TERRAIN CONTROLS ON THE DISTRIBUTION OF TREE SPECIES DIVERSITY AND STRUCTURE IN TROPICAL LOWLAND AND TROPICAL MONTANE FOREST

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ABSTRACT

This thesis examines the micro-scale variability in tree species composition, diversity and tree structure through a combination of ground-based plot studies and computer-based analyses of terrain characteristics in two contrasting tropical forest sites; a tropical montane cloud forest environment, and a lowland Amazonian forest environment. The aim is to measure the micro-scale spatial variability in tree species diversity, composition and structure in tropical forests, and to quantify the role of topography, through both direct and indirect resource partitioning (of essential resources such as energy and water), in controlling this variability. Ten 25m x 25m plots have been established in each site, distributed widely around the region. High-resolution digital elevation models (DEMs) have also been generated for each site, and a range of 12 terrain-based characteristics calculated which capture some of the likely controls on essential resources such as light and water.

Tree diversity and composition is found to vary significantly between plots in each study site, with species richness varying from 31 to 52 species in a montane forest, and between 31 and 82 species in the lowland Amazonian site. Analyses of habitat associations of tree species with respect to the terrain characteristics showed that 36% of compositional variability in the montane site is explained by elevation, whilst just 16% of compositional variability is explained in the lowland site, also through elevation (though this pattern is attributed to an edaphic gradient brought about by river migration). This indicates that some habitat association occurs, but that a significant portion of compositional variability remains unaccounted for, at least using the terrain characteristics used in this study. This leads to the conclusion that a combination of equilibrium and non-equilibrium, both abiotic and biotic based processes are maintaining diversity in tropical forests.

When diversity patterns are examined, a mid-elevation tree diversity peak is observed in the montane site ($R^2 = 0.70$, highest diversity at 1850 m), a pattern attributed to a combination of the mid-domain effect and species-area relationships. Furthermore, species richness is found to correlate significantly with slope mean curvature, with greater richness found on convex slopes ($R^2 = 0.73$). Fewer patterns are found in the lowland site, with generally lower diversity in the more frequently flooded sites, though no terrain-based patterns are found to explain variability in diversity between non-flooded sites.

Structure is observed to vary significantly between sites, and between-plots within each site yet surprisingly little of this variability is explained by terrain-based characteristics. Indeed, not even a significant elevational gradient in forest structure was observed in the montane site, though TopModel (a terrain characteristic indicative of soil moisture) explained 67% of variability in the DBH/Height ratio. The interpretation of this result was inconclusive. In the lowland site two marked clusters in structure were evident, separating higher and lower elevation plots. The shorter stature found in the low elevation plots was attributed to the disturbance effect of regular flooding. No further terrain-based correlations with structure were found.

Finally, analysis of spatial heterogeneity of terrain and its relationship with tree diversity indicated that regions spatially heterogeneous in elevation in the montane environment were also more diverse ($R^2 = 0.53$). In the lowland site no significant correlations were observed.

Overall this thesis has found some interesting correlations between terrain characteristics and tree species composition and diversity, and has provided some novel methodologies for testing the processes behind the maintenance of species diversity in tropical forests. These results lead to the conclusion that a combination of equilibrium and non-equilibrium, abiotic- and biotic- based processes are maintaining diversity in tropical forests.

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Chapter 1

1 Research goals and introduction

This opening chapter presents the aims and objectives of the study, and a brief overview of the research strategy and structure of the thesis. This sets the context for the review of associated literature found in Chapter 2.

1.1 Hypothesis

Tree species diversity, forest structure and species composition in tropical forests are heterogeneously distributed in space at the micro-scale, and topography plays an important role in generating this spatial variation.

1.2 Aim

The aim of this thesis is to measure the micro-scale spatial variability in tree species diversity, composition and structure in tropical forests, and to quantify the role of topography, through both direct and indirect resource partitioning (of essential resources such as energy and water), in controlling this variability.

1.3 Objectives

Tree species diversity and structure in tropical forests are heterogeneously distributed across the land surface, a notion strongly supported in the literature with differences in diversity, composition and structure observed at a broad range of spatial scales (for example Pitman, 2000; Hawkins et al., 2003; Hawkins and Diniz-Filho, 2004). A central issue in tropical ecology is to understand the processes which drive this spatial variability since those processes must be at least part responsible for the maintenance of high levels of tree diversity in tropical forest systems. Since trees are the dominant structural organisms of tropical forests, tree species diversity is also central to theories explaining why these forests are also so diverse in other plant and animal groups.

In this thesis I endeavour to use methods of terrain analysis to quantify environmental conditions (controlled through topography) at the micro-scale, and liken species diversity and composition (principally) and tree structure (secondarily) to these environmental conditions, to understand the important interaction between environment and diversity in tropical forests. The term micro-scale is used in this thesis to refer to spatial variability at the local scale, over distances of 20m – 100m depending on the degree of topographic variability, though this may also be referred to as the plot-landscape scale.

Specifically, the objectives of this thesis are:

1. To use field-collected data on tree diversity, composition and structure in tropical forests to quantify the degree of spatial variation at the micro-scale.
2. To examine the relationship between topographic characteristics and species composition in order to assess the degree of topographically controlled habitat association in tropical tree species.
3. To identify the role of topographic characteristics on maintaining levels of tree diversity, through the control of essential resources

4. To identify the role of topographic conditions in generating distinct structural characteristics in the forest, and how this may control or be controlled by variation in tree species diversity.
5. To quantify the effect of spatial environmental heterogeneity in the generation and maintenance of tree species diversity at the micro-scale.

Using two contrasting study sites found in a tropical montane cloud forest (TMCF) in Colombia and a tropical lowland forest (LRF) in Amazonian Ecuador, this thesis combines intensive field-based plot measurement of diversity, composition and structure of tropical trees, and compares the patterns of spatial variation found in the field with the topographic conditions as measured through high resolution digital elevation models. A number of terrain derivatives, some of which control the spatial distribution of essential resources (energy and water), are applied for this purpose. In addition to direct comparison of topographic conditions with the observed structure and diversity at the site of each plot, the role of spatial heterogeneity in these topographic conditions is also examined.

The research presented in this thesis is principally empirical and academically driven, but these analyses are applied within the context of the current debate on theories on the *maintenance* of species diversity in tropical forests (discussed in Section 2.3), and its implications for science-based species conservation planning. For the latter point, some effort is maintained to make the methodology used here easily applicable to other regions, by using readily available sources of data and replicable methodologies.

This research is innovative in the field of tropical ecology in the following ways:

- Though habitat associations of tropical tree species have been studied with respect to topography (see Section 2.3.2), only basic topographic characteristics have been used (slope, elevation and landscape unit) whilst this thesis applies advanced methods of terrain analysis to examine habitat associations in tree species composition for a wide variety of resource-based terrain characteristics over a range of scales.
- There are few examples of studies which endeavor to find relationships between quantified topographic characteristics and tree *diversity* in tropical forests (see Section 2.3.3.5), and this thesis is the first known example of applying terrain analysis to understanding micro-scale spatial variability in diversity.
- Although there is a strong theoretical body of literature stating that environmental heterogeneity is significant in shaping spatial variability in diversity in tropical forests (see Section 2.5), this has never been rigorously tested in tropical forests and this thesis makes a first attempt through a combination of field data collection and analyses and the application and validation of spatial models for diversity control.

This thesis focuses on the role of the environment on tree diversity, composition and structure, though it is important to acknowledge the important role of biotic processes (especially ecological interactions such as competition, allelopethy, or herbivory etc.). Although these are not analysed here, nor thoroughly discussed in the text, biotic interactions have also been found to be important in the maintenance and generation of diversity (Huston, 1994). The objectives of this thesis are only related to environmental interactions, but it is important at this point to note that biotic interactions are also of importance but not centrally addressed.

It is also important to emphasize that the direct role of soil on tree diversity, composition and structure is not explicitly analysed in this thesis (no soil sampling was performed), though it is regularly discussed in the text. This is in order to ensure that the methodology applied here is readily applicable to other regions, only requiring topographic data. However, soil attributes are often strongly controlled by topography, and the possible significance of specific topographic characteristics on soil type and quality is discussed both in the literature review (Section 2.3.3.4) and in the analysis chapters. In this sense no direct measurement of soil-diversity relationships are made, but topography is used a possible indicator of some soil conditions.

1.4 Overview of this thesis

This thesis is split into seven chapters. They are structured in a way to lead the reader through the theoretical and empirical background of the research problem, explain and justify the research design and present results in the three major thrusts of the thesis, that of micro-scale variation in composition and diversity, micro-scale variation in structure and the role of spatial environmental heterogeneity in species diversity. Specifically:

1.4.1 Chapter 1

This short chapter has introduced the aims and objectives of the thesis, and has outlined the general structure of the thesis.

1.4.2 Chapter 2

Some background is provided on the theoretical and empirical context of the thesis, reviewing the state of knowledge of key themes related to the objectives. Specifically the chapter outlines the context of biodiversity and tropical forests, stressing the importance of conservation and the high levels of diversity found in tropical forests. Some information is provided on the role of tree species diversity to overall biodiversity in tropical forests. A brief introduction on spatial variation in diversity is provided along with an introduction to the equilibrium and non-equilibrium hypotheses for species diversity maintenance in tropical forests. Specific attention is given to the theoretical and empirical findings in relation to elevational gradients (of particular relevance to the TMCF site) and habitat associations (a topic under vigorous debate in relation to LRF). A brief summary of interactions between environment and tree diversity and structure is presented. The chapter finishes by introducing the theme of spatial heterogeneity, covering both theoretical and measurement aspects.

1.4.3 Chapter 3

Chapter three presents the research strategy and methodology, starting by introducing the study sites. The chapter then provides information on the desk-based terrain analysis of topography and environmental data. Although terrain analysis is not discussed in chapter 2, theoretical issues related to the calculation of the specific terrain characteristics used in the thesis are analysed in this chapter. Field methodologies are then discussed, and the methods for integrating field-based data with the terrain characteristics are introduced. The chapter finishes by introducing the methodology for quantifying spatial environmental heterogeneity.

1.4.4 Chapter 4

Chapter four starts the results and analysis section of the thesis, examining the topographic controls on tree species composition and diversity. For each site (TMCF and LRF) a brief description of diversity, composition and structure is given, firstly at the site-level and secondly at the plot-level through between-plot comparisons (Objective 1). Statistical analyses are then presented to identify the degree to which composition is controlled by terrain characteristics (Objective 2). The chapter also examines the topographic controls on species diversity (Objective 3). The chapter is structured firstly by site, then by compositional and diversity patterns. The chapter concludes by examining the differences between each site, and providing some preliminary conclusions.

1.4.5 Chapter 5

Chapter five examines the tree structural variability at the two sites, examining both the average structural characteristics for each site and each plot within each site, but also the distribution of structural forms. Effort is made to identify the topographic controls on structure through statistical analyses (Objective 4). Some analysis and discussion is provided on the complex relationship between diversity and structure, though this is limited in scope due to data restrictions. As in Chapter Four, this chapter concludes by summarizing the key results, though conclusions are left for Chapter Seven.

1.4.6 Chapter 6

Chapter Six exclusively examines the role of spatial environmental heterogeneity on tree species diversity (Objective 5), through presentation of the results of the environmental modelling and comparison with the plot data, for each site separately. Multi-variate statistics are applied to the results of previous chapters to provide a broader vision of spatial variability in diversity taking into account both terrain characteristics and their spatial heterogeneity.

Chapter 7

Although preliminary conclusions are provided at the end of each analysis chapter (4-6), this chapter attempts to coherently present the most important findings and place them within the context of current literature and theory presented in Chapter Two.

Chapter 2

2 Literature review

2.1 Introduction : The biodiversity and conservation context

The world's biodiversity is being lost at a staggering rate, and conservation of biological resources is now a challenge that all nations must strive to achieve, and is being pursued through international treaties such as the Convention for Biological Diversity (CBD). Though this thesis is not directly oriented towards conservation objectives, it is important that any study of biological diversity be placed within this context, as science plays an important role provision of accurate biological information and in the search for practical solutions to biodiversity loss.

The overall goal of the Convention on Biological Diversity (Article 1, CBD, 1992)) is "….to conserve and sustainably use biological diversity for the benefit of present and future generations". Under this agreement, which most countries have signed to, each country is required to provide an inventory of biological resources within the country, and to pro-actively ensure its conservation. Parties to the Convention are committed to develop effective and scientifically sound protocols and methodologies to conserve biological diversity, that is ecosystem, species and genetic diversity. In the field of *in situ* conservation, the CBD calls on nations to:

> "Develop, where necessary, guidelines for the selection, establishment and management of protected areas or areas where special measures need to be taken to conserve biological diversity."
>
> Article 8 (CBD, 1992)

Biological diversity is of importance to the world for numerous reasons. Firstly, humans throughout history have used biological resources to for food, fibre and fuel. Alonso et al. (2001) report that close to 30 percent of pharmaceuticals on the market today have been developed from plants and animals. Some of these uses include "antibiotics extracted from fungi and from sources such as the African clawed frog's skin, an extract of the saliva of the vampire bat is used in treatment for hardening of the arteries, wild yams contain chemicals with anti-inflammatory properties and ovarian and breast cancer treatments have been developed from the bark of the Pacific yew tree found in the northwestern United States" (Alonso et al., 2001). Our entire agricultural system is built upon biodiversity. Of some 270,000 described species of plants, 30,000 are edible, and 7,000 of these have been actively cultivated over history (FAO, 1997). A small percentage of the world's biological diversity has actually been screened for potential uses, and a potentially significant percentage of the world diversity has not even been discovered or catalogued (Erwin, 1991; Johnson, 1995). The extent to which biodiversity will provide solutions to new threats in the future is unknown (Aylward and Gammage, 1992), especially as society faces an uncertain environmental future in the face of rapid land-use and climatic change. On top of these tangible uses, biodiversity has been shown to be of importance for ecosystem functioning (Naeem et al., 1994; Folke, 1996; Johnson et al., 1996; Fonseca and Ganade, 2001; Wolters, 2001; Kennedy et al., 2002; Worm et al., 2002), and amongst other things maintains global biogeochemical and hydrological systems. However, the functional role of biological diversity is still not fully understood (Bengtsson, 1998; Wardle, 1999), and is the subject of considerable discussion. Finally, conservation of biodiversity is also considered important for what are generally termed "spiritual" reasons, including that humans have a responsibility to conserve the worlds biodiversity regardless of its significance or value (Ehrenfeld, 1988; Wilson, 1992).

Despite this economic, functional and spiritual importance, little has been achieved to halt or reduce what is being termed the sixth great biological extinction (Pimm et al., 1995), and continued efforts are required to halt what is believed to be an irreversible loss (Wilson, 1992).

Though this thesis does not directly address conservation issues with respect to biodiversity, it is hoped that accurate spatial information on *where* diversity is found will help provide more informed decision-making on biodiversity conservation. This literature review focuses on patterns of variation of species diversity, composition and structure of trees in tropical forests. Emphasis is made to highlight studies in tropical forest environments, though important papers from other biomes are also presented. In most cases there is greater volume of both empirical and theoretical studies for lowland tropical forests compared with the less-studied tropical montane forest environments, though the same can also be said for temperate versus tropical environments.

The chapter begins by reviewing diversity in tropical forests, providing the context of this study. Some discussion is provided as to the significance of tree diversity for total forest biodiversity, followed by a more detailed introduction of tropical forests, and specifically the two types of tropical forest studied here. The chapter then moves on to the central issue of the thesis, that of micro-scale spatial variation in diversity and composition, presenting both theoretical perspectives and empirical results. Some of the abiotic driving mechanisms of diversity are also briefly discussed, though there is an large volume of literature in this area that cannot be covered in detail within this chapter. The chapter then moves on to discuss spatial variation in structural patterns in tropical forests, with special reference to the important interaction between structure and diversity, through partitioning of resources (principally light), though literature on this is scarce. Finally, the chapter provides some background on the concept of spatial heterogeneity, and its significance to diversity and composition in tropical forests, and concludes with a discussion on sampling in tropical forests, an important bridge to the following chapter of materials and methods. What is not discussed here are general techniques for terrain analysis and environmental modelling issues, as this is not the focus of the thesis rather these are tools which are used here for the study of tropical forest diversity and structure. In general terms, terrain characteristics are chosen and used in this thesis to represent partitioning of essential resource, principally energy and water. Though some biological literature presented in this chapter use topographic characteristics in the study of diversity, composition or structure, these examples are few and often limited in scope. A specific discussion of the terrain characteristics used in this thesis is reserved to the methods chapter (Chapter 3), where not only the terrain analysis methodology is presented but also a detailed analysis of the reason for its use, its potential biological significance in terms representing essential resources, and the issues involved with its calculation.

2.2 Diversity in tropical forests

Tropical forests cover approximately 7% of the global terrestrial surface, across the continents of Asia, Africa and Latin America, and are thought to contain over half of the world's species (Wilson, 1992). There is a great deal of variability in tropical forests around the globe, with a broad range of structures and species compositions. Asian forests tend to be dominated by Dipterocarps (Whitmore, 1984) whilst in the neotropics tropical forests are not dominated by any particular family though Leguminosae are typically most common (Gentry, 1990), though within these broad regions there is significant compositional variation. Tropical forests contain overwhelming levels of diversity compared with their temperate counterparts (Huston, 1994), though biomass is comparable or even less than in temperate forests (Whittaker and Niering, 1975). Whilst 1-Ha in a particularly diverse temperate forest may contain 15-20 tree species (greater than 10cm diameter at breast height (DBH)), a tropical forest may contain over 200 tree species (Gentry, 1990; Huston, 1994; Hawkins et al., 2003). Indeed, Whitmore et al. (1985) reports 233 vascular plant species in just 100m^2 of lowland tropical forest in Costa Rica, equivalent to one-sixth of all flora of the British Isles.

Despite being a treasure trove for biological diversity (Wilson, 1992; Crawley, 1997), and of great importance for the global climate system (Melillo et al., 1996), tropical forests are also undergoing rapid loss through deforestation for agricultural expansion and logging (Skole and Tucker, 1993; Melillo et al., 1996; Lambin and Ehrlich, 1997; Maio Mantovani and Setzer, 1997; Read et al., 2003). Deforestation rates vary between regions and continents, with Fearnside (1990) using satellite remote sensing (LANDSAT TM images) to approximate deforestation rates of 0.5% yr^{-1} in the Brazilian Amazon (21,130km^2 lost per year 1978 - 1989, of the total 4,000,000 km^2 of Amazonian forest). There is considerable uncertainty in monitoring the true rates of deforestation across regions (Grainger, 1993), but most approximations range from 0.5 – 1.3 % per year (FAO, 1990).

The term tropical forest refers to all forests within the tropical region (typically defined as between the Tropics of Cancer and Capricorn), including tropical dry forests, tropical montane forests, tropical montane cloud forests and lowland rain forests, amongst others. The physical environment for each of these types of forests is different, resulting in different levels of species diversity, different species compositions and different forest structures (Huston, 1994). A complete review of the different types of tropical forest is a available in Burley et al. (2004). This study examines diversity, compositional and structural patterns in a tropical lowland rain forest (LRF) and a tropical montane cloud forest (TMCF), which are described later in Section 2.2.2.

2.2.1 Relationship between tree diversity and biodiversity

This study only examines tree diversity in tropical forests, but the degree to which tree diversity is related to total biodiversity (i.e. diversity in all other groups of organisms) has been the subject of a number of studies. According to Huston (1994), organisms can be sub-divided into two classes - structural and interstitial. Structural organisms actually form the physical environment (examples include trees and corals) and to a certain extent alter the physical surroundings (e.g. microclimate), whilst interstitial organisms inhabit this environment (examples are insects, birds, vertebrates, herbaceous plants etc.). Different processes and factors affect these two types of organism, with structural organisms directly affecting the diversity of the interstitial organisms. Ecological theory further predicts that loss of biodiversity at the base of the ecosystem (basal species), for example plants, will impact on the whole system (Siemann et al., 1998; Knops et al., 1999). Though theory clearly emphasizes the importance of plant diversity (and especially tree diversity) on 'total' biodiversity, and many authors cite tree diversity as being strongly correlated with diversity in other groups (Huston, 1994), empirical studies show conflicting findings as to the validity of this relationship (Su et al., 2004). Ingerpuu et al. (2001) show vascular plant species richness to strongly correlate with bryophyte species richness ($r = 0.76$, $p = 0.007$) in 10 different stands in an Estonian boreo-nemoral moist forest. Similarly, Aptroot (2001) found that an Elaeocarpus tree in montane forest in Papua New Guinea showed the presence of over 200 species of ascomycetes, including 173 lichenized ascomycetes, many of which are thought to be host-specific. Nieder et al. (2001) further discuss host-specificity with respect to epiphytes, providing a strong case for a strong (one-way) relationship between tree diversity and epiphytic and bryophytic diversity. There are other significant correlations in the literature between plant species richness and butterflies (Simonson et al., 2001), arthropods (Siemann et al., 1998), tetrapods (Barthlott et al., 1999), herbivores and predators and parasites (Knops et al., 1999), amphibians, mammals, birds and reptiles (Currie, 1991) and belowground biota (Wardle et al., 2004), though it is important to note that the majority of these studies are not all in tropical forests. However, some studies fail to find such relationships, for example between butterfly richness and plant species richness in Madagascar (Kremen, 1992), and in the British Isles little coincidence between hotspots in butterflies, dragonflies, liverworts, aquatic plants and in breeding birds are found (Prendergast et al., 1993). In tropical forests specifically, Lawton et al. (1998) found few relationships between changes in richness in one group of taxa with changes in an array of other groups (taxa of butterflies and insects) under some kind of habitat modification. Unfortunately this study did not include tree (or plant) species. These findings amongst others lead Su et al. (2004) to conclude that cross-taxon relationships are site and taxon specific and no general rule can be extracted. However, the significant levels of host-specificity to plant species identified in tropical forests, for example in arthropods (Erwin, 1982; Erwin, 1991) or fungi (Aptroot, 2001), make it highly likely that greater plant diversity also signifies to a certain extent greater diversity in other taxa.

In conclusion it cannot conclusively be stated that high tree species diversity in tropical forests indicates high diversity in other taxa, though there are undoubtedly important processes whereby tree diversity should theoretically generate high diversity in other groups. These mechanisms include host-specificity, the fact that trees are a basal species in the ecosystem, and through their structural role in the forest filter largely homogenous physical inputs (solar radiation, temperature and rainfall) to create a heterogeneous under-canopy. Furthermore, evidence of direct-cycling of nutrients by tropical trees affects edaphic conditions immediately around the individuals (Clinebell II et al., 1995) creating a mosaic of physical and chemical soil conditions, broadening the resource-niche space and potentially encouraging greater diversity in other taxa (especially belowground biota and herbs and shrubs). Quantification of the cross-taxon congruence in tropical forests through coordinated plot studies would be a significant achievement for tropical ecology, but for the purposes of this thesis it is likely that tropical tree diversity is to a certain extent representative of biodiversity as a whole.

2.2.2 Diversity and structure in the study sites

This study examines diversity, structure and composition of trees in two tropical forests in the Northern Andes and Choco Biogeographic Region (Gentry, 1982), and in the western Amazon (Andean fringe), both of which represent global conservation priorities and contain very high levels of biological diversity.

The northernmost part of the Andes is subdivided into three mountain ranges that generate a very complex geographical pattern of exceptional biological diversity (McNeely et al., 1990; Stattersfield et al., 1997). The Colombian Andes are also the most densely populated areas in the country (CIESIN, 1998), hence the last remnants of Andean montane forests are priorities in the national (IaVH, 1997), and international conservation agenda (Barthlott et al., 1999; Myers et al., 2000). Colombia ranks among the Earth's highest conservation priorities due to its exceedingly high diversity coupled with the threats posed by human development and commercial resource exploitation (Dinerstein et al., 1995). It is one of the richest countries in terms of species diversity per unit area comprising an estimated 14-15% of the planet's flora and fauna in 0.77% of its surface (International, 1997). Furthermore, Johnson (1995) ranked Colombia first in the world in terms of species richness in birds (1,752 species) and butterflies (3,500 species), and second in terms of plants (45,000 species) and amphibians (407 species). Since many plant and animal species have not been documented, particularly in tropical forests (Claridge, 1995), the documented diversity of Colombia is expected to increase substantially with further biological inventory work.

The western Amazon (bordering the Andean fringe in Peru, Ecuador and Colombia) is also identified as one of 20 global biodiversity priorities (Myers et al., 2000). Pitman (2000) established a network of plots in Ecuador and Peru, finding extremely high diversity in tree species throughout the region, with other plot studies in the region further confirming this (Duivenvoorden, 1994; Duivenvoorden and Lips, 1995; Romoleroux et al., 1995). The reasons for the high levels of plant diversity found in the Amazon regions of Ecuador, southern Colombia and Northern Peru are the topic of heated discussion, with Prance (1982) proposing evidence of this region being a Pleistocene forest refuge.

The two sites studied here represent two contrasting tropical rain forest types of the Neotropics; tropical montane cloud forest (TMCF), and lowland rain forest (LRF).

2.2.2.1 Neotropical Tropical Montane Cloud Forests (TMCF)

Cloud forests are defined according to the presence of forest in areas of frequent or persistent ground level cloud (Bruijnzeel and Proctor, 1995), and occur in both temperate and tropical environments. Tropical montane cloud forests (TMCF's) are exclusive to mountains in tropical regions. Their altitudinal distribution is highly variable depending on climatic factors, with TMCF occurring as low as 350m in coastal regions where fog forms at lower altitudes, stretching as high as 3,500m in inland mountain systems such as the Andes (Bruijnzeel and Proctor, 1995). TMCF occurs in three regions of the globe; SE Asia, Central Africa and Central and South America.

In 1970 they were estimated to cover 50 million hectares, but reported deforestation rates in excess of 1.1% per year (greater than that for lowland rainforests) has caused a serious reduction in their coverage, putting them at serious risk (Hamilton et al., 1995). These deforestation rates are caused by land hunger and the spatial expansion of agriculture, and are predicted to continue under the current population explosion in many of the areas where TMCF's occur (CIESIN, 1998). Castaño (1991) approximates that just 10% of Colombia's original TMCF now remains. Furthermore, there is now growing concern as to the effect of climate change on these ecosystems (Loope and Giambelluca, 1998; Pounds et al., 1999; Still et al., 1999).

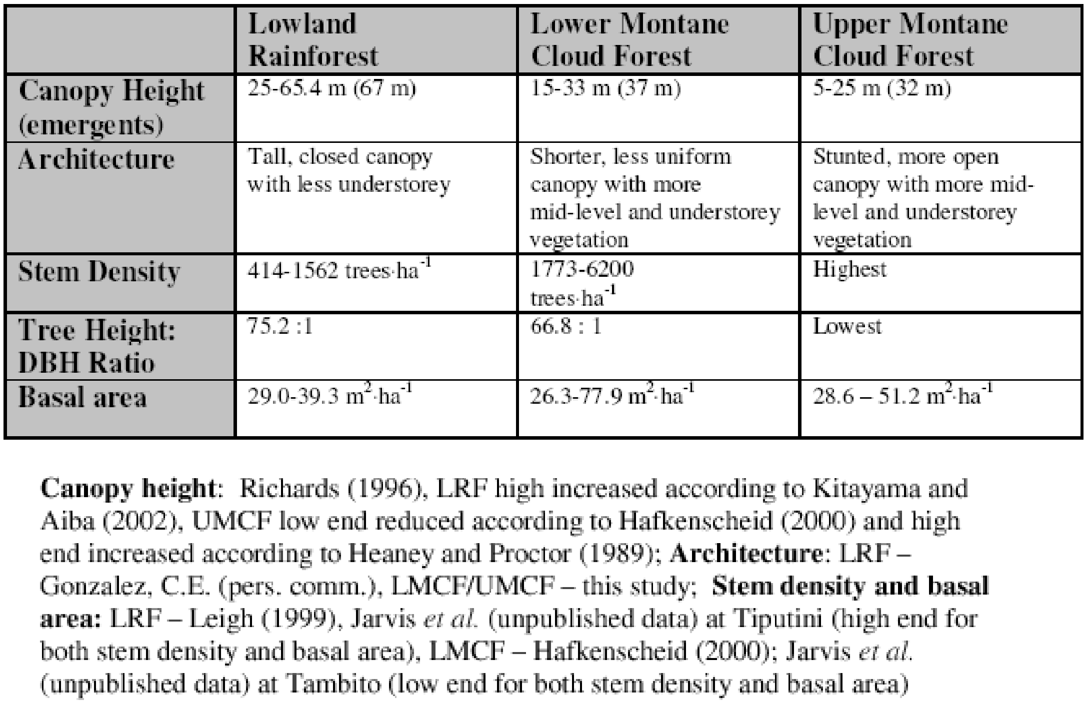
The hydrological significance of TMCF has been shown to be important for downstream water resources (Bruijnzeel and Proctor, 1995), due to their constant provision of streamflow even during the dry season (Zadroga, 1981), brought about by considerable volumes of cloud interception throughout the year (Gonzalez, 2000).

Tropical montane cloud forests are renowned for the large numbers of endemic species, highly dependent on their climatic environments (Bubb et al., 2004). This is especially the case for plants (Kappelle, 2004; Leimbeck et al., 2004), and birds with Long (1995) reporting that ten per cent of the world's 2,609 restricted-range bird species are confined to or mainly found in cloud forests. TMCFs also contain exceptional levels of diversity in epiphytes (Nieder et al., 2001), bryophytes and orchids (Muller et al., 2003), with a high concentration of threatened plant species and some important rare-agricultural wild relatives (Bubb et al., 2004). The best plot based study of plant diversity in TMCF in the neotropics is a study by Clinebell II et al. (1995) presenting 69 lowland and montane 0.1Ha plots established by Alwyn Gentry around the entire continent, with 13 plots throughout the Andes above 500m (ranging from 560m – 3000m) having an average of 109 species in the 0.1 Ha (DBH > 10cm).

More specifically to the region around Tambito (an Andean site on the western slope of the western cordillera, placing it within the Choco Biogeographc Region), plot studies of plant species diversity in the Choco Biogeographic Region on the Pacific Coast of Colombia and Ecuador confirm exceptionally high levels of diversity (Gentry, 1990, 1995; Galeano et al., 1998). Specifically, Galeano et al. (1998) studied all vascular plant species in 0.9Ha of forest (in 12 transects) finding a record 970 species for that sampling scheme, with Araceae, Cyatheaceae, Piperaceae and Rubiaceae being the most dominant families. In all, there are thought to be some 8,000 vascular plant species in the Choco Biogeographic Region (Forero and Gentry, 1989), though large tracts of the forest are unknown to science, especially in the exceptionally wet (and remote) parts (Galeano et al., 1998).

Tree height in TMCF is generally less than in the lowlands (Table 1), with reported canopy heights of 5-33m in TMCF compared to 25-65.4m in LRF (summarised in Letts, 2003), though emergent trees still reach great height in TMCF, with Kappelle

(2004) reporting emergent trees of 33-55m height in Costa Rica. Most studies report stem density to increase with altitude, with Kappelle (2004) reporting average stem densities for TMCF in the region of 500-1000 stems Ha^{-1} for TMCF counting all stems with DBH > 5 cm, and 1600 – 3500 stems Ha^{-1} when all individuals with DBH > 2.5cm are counted.



	Lowland Rainforest	**Lower Montane Cloud Forest**	**Upper Montane Cloud Forest**
Canopy Height (emergents)	25-65.4 m (67 m)	15-33 m (37 m)	5-25 m (32 m)
Architecture	Tall, closed canopy with less understorey	Shorter, less uniform canopy with more mid-level and understorey vegetation	Stunted, more open canopy with more mid-level and understorey vegetation
Stem Density	414-1562 trees·ha^{-1}	1773-6200 trees·ha^{-1}	Highest
Tree Height: DBH Ratio	75.2 :1	66.8 : 1	Lowest
Basal area	29.0-39.3 m^2·ha^{-1}	26.3-77.9 m^2·ha^{-1}	28.6 – 51.2 m^2·ha^{-1}

Canopy height: Richards (1996), LRF high increased according to Kitayama and Aiba (2002), UMCF low end reduced according to Hafkenscheid (2000) and high end increased according to Heaney and Proctor (1989); **Architecture**: LRF – Gonzalez, C.E. (pers. comm.), LMCF/UMCF – this study; **Stem density and basal area:** LRF – Leigh (1999), Jarvis *et al.* (unpublished data) at Tiputini (high end for both stem density and basal area), LMCF – Hafkenscheid (2000); Jarvis *et al.* (unpublished data) at Tambito (low end for both stem density and basal area)

Table 1 Structural parameters for LRF and TMCF, from Letts (2003), based on studies by Richards (1996), Kitayama and Aiba (2002), Hafkenscheid (2000), Heaney and Proctor (1989), and Leigh (1999) and this study.

2.2.2.2 Tropical Lowland Rainforest (LRF)

Tropical lowland (evergreen) forests occur in perhumid lowland climates where water stress is either intermittent or non-existent, typically below 1200m elevation

(Whitmore, 1998). LRF is principally found in the Neotropics, in the Amazon region and along the Pacific coast, though there are also lowland rain forest regions in Africa. In the Amazon region, with approximately 4,000,000 km^2 of LRF, the forest is often further split into vegetation types related to flooding frequency, with terra firme forest found on higher relief not subjected to flooding and várzea forest which is seasonally flooded, sometimes for extended periods of time.

Based on Alwyn Gentry's 0.1Ha plots established throughout the Neotropics, an average of some 149 species are found per plot in the lowlands (< 500m elevation), with all individuals with DBH > 10cm (Clinebell II et al., 1995). This is considerably higher richness than was found in montane plots. In and around the Yasuni National Park region in Ecuador, there is documented high diversity in a 25-Ha plot (Valencia et al., 2004), and at the time of publication in 1994 this area had the highest recorded plant diversity per hectare in the world (based on the sampling method), with 473 species (DBH >5cm) found in a 1-Ha square forest plot, with Fabaceae, Lauraceae and Sapotaceae being the most dominant families (Valencia et al., 1994).

Tree height in LRF is typically greater than in TMCF, with a higher canopy, lower stem density and greater basal area. Clark and Clark (2000) report stem densities of 462 – 504 stems Ha^{-1} in La Selva in Costa Rica (30m elevation) counting all individuals DBH > 10cm. Webb et al. (1999) report average canopy height of 14.9 – 22.9m, stem densities of 550 – 945 stems Ha^{-1}, and average DBH of 23.5 – 25.6cm in a lowland rain forest counting all individuals DBH > 10cm in American Samoa (48m – 339m), with Proctor et al. (1983) reporting similar densities of 615 – 778 stems Ha^{-1} (DBH > 10cm) for an LRF in Sarawak, with basal area ranging from 28 – 57 m^3 Ha^{-1}.

2.3 Spatial variation of tree diversity and composition in tropical forests

Spatial variation in species composition and diversity occurs at a range of scales, from global to regional to the micro-scale, and the processes behind such variability are different depending on the scale in question (Condit et al., 1992). On the global scale, latitude is often cited as explaining the strongest global-level spatial variation in diversity, with a general decline in diversity with greater latitude, though latitude itself is not the physical driving mechanism, but more specifically climate is amongst other factors (discussed in detail in Hawkins and Diniz-Filho, 2004). Within tropical forests, that have the highest levels of diversity on the planet, there is also a significant degree of spatial variability in diversity and composition at a range of spatial-scales, from the continental scale (for example Gentry, 1990) down to the regional scale (for example Gentry, 1995; Kress et al., 1998) and the local scale (discussed in Rosenzweig, 1995). Within this section the local-scale drivers of spatial variation of diversity and composition will be reviewed, as this is the scale relevant to this study.

However, spatial patterns in diversity and composition cannot be discussed without the important consideration of the temporal dimension. The spatial pattern of diversity observed today is at least in part a function of temporal history over a range of timescales (Smith and Huston, 1989; Huston, 1994). In tropical forests, temporal variation in the context of large spatial and temporal scales is discussed in depth with respect to refuge theory (Gentry, 1982; Prance, 1982), whereby it is hypothesized that the current distribution of plant diversity hotspots is brought about by long-term climatic stability in these zones (though significant evidence is now available that refutes this theory, but is not discussed here), both in the Amazon region (Prance, 1982) and the Choco Biogeographic Zone (Gentry, 1982). Temporal variability at this broad-scale is of little relevance to this study, but the micro-scale spatial variability in diversity central to this thesis is a function of shorter time-scale dynamics (Condit et al., 1992), principally gap dynamics and succession, though broader-scale disturbance regimes (such as drought (Condit et al., 1992), or tropical storms) may also impact the micro-scale configuration of species composition and diversity.

There are two over-arching hypotheses for the maintenance of high levels of species diversity through time in tropical forests, eloquently described by Denslow (1987) asking whether tropical forests comprise of "sets of highly coevolved niche-differentiated tree species in stable or semi-stable floristic assemblages", the so-called equilibrium hypothesis, or if tropical forests consist of "diffusely coevolved, broadly generalist species which slowly drift in relative abundance within a few large life-history guilds", the so-called non-equilibrium hypothesis. Hubbell (1979; Hubbell and Foster, 1986) has been the main proponent of non-equilibrium processes acting to maintain species diversity. The non-equilibrium hypothesis, or "null" model of tree dynamics holds that "species-rich tropical tree communities are maintained on a local scale by a balance of extinction and immigration, and on a global scale by a balance of extinction and speciation" (Yu et al., 1998). All species are considered ecologically equivalent, such that species having equal initial abundances have equal probabilities of extinction or fixation. Also key to Hubbell's null model is disagreement over the existence of density-dependence in tropical forests (Janzen, 1970; Connell, 1971), and the implication that species on the whole are adaptively equivalent. Density dependence (the so-called Janzen-Connell model in tropical forests) dictates that individuals of the same species are likely to perform poorly around each other, due to higher concentrations of host-specific natural enemies (fungal pathogens and herbivores) and as they compete for the same resource-niche, subsequently diminishing growth and survival. Advocates of the non-equilibrium theory for the maintenance of species diversity have provided empirical data rejecting the existence of density-dependence in tropical forests (Hubbell, 1979; Condit et al., 1992). Equilibrium based explanations for species diversity centre on the concept of niche differentiation in tropical species, first advocated by Ashton (1977), and since supported by studies such as that of Phillips et al. (2003), and support the existence of the Janzen-Connell model of density-dependence. The validity of the non-equilibrium hypothesis has been questioned, with Terborgh et al. (1996) providing evidence from Peru of strong density-dependence. In his study, Terborgh and colleagues test the idea that in a non-equilibrium state, a disturbed forest would not necessarily regenerate to its former composition. Other authors have since provided further evidence supporting a certain degree of determinism in species composition in tropical lowland forests (Pitman et al., 1999; Pitman, 2000; Pitman et al., 2001), and an extensive and vigorous discussion of equilibrium vs. non-equilibrium hypotheses is present in the literature (see for example Yu et al., 1998). Currently there is strong empirical evidence supporting both equilibrium and non-equilibrium hypotheses, and tropical ecology continues to rigorously debate the issue, though some accept that a combination of both mechanisms are at play in tropical forests (Brokaw and Busing, 2000). In an attempt to examine the existence of equilibrium or non-equilibrium dynamics in a tropical rain forest in Malaysia, He et al. (1996) found no clear spatial pattern in diversity but concluded that a large amount of undetermined variation may originate from small-scale processes (<20m). This thesis in part attempts to provide more empirical evidence to fuel the equilibrium vs. non-equilibrium discussion, through testing of habitat associations and spatial partitioning of diversity and composition in different topographically controlled niches at the micro-scale.

Whichever theory for the maintenance of species diversity in tropical forests is taken, it cannot be denied that forests change considerably in both the long- and short- term. Condit et al. (1992) provides data on short-term dynamics in species composition and diversity in a 50-Ha plot in Barro Colorado Island, showing that although species richness remains unchanged some 40% of the species (approx. 300 in total) changed in abundance by more than 10% in just 3 years. Temporal dynamics must be carefully considered throughout this study, as measurement of diversity at any one time is just a snapshot of a temporally dynamic system.

Specifically to lowland tropical forests, science is only beginning to understand in any detail how variable species composition and diversity is over space (Pitman, 2000). It has long been established that tropical tree species tend to occur in low densities in Amazonian forests, with Black et al. (1950) stating that the average density of an Amazonian tree species is less than 1 individual Ha^{-1}. Over the years this figure has not changed much despite intensive plot studies throughout the region, with Pitman et al. (2001) concluding that the commonest species rarely exceed 90 individual Ha^{-1} and often account for just 3-12% of all stems. This also means that a 1-Ha plot is likely to capture a small-subset of all species in the local pool, and through lack of large enough datasets ecologists are only just beginning to understand the geographic patterns of species distributions in the Amazon (Pitman, 2000).

Within this section, two specific themes of geographic variation in composition and diversity are examined in detail, namely the role of elevational gradients on diversity (particularly relevant to TMCF environments) and habitat associations of tropical tree species (elevational gradients in *composition*).

2.3.1 Elevational gradients in diversity

Elevational gradients of diversity have been the subject of many studies, as they represent a natural environmental gradient and a perfect opportunity for examining the factors and processes that generate and maintain species diversity (Sanders, 2002). Adiabatic-lapse rates dictate that temperature decreases with elevation through a lowering of atmospheric pressure, but elevational gradients also often represent gradients in wetness (through both rainfall, accumulated soil moisture, fog inputs and reduced evapotranspiration) (Whittaker and Niering, 1975).

Elevational gradients are often seen as a mirror of the latitudinal gradient in richness (Stevens, 1992), with global patterns in species richness often being described by a decrease in richness with greater latitude (Hawkins and Diniz-Filho, 2004), and at any single latitude a decrease in richness with elevation (Rahbek, 1997). This simplified view of elevational gradients however is not supported by all studies (Lees et al., 1999; Colwell and Lees, 2000; Sanders, 2002), and considerable literature is available on both the empirical patterns (Terborgh, 1977; Vasquez and Givnish, 1998; Grytnes, 2003) and the theoretical explanation of these patterns (Stevens, 1992; Rahbek, 1997).

In general terms, two patterns in richness have been identified along the altitudinal gradient for different habitats and for different taxa: a monotonic decrease in species richness with elevation (Terborgh, 1977; Vasquez and Givnish, 1998) and a unimodal hump-shaped (the shape of a normal distribution) mid-elevation peak in richness (Whittaker and Niering, 1975; Lees et al., 1999; Colwell and Lees, 2000; Nor, 2001; Kessler, 2002; Vetaas and Grytnes, 2002; Brehm et al., 2003), with Grytnes (2003) finding both patterns in seven transects in Norway.

Several explanations are provided as to the mechanism behind such relationships. The influence of area on species richness is stated to be "one of community ecology's few genuine laws" (Schoener, 1976). Indeed, species-area relations have been discussed for nearly a century in the ecological literature (Gleason, 1922), and recently reviewed by Lomolino (2000). Many authors have examined the effect of area specifically on species richness in elevational gradients, finding it to be important (Whittaker and Niering, 1975; Stevens, 1992; Rahbek, 1997). In simple terms, assuming that an elevational gradient is representative of a floristic gradient, greater area at any elevation would increase the probability of higher species richness.

Some authors also contend that mid-elevations are habitat-sinks due to the high probability of range-overlap (termed the mid-domain effect), because species ranges are bounded by the highest and lowest elevation possible in the region (Colwell and Lees, 2000).

Rapoport's rule (originally conceived in the context of the latitudinal gradient, but adjusted to the elevational gradient) interprets elevational patterns in richness based on the observation that there is greater temporal climatic variation in higher elevations, Stevens (1992) and subsequently Blackburn and Gaston (1996), advocated that species elevational ranges increase with elevation. The result, according to Stevens (1992) is a monotonic decrease in richness with elevation.

Others liken the elevational gradient simply to productivity, and contest that patterns in species richness are merely a function of the productivity gradient, with different productivity versus diversity theories explaining the monotonic (for example Hutchinson, 1959; Macarthur, 1965) and hump-shaped patterns in species richness (for example Tilman, 1982; Rosenzweig, 1995).

Empirical evidence of the elevational gradient in richness in tropical forests is variable, with Kappelle (2004) reporting that the richness in flowering epiphytes decreases with increasing altitude, whilst pteridophytic plant groups (particularly ferns and mosses) increase in richness with altitude, whilst Vasquez and Givnish (1998) find a gradual decrease in vascular plant richness from lowland tropical dry forest to tropical montane cloud forest in Mexico. Based on the Clinebell et al. (1995) compilation of 0.1Ha tree plots distributed throughout the neotropics, no clear elevation pattern was found, although high elevation plots tended to have lower species richness.

Tests of the theoretical controls on elevational gradients in richness conclude that multiple factors determine the patterns. Sanders (2002) finds a mid-elevation peak in diversity in ant species richness in three US States, attributing the patterns to both species-area effects and Rapoport's rule. Similarly, Rahbek (1997) tested four null models (Rapoport's, monotonic productivity, hump-shaped productivity and area/geometric constraints) using bird diversity in South America as an example, rejecting in this case Rapoport's rule and the monotonic productivity model. In reality, evidence suggests a large degree of site-specificity in richness and elevational gradients, and patterns are likely a cause of a combination of processes, including species-area, productivity and Rapoport's rule. Mid-elevation peaks tend to be more common than monotonic patterns, but there are few clear examples of either for vascular plant species richness in elevational gradients in the tropics.

2.3.2 Habitat associations among tropical forest tree species

A central question in understanding the geographic distribution of tropical rain forest tree species, and indirectly to the maintenance and spatial variation in species diversity, is the degree to which abiotic or biotic factors restrict or limit fine-scale geographic distribution. Lowland rain forest species have historically been considered to be generalists (Pitman, 2000), though some authors have suggested edaphic specialization in lowland rain forest tree species (for example Clark et al., 1998; Palmiotto et al., 2000). Central to equilibrium-based explanations of tropical forests diversity is the concept of niche-differentiation, and this has been tested through studies of habitat association presented in this section.

In LRF, there are two clear scales of habitat association in tropical tree species (Pitman, 2000). There is little doubt of the clear compositional differences between flooded (varzea) and non-flooded forest (terra-firme) (Phillips et al., 2003) brought about by different degrees of flooding tolerance of the species present (Pitman et al., 2001). However, there is a more controversial debate on the degree of habitat association amongst tropical tree species within these broad forest classes.

In the 1960's and 1970's some studies, particularly from Dipterocarp forests in the old world, presented evidence that fine-scale species distributions in tropical forests are driven by habitat preferences (Ashton, 1964; Wong and Whitmore, 1970; Austin et al., 1972; Ashton, 1976). A number of subsequent studies examined similar relationships (Newbery et al., 1986; Baillie et al., 1987). In most of these cases parent material was identified as the most important physical factor driving fine-scale distribution patterns (Austin et al., 1972; Baillie et al., 1987), though not all studies found evidence of strong habitat preferences in tropical forest species (Wong and Whitmore, 1970; Newbery et al., 1986).

More recently a resurgence of the issue has resulted in a half dozen of focused studies published over the past 5 years. The majority, based in Neotropical lowland forests (except for Webb and Peart (2000; Debski et al., 2002; Potts et al., 2002; Palmiotto et al., 2004)), have looked in detail at habitat associations within forest types in search of explanation of micro-scale variability in tree composition and diversity. Indeed, the concept of habitat heterogeneity and tree species specialization has become central to theories explaining the maintenance of tropical tree species diversity (discussed in detail in Pitman, 2000; Harms et al., 2001), and especially related to the non-equilibrium theory of Hubbell and Foster (1986).

Tuomisto et al. (2003) provide three useful models for evaluating micro-scale tree species distributions and habitat associations in LRF, terming them the random-walk, uniformity and the environmental heterogeneity model. The random-walk model is based on a simple view of the non-equilibrium hypothesis proposed originally by Hubbell and Foster (1986), whereby species are randomly distributed across the landscape, but spatially-autocorrelated due to dispersal limitations. Stochastic processes, such as tree-fall, principally drive this model of tree species distribution. Under this model, species presence is not indicative of presence of any other species, and floristic similarity is expected to decrease with inter-site difference. The uniformity model (or more accurately "more-or-less" uniformity) is based on Pitman et al. (1999; 2000; 2001) and Terborgh et al. (1996), with generally constant species composition over wide-areas. Most species are expected to be widespread, and their presence at a site is non-random, but due to a biological characteristic which makes them compete successfully and dominate over a wide range of forest tracts (Pitman et al., 2001). After a disturbance, a similar species composition is expected to recover (Terborgh et al., 1996). In this sense, species composition is expected to vary little with local site conditions, and spatial auto-correlation is not necessarily present. The final model, environmental heterogeneity, advocated by (Poulsen and Balslev, 1991), and the variable composition brought about by non-random, spatially auto-correlated environmental heterogeneity. In the case of this study, Tuomisto et al. (2003) rejects the uniformity model, lending support to a combination of the random walk model and the environmental heterogeneity model, concluding that it is edaphic variability that most strongly segregates the species.

These three models for examining habitat associations in tropical trees present a useful means of evaluating the processes behind specialization or generalization in tropical species, capturing contemporary theories of equilibrium, non-equilibrium and combined dynamics.

Harms et al. (2001) found that 82% of species in a 50-Ha plot in Barro Colorado Island showed no habitat association with basic landscape units, concluding that specialisation plays a limited role in spatially distributing species composition and diversity, lending support to the "uniformity" theory advocated by Pitman et al. (1999). Valencia et al. (2004) find some habitat association related to landscape units in a 50-Ha plot in Yasuni National Park in Ecuador with 25% of species showing habitat specialisation, but conclude in favour of the random-walk model attributing the environmental heterogeneity effect on tree species distributions as only minor. Webb and Peart (2000) lend support to the environmental heterogeneity model, through examination of habitat associations in 45 species in a mixed dipterocarp forest in Borneo, finding 44% of species to have habitat specialization to light and physiographic conditions, but still they fail to account for fine-scale distributional patterns in the remaining 56% of species. Phillips et al. (2003) perform a more rigorous analysis of habitat association amongst 849 Amazonian species across 88 plots, focusing on edaphic constraints to species distribution and finding that 77% of species are significantly related to edaphic habitat, lending strong support to the environmental heterogeneity model. Mantel tests are used in this case to examine distance related floristic similarity (central to the random-walk model), finding only a weak distance related effect. Vormisto et al. (2000) also found strong edaphic specialization in four plant groups (melastomes, palms, trees, and pteridophytes), also using Mantel tests, though in a later paper (Vormisto et al., 2004) the degree to which palm distributions are related to topography is questioned. Clark et al. (1999) approximate that 30% of species in La Selva, Costa Rica, have edaphically biased distributional patterns, and Potts et al. (2002) find 43 out of 60 species studied to have some degree of edaphic specialization, both of these cases providing a strong case for the environmental heterogeneity model.

There are fewer studies and much less theoretical background available for species habitat associations in TMCF environments, though limitations to species ranges are likely to be far clearer due to the sharper environmental gradients. Vasquez and Givnish (1998) examined elevational gradients in family composition, showing clear gradients in abundances for certain families. Sugden (1982) presents similar evidence of altitudinal zonation for some selected tree species in a Colombian cloud forest, also showing clear patterns of elevational limits to distribution. Furthermore, many botanical monographs and species descriptions present elevational range as a factor in describing species distribution. Though these studies are few, there is little doubt that elevational gradients represent strong floristic gradients too, however no studies examine habitat association at the fine-scale based on topographic characteristics in TMCF environments.

In conclusion, there is no single model for habitat association in lowlands that stands out as the dominant process, with different results for different sites and different habitat measures (edaphic or landscape/topographic), though the more rigorous and data rich studies (namely Phillips et al., 2003) find clearer patterns of specialization in tropical tree species, especially related to edaphic conditions. Attention however is brought to the possible role of direct-cycling by trees, whereby tree species themselves control in some part the edaphic conditions around them through litterfall, suggested by Clinebell et al. (1995). However, none of the studies of habitat association for LRF and TMCF presented in this review use DEM-derived topographic variables beyond simple elevation, slope, or landscape unit. In most cases, landscape unit is defined through a combination of rules of elevation, slope and convexity, none of which are calculated in the context of a GIS (for example Valencia et al., 2004). This lack of quantified terrain analysis is clearly a research gap in tropical studies, despite an early paper applying GIS terrain analysis to explain compositional variation in a temperate forest in West Virginia (Twery et al., 1991).

2.3.3 Environmental controls on diversity

Whittaker (1999) states that 'most ecologists have to contend with systems of bewildering complexity, in which it is hard to separate the wood from the trees', and nothing could be truer in the context of discussing environmental interactions with diversity. There is a massive amount of published material that discusses environmental interactions with diversity, covering many different ecosystems and many different taxa. Effort is made in this section to maintain the literature review brief and focused on micro-scale environmental drivers of tree or plant diversity in tropical forests. In general terms, readers particularly interested in this section are strongly urged to consult Givnish (1999), who provides a comprehensive review of environmental interactions with diversity in the context of tropical forests.

The discussion presented here is separated into diversity relations with climate and productivity, light environment and gap dynamics, other types of disturbance, soil quality and finally topography and topographic heterogeneity, though in reality these distinctions are fairly arbitrary as many of these factors are related or act in combinations to affect plant diversity (see for example discussion on the combined effect of productivity and disturbance on diversity in Kondoh, 2000).

2.3.3.1 Climate and productivity

The productivity-diversity relationship is denied by few, but there is heated debate as to the shape of the relationship, with a number of very detailed reviews on the subject (Maranon and Garcia, 1997; Givnish, 1999; Waide et al., 1999; Schmid, 2002). Productivity strictly speaking in this context is defined as the ‘rate of conversion of resources to biomass per unit area’ (Waide et al., 1999), though many authors examine the relationship in the context of water or energy gradients as surrogates of productivity (see Hawkins et al., 2003 for an example).

Waide et al. (1999) present a comprehensive survey of literature on the productivity-diversity relationship, finding that 30% of 200 related articles report a unimodal pattern, 26% a monotonic increase, 12% a monotonic decrease and 32% of articles found no significant pattern at all. But in general, the contemporary literature strongly supports the unimodal relationship, with Weiher (1999) going as far as suggesting it may become an "ecological law" alongside the species-area law of Schoener (1976). However, the debate is far from over, and field-based results showing the contrary cannot be overlooked. Chase and Leibold (2002) contest that the different patterns found are a function of scale, and that the relationship changes shape depending on the scale of study, with a unimodal relationship at the local scale and a monotonic increase at the regional scale. This is also supported by Weiher (1999), and has been strongly supported by Waide et al. (1999).

Perhaps the most comprehensive and frequently cited regional scale test of the productivity-richness relation has been provided by Currie (1991), who found a strong monotonic increase in tree species richness along a potential evapotranspiration (as a surrogate of productivity) gradient across the USA. However, specifically to tropical forests Waide et al. (1999) report that there are few examples of clear relationships between productivity and diversity in tropical forests. The clearest example of climate-diversity relations in tropical forests is that of the high diversity found in regions of high precipitation at both the local scale (Huston, 1980; Phillips et al., 1994) and regional scale (Gentry, 1982; Clinebell II et al., 1995; Gentry, 1995). Wright (1992) also contends that greater seasonal variability in precipitation reduces plant diversity. No other clear patterns have been found.

There are a plethora of explanations as to *why* a productivity-diversity relationship exists. Those that refer to both local scale productivity gradients and diversity include competitive exclusion and environmental stress (Huston, 1979, 1994), changes in environmental heterogeneity with productivity and plant abilities to resist predation (Givnish, 1999; Waide et al., 1999), though there is no agreement on a robust explanation, and patterns and processes tend to vary on a site-by-site basis (Givnish, 1999). Because of the inconclusive nature of the literature and high degree of site-specificity evident, this is not discussed here in great detail, though readers interested in more in depth presentation and discussion of the various hypotheses to explain the productivity-diversity relationship are referred to Waide et al. (1999).

2.3.3.2 Light environment and gap dynamics

Disturbance in ecology is defined as 'any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment' (Pickett and White, 1985). Disturbance in tropical forests includes herbivory, predation, climatic variability, but perhaps the most common and controversial forms of short-term disturbance in tropical forests are those of tree-fall or branch-fall, resulting in an environmental and ecological response referred collectively as gap dynamics (Denslow, 1987).

Prior to discussing the implications of gap dynamics on tree species diversity, some background is provided on the process of gap formation in tropical forests. In a large census of gaps in 12-Ha of primary forest in French Guiana, Van Der Meer and Bongers (1996) found 1.5% of trees (DBH > 10cm) fell in a single year, with 1.3% of individuals losing a large branches. Some 4.9% of the standing basal area was found to be damaged or felled in a single year. Key characteristics in studying gap dynamics include the gap size, orientation, frequency (i.e. temporal variability) and distribution (i.e. spatial variability). Hubbell et al. (1999) contend that gaps occur randomly in both space and time, though some empirical evidence concludes the contrary. Salvador-Van Eysenrode et al. (2000) conclude for an Ecuadorian western Amazonian rain forest that gaps form stochastically in time, but are spatially clustered (in TBS – the same study site as the thesis). The spatial clustering contributes to increased wind turbulence around existing gaps, soil properties, topography (also confirmed by Poorter et al., 1994), and possibly biotic factors such as fungal attacks (Uhl et al., 1988). Nelson et al. (1994) also finds tree falls to be non-stochastic in space, this time using remote sensing to map the frequency of large blowdowns in the Brazilian Amazon, though the study detects broad-scale variability in tree fall due to storm occurrence and rainfall. Though this scale of variability is not relevant to the micro-scale discussed here, the implication of higher frequency in areas of greater rainfall may mean that on the local-scale tree falls are more frequent in areas of higher soil moisture. The micro-scale variation in the spatial distribution and nature of gaps with relation to topography has been studied by Gale (2000) in the Pacific lowlands in Ecuador, finding higher concentrations of gaps in upper- and mid- slopes, with the lowest occurrence of gaps on ridges. The reasons for which were principally attributed to wind, with leeward slopes being most exposed. Given these observed patterns, topography is a key variable that affects (through direct and indirect mechanisms) the probability of a tree-fall (Gale, 2000), and so some of the terrain characteristics developed in the next chapter capture elements of gap dynamics.

The effect of a gap on the light environment is dramatic. Under closed-canopy conditions, the understorey typically receives only 1% of full sunlight in energy receipt, with a 200m^2 small gap receiving 9% full sunlight and a large 400m^2 gap receiving 25-35% full sunlight (all in terms of photosynthetic photon flux density – PPFD) (Chazdon and Fetcher, 1984). This increase in light intensity is crucial for germination of light demanding seedlings and saplings (Denslow, 1987; Meer et al., 1998; Dalling et al., 1999). It also provides a diverse set of light-related niches, with both vertical and lateral penetration of light to the sub-canopy and understorey (Terborgh and Mathews, 1999). Tomlinson (1987) describes many of the types of tree architecture existing in tropical forests including monolayer or deep cylindrical crowns, and leaf angles and orientations, many of which are adaptations related to light receipt. Some species are clearly better adapted to specific light environments than others, with some studies showing this to be the case through focused comparisons of specific species, examining their morphological and physiological strategies for surviving in different light environment (Dalling et al., 1999; Terborgh and Mathews, 1999). Aside from gaps, canopy structure and topography has also been shown to affect the light environment, with Tateno and Takeda (2003) showing higher levels of light availability at the forest floor on steeper slopes, due to a combined effect of vertical and lateral penetration of the canopy.

Gap dynamics are central to many contemporary theories of species diversity maintenance in tropical forests. Recent literature on non-equilibrium dynamics in tropical forests has focused on gap dynamics, arguing that this process, stochastic in both space and time, results in chance occupants rather than the best adapted species recruiting in the micro-environment (due to dispersal limitations). Hubbell et al. (1999) first coherently presented this theory, providing compelling evidence of non-species specific recruitment in gaps in a 50-Ha plot on Barro Colorado Island, as well as undifferentiated levels of vascular plant species richness in gaps and in closed canopy forest.

Hubbell's paper once again stirred an intense discussion on equilibrium vs. non-equilibrium maintenance of diversity, excellently reviewed by Brokaw and Busing (2000). The resultant effect on species diversity if the non-equilibrium theory is accepted is one of relatively little variability (i.e. equal levels of diversity in both gaps, early regeneration and regenerated forest, although this is only observed when diversity is measured as richness per stem). Conversely, the opening of a greater diversity of niches along the light gradient from the center of the gap to the surrounding canopy-covered understorey (often referred to as the gap-understorey continuum) means that gaps generate higher levels of species diversity under the equilibrium theory of niche-partitioning (Brokaw and Busing, 2000).

However, the intermediate disturbance hypothesis (IDH) is also an additional aspect of gap dynamics central to theories of tree species diversity. The IDH was first proposed by Connell (1978) for both tropical forests and coral reefs, and was reviewed more recently with special reference to tropical forests by Sheil and Burslem (2003). The hypothesis dictates a hump-shaped unimodal curve of diversity along a disturbance gradient, measured in terms of frequency or intensity. Connell (1978) suggests a successional process, whereby colonizing species (good dispersers, shade intolerant and fast growing) at first establish in the gap. The second stage of succession involves the slower establishment of shade tolerant species, which compete with the colonizers for energy and water in a state of coexistence. The final stage involves the competitive exclusion of the colonizers, and the dominance of shade tolerant species. Connell suggests that the middle successional stage is most diverse through the existence of both colonizers and shade-tolerant species, therefore sites with intermediate levels of disturbance frequency and intensity tends to maintain the greatest number of species.

In a survey of 197 published works making empirical tests of the IDH, Mackey and Currie (2001) find that the majority of studies find no significant relation at all of a unimodal pattern of species richness along the disturbance gradient (36%), with just 17% confirming a mid-disturbance peak. This study included a broad range of taxa and ecosystems, but for the tropics there are very few examples. Hubbell et al's (1999) model of the effect of gap dynamics on species diversity rejects the IDH, despite both models being marked as non-equilibrium models. But a more recent study shows very strong empirical evidence for the existence of a peak in diversity along a disturbance gradient in tree falls in Guiana (Molino and Sabatier, 2001). In their review, Sheil and Burslem (2003) discuss in detail these two contrasting studies and actually suggest that Hubbell's results are consistent with the IDH, with site-specific conditions leading to the confused pattern. In conclusion, more large-scale and long-term studies are required to further understand the role of the IDH, but there is fairly compelling evidence of at least some variability in tree diversity being explained by gap dynamics and the IDH.

Putting gap dynamics to one side, there is also the important issue of light quality in tropical forests, especially in montane environments. Letts (2003) discusses in depth two aspects of light quality; photosynthetically active radiation (PAR) and ultra-violet radiation (UV). PAR refers to the frequencies of solar radiation used by plants in photosynthetic production, and is not a constant percentage of total solar radiation, varying depending on atmospheric attenuation through cloud cover (Letts, 2003).

Spatially varying levels of PAR therefore have potentially important implications for composition, diversity and structure. For example, in terms of structural implications, Flenley (1992) observed that light-demanding plants grown in high humidity and lowered PAR are tall, with long internodes and large, thin, pale green leaves.

Ultra-violet radiation can cause damage to macromolecules (Letts, 2003). For example, Teramura (1983) showed that seedling growth is stunted following exposure to UV-B radiation. Ultra-violet radiation is important in montane forests, as TMCF vegetation is exposed to higher UV-B radiation than any other forest biome as a result of the short path-length of incident radiation (Ziska, 1996) and the reflection from clouds below, which may increase UV-B radiation by up to 70% (Flenley, 1995). Caldwell et al. (1980) finds that ultra-violet radiation levels increase substantially with altitude. Numerous studies have indicated plant adaptations to high UV radiation levels (Sullivan et al., 1992; Ziska et al., 1992; Ziska, 1996), implying that high levels of UV radiation may have an important effect on tree composition and structure specifically. The degree to which light quality (PAR and UV-B) affects species diversity and composition has not been studied.

2.3.3.3 Other disturbances

Although gap dynamics are undoubtedly the dominant micro-scale disturbance process in tropical forests (Denslow, 1987), other temporal disturbances have been observed to affect species composition and diversity. Condit et al. (1992) provide a detailed account of the effects of drought on Barro Colorado Island, causing widespread mortality in species with different degrees of drought tolerance. Although the disturbance was equal in severity across the whole region, spatial heterogeneity and non-homogeneous distribution of species likely means that the drought may affect change in the spatial distribution of diversity on the micro-scale, although this was not studied. Another type of disturbance of great importance to lowland rain forests is that of flooding, caused by river level fluctuation of as much as 14m, which can submerge large tracts of forest for periods from a few days to 270 days (Junk et al., 1989). Ferreira (1997) finds species richness to be lower in heavily flooded regions, largely to do with dominance of a handful of species well adapted to prolonged root submergence, though in a later study finds no clear relationship in species richness across three landscapes with low, intermediate and high frequency of flooding (Ferreira, 2000).

Intermediate-scale disturbances have also been found to affect forest dynamics, including the effect of river-meandering (Salo et al., 1986). Salo and colleagues use satellite images to conclude that 27% of lowland rain forest in the Western Amazon exhibits evidence of recent erosional and depositional activity, suggesting that this disturbance is another important process in maintaining high diversity in Amazonian forest through prevention of competitive exclusion and creation of environmental heterogeneity. Furthermore, studies in western Amazon also indicate that river meandering may have been stronger through enhanced flows in the recent past as a result of tectonic activity (Rasanen et al., 1986). This intermediate scale disturbance affects the successional stage of forest, as well as altering the substrate for soil formation (Huston, 1994), though little other attention has been given to the role of river-meandering in studies of tropical lowland forest diversity.

2.3.3.4 Soils and nutrients

Though this study does not explicitly include soil in the fieldwork nor desk-based modelling, many topographic factors are indicative of soil texture and soil quality, and there is an extensive body of research which examines edaphic specialization in species (discussed previously in Section 2.3.2), and the role of edaphic conditions on species diversity (discussed here).

There are a number of studies that have used digital elevation models (DEMs) to map soil attributes (for example Bui et al., 1999; Ryan et al., 2000), typically texture (Gobin et al., 2001), nutrients (Chen et al., 1997) and organic matter content. However, these methods often require large calibration and validation datasets, including soil surveys or geological maps, and are not performed in this thesis for reasons outlined in Chapter 1. However, some topographic characteristics are likely to capture soil gradients, and these must be considered in the analysis. Topography plays an important role in controlling the distribution of soil quality (discussed in the next paragraph), but the distribution of soil texture is highly dependent on soil substrate (Takyu et al., 2002) and many topographic patterns in soil texture tend to be site-specific (Gobin et al., 2001).

In terms of plant diversity, nutrients (in much of the literature referred to simply as soil quality) have been found to be both beneficial and detrimental to species richness, with contrasting results of monotonic increase in richness across an increasing soil nutrient gradient (Proctor et al., 1983; Palmiotto et al., 2000), a unimodal distribution with species richness peaking in mid-nutrient levels (Huston, 1982), and monotonic decrease in richness across the nutrient gradient (Hall and Swaine, 1976; Huston, 1982; Oliveira and Mori, 1999). There are text-book examples of the latter relationship, where nutrient-poor soils harbor low tree diversity in the caatinga in Amazonia and kerangas in SE Asia (Whitmore, 1998). Huston (1994) contends that these patterns are spurious, originating from the co-linearity between precipitation and nutrient levels (representing a productivity gradient, producing a unimodal pattern), and that nutrients are indeed of little importance in controlling species richness. Clinebell et al. (1995) argue the same, using detailed soil data in 69 0.1-Ha tree plots of Alwyn Gentry, finding species richness to be independent of soil quality, as well as clear inverse correlations between precipitation and soil nutrient concentrations (principally through greater leaching). However, Oliveira and Mori (1999) provide evidence that high precipitation is not necessarily synonymous with poor soils, providing support for the argument that low nutrient content in soils reduces growth rates and stimulates competition, maintaining high diversity and preventing competitive exclusion (Berendse, 1999). In conclusion, a number of studies present different relationships between soil quality and diversity, and the nature of this relationship may indeed be site-specific.

Many studies of edaphic specialization and soil quality - diversity relations use topography as a factor in determining the edaphic conditions, finding that valley or toe slope regions tend to have fertile soils and ridge landscapes have low fertile soils (Clark et al., 1998; Clark et al., 1999), due primarily to greater degrees of leaching on convex slopes.

2.3.3.5 Topography

Although topography itself is not a physical resource crucial to plant growth and survival, it is a fundamental environmental variable which partitions critical resources such as energy, light and nutrients. Many studies already discussed in Section 2.3.2 use topography to identify habitat specialization, based on the physical environmental conditions found in different topographically defined landscape units (valley, slope, ridge etc.). Although habitat association of species with relation to topography has already been discussed, there are also a select few studies that examine micro-topographic patterns of diversity (rather than composition). Webb et al. (1999) presents the most detailed direct analysis of topographic patterns in diversity variation in a tropical rain forest in American Samoa, finding significantly higher tree species richness on ridges compared to slopes and valleys. No detailed analysis of the reasons behind this is provided, but the authors do mention the possible role of frequent visits by birds and large insects to the more exposed ridges, thus increasing seed deposition. This is the only suggestion of such a process in the literature and may be of relevance for further testing, though the high diversity on ridges might also be due to the documented lower soil quality (Clark et al., 1998; Clark et al., 1999), and of the negative monotonic nutrient-diversity relationship discussed in Section 2.3.3.4. Koponen et al. (2004) also studies micro-topographic patterns of tree species richness variability in a tropical freshwater swamp forest in French Guiana, finding greater richness in lower-sites more regularly flooded, though the extent of the topographic analysis was in fact in the distinction of lower and upper sites. Finally, Enoki (2003) presents analysis of species composition on different "topographic indices" (slope and a basic measure of mean curvature termed 'configuration'), finding that species composition was somewhat related to topographic indices, though no pattern in terms of species richness was evident. Unfortunately the steepness and configuration variables were not measured using robust techniques of terrain analysis.

With the part exception of Enoki (2003), no studies have thoroughly analysed species composition or diversity patterns with relation to a broad range of quantified topographic characteristics, making this thesis the first example of this kind of analysis applied to tropical forest composition and diversity studies.

2.4 Spatial variation of structure in tropical forests

This section provides a brief review of literature on structural variability in tropical forests. It is less thorough than the review already presented for diversity, as it is relevant to only one objective, though there is also less theoretical debate on the topic.

As already presented in Section 2.2.2.1 and Section 2.2.2.2 structure varies significantly between tropical forest ecosystems, with many documented reductions in stature and increases in stem density with greater elevation (Pendry and Proctor, 1996; Pendry and Proctor, 1997; Kappelle, 2004), but there is also micro-scale variability aside from elevational gradients (for example Robert and Moravie, 2004). Aubréville (1938) first coined the phrase ‘forest mosaic’ to describe the micro-scale variability in forest structure, producing a diverse set of micro-environments in the canopy, sub-canopy and understorey. Since then detailed studies of gap dynamics and succession have described much of this variability (discussed in Section 2.3.3.2), but there is still a large degree of spatial variability in structure which is not accounted for by disturbances (Schaik and E, 1985) which has been overlooked in the literature (Trichon et al., 1998).

The elevational gradient in stand height has been attributed to many factors, including high humidity (Odum, 1970), nutrient limitation (Vitousek, 1984; Vitousek and Sanford, 1986), low temperature (Kitayama and Aiba, 2002), soil acidity (Hafkenscheid, 2000), leaf wetness (Letts, 2003) and cloud cover (Grubb, 1977; Letts, 2003). Once again, a certain degree of site-specificity is evident in the literature, but all these studies only use elevational data and do not perform analyses of micro-scale variation which may provide a clearer picture of the factors at play in reducing tree stature.

In terms of micro-scale variability in tree structure without considering the elevational gradient, Robert and Moravie (2004) find no patterns in diameter distributions with respect to slope, but do find that the height of a tree per unit diameter does increase on gentler slopes. Webb et al. (1999) analysed forest structure in different topographic landscape units (ridge, slope and valley), and found stem densities to be highest on ridges with a limiting maximum diameter on ridges, a low stature and a respective low height/diameter which they attribute to windcropping. In general, there are few studies of micro-scale forest structure variability beyond the extensively researched role of gap dynamics.

2.4.1 Structure – diversity interaction

Also of relevance to this thesis is the relationship between structure and diversity, though there is very little available in the literature about this two-way relationship. Many of the equilibrium based theories of species diversity and gap dynamics are based on the diversification of niches through a disturbance that drastically changes forest structure. However, beyond these stochastic and drastic structural changes, structural heterogeneity in a closed canopy also potentially increases the number of niches available in the light environment (Huston, 1994), though there is little literature which explicitly investigates this theme.

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Givnish (1999) reports that amongst other factors that have been found to generate high species diversity in tropical forests, there is a negative effect on diversity with increasing diameter at breast height (DBH), and a positive effect with increased stem density and forest stature. The reasons behind such relationships are questionable, and may be statistical artifacts of diversity indices, or co-linearity between already discussed drivers of forest structure (Section 2.4).

Also of importance when considering this relationship is the potential circular nature of the comparison, with different species themselves having very different structural forms (Tomlinson, 1987), therefore it would be expected that highly species diverse sites would also be structurally heterogeneous. Furthermore, under Huston's (1994) categorizing of interstitial and structural organisms, it is also expected that a diverse structural environment (however this be generated) provides a diverse set of niches for organisms in other groups, such as insects, amphibians and small mammals. This is to some degree confirmed by empirical studies (for example Tews et al., 2004). In this sense, structural heterogeneity may in fact be a more suitable indicator of diversity in other taxa than in trees (for which the lack of relationship has been discussed in Section 2.2.1).

Though there are a number of possible theoretical linkages between structure and diversity, there are few empirical studies that explicitly study this two-way relationship, as it is clearly very difficult to separate cause and effect. In this thesis a brief examination of this relationship will be made.

2.5 Spatial environmental heterogeneity and its quantification

The term environmental heterogeneity is used in a number of different senses in the literature, making discussion of the topic confused without an accurate definition. Environmental heterogeneity within the context of this study refers to the diversity of environments within a certain local spatial extent, for this reason it will be referred to as spatial environmental heterogeneity in order to stress the spatial nature of the variable. Spatially environmentally heterogeneous sites therefore exist where there are sharp gradients in whatever environmental factor is being examined. Many different terms are used to portray the same phenomena, including habitat heterogeneity, habitat diversity, habitat complexity, structural heterogeneity, and spatial complexity (Tews et al., 2004).

Spatial environmental heterogeneity has long been associated with diversity at both the species level (Huston, 1994; Rosenzweig, 1995) and the genetic level (Hedrick et al., 1976; Hedrick, 1986; Volis et al., 2004), though as Araújo et al. (2001) point out this positive relationship has often been ‘assumed rather than measured’. The role of environmental heterogeneity on species diversity is in theory strongly supported by Macarthur (1969), stating that ‘the number of species that stably coexist in an area is dependent on the relative abundance of limiting resources and the range of values over which these resources are distributed’, and many authors have since supported the positive relationship between spatial heterogeneity with related niche-based justifications (Ricklefs, 1977; Tilman, 1982).

Despite what appears to be general acceptance of the relationship between spatial environmental heterogeneity and diversity (Huston, 1994), there are few empirical tests of the relationship, and in some case the methods used are less than satisfactory. Positive relationships between spatial environmental heterogeneity and plant diversity have been found at the local (Nilsson et al., 1989; Burnett et al., 1998; Barberis et al., 2002; Lundholm and Larson, 2003) and regional scale (Rey Benayas and Scheiner, 2002; Pausas et al., 2003). In these studies environmental heterogeneity has been measured based on topography (Harner and Harper, 1976; Burnett et al., 1998; Barberis et al., 2002), soil substrate (Nilsson et al., 1989), or soil depth (Lundholm and Larson, 2003). Only one study reports a poor relationship between richness in vertebrates and higher plants and spatial environmental heterogeneity (Araujo et al., 2001). None of these studies are performed in tropical forests, all originating from temperate ecosystems.

Lundholm and Larson (2003) are the only authors to observe an important unimodal relationship between environmental heterogeneity and the productivity gradient, showing clearly in a limestone pavement that the greatest heterogeneity (based on microtopography and soil depth) is found in the middle of the productivity gradient.

This has important implications for the many studies that have observed unimodal diversity peaks in mid-productivity levels (discussed in Section 2.3.3.1).

However, the measurement of spatial heterogeneity in many of these studies is highly variable, and in some cases questionable. Most apply grid or transect methods, whereby fine-scale environmental data is degraded to a coarse-scale grid of environmental heterogeneity through analysis of range, richness, standard deviation, variance or evenness of environmental conditions within each coarse-scale grid (Burnett et al., 1998; Pausas et al., 2003). In other cases, the method used to quantify environmental heterogeneity is ambiguously described (Harner and Harper, 1976). These methods should not be confused with measurement of habitat heterogeneity in the landscape ecology literature, which tend to focus on factors such as habitat patch types, patch arrangement and patch shape (Li and Reynolds, 1994), referring more to land-use, and which are less relevant to this study as the forests studied here are non-fragmented.

To the best knowledge of the author, there have been no rigorous and quantified tests of the role of spatial environmental heterogeneity at the local scale on tropical tree diversity in the humid tropics. The concept of environmental heterogeneity in tropical forests provides a degree of unification between non-equilibrium and equilibrium based theories of species diversity maintenance. If in lowland rain forests the random occurrence in both space and time of tree and branch fall means that recruitment in gaps is dominated by chance occupants (Brokaw and Busing, 2000), but that there is also some degree of niche-specialization in some tree species (for example Phillips et al., 2003, also discussed in depth in Section 2.3.2), spatially heterogeneous environments would potentially provide a diverse local seed pool for gap recruitment because habitat preferences would mean that the pool of potential immigrants were diverse, increasing the chances that a specialist to the conditions in the gap may arrive through short-distance seed dispersal. The potential implication of a greater number of specialist species finding their particular niche is likely to increase diversity, through optimizing the resource-partitioning, potentially increasing the different number of species that the community may support (Hill and Hill, 2001). In spatially heterogeneous landscapes, the rapid arrival of specialists to a gap may speed up the process of succession and increase levels of competition, resulting in there being greater diversity in temporally dynamic regions (i.e. possibly a left-skewed IDH curve).

In this sense, the potential role of spatial environmental heterogeneity on tropical tree diversity is through explicitly spatial processes such as seed dispersal, predation, herbivory and competition. With respect to seed dispersal, there is a great deal of literature on seed dispersal mechanisms (for example Howe and Smallwood, 1982; Chambers, 1994; Wehncke et al., 2003), and a great volume of studies which quantify seed dispersal processes for specific taxa in tropical forests (Peres and Baider, 1997; Wenny, 1999; Yumoto et al., 1999), many finding the majority of seed dispersal processes acting over distances in the region of 20m – 1km, with the majority of seeds traveling less than 200m (Wehncke et al., 2003).

At this point much of this discussion is pure conjecture with a number of different ways of hypothesising the role of environmental heterogeneity on diversity. It is best to test for diversity relationships with spatial heterogeneity then analyse the potential mechanism behind the pattern, though within the scope of this thesis this is a large theme and only the first step in the analysis of spatial environmental heterogeneity can be achieved here.

2.6 Field sampling methods

A recent article by Phillips et al. (2003) reviewed different sampling methods for studies of forest diversity and dynamics. Though these results were too late to impact on the field-based gathering of diversity, composition and structure data for this thesis, it is nevertheless worth a mention here. A comparison of effort (in terms of person days) and results of floristic inventory were made for 0.1-Ha plots (made up of ten 2m x 50m plots) and 1-Ha plots (square, 100m x 100m), finding that the smaller 0.1Ha plots were more efficient in terms of capturing floristic inventories with the minimum of effort. However, the best choice of plot size and shape is heavily dependent on the ecological questions being raised.

When considering field sampling methods and possible field sampling errors, attention is especially raised to the temporal dynamism of tropical forests, explicitly discussed in Section 2.4, and its relation to plot studies. Though long-term and large-scale projects such as that undertaken in Barro Colorado Island benefit from frequent censuses over time, and many other large-scale plot-based monitoring projects are now underway (Burslem et al., 2001), this study is based on diversity data from a single snap-shot in time. Small plots are used in this study to capture the micro-scale variability central to the objectives outlined in Chapter 1, but this also makes the plot studies particularly sensitive to stochastic processes such as tree-fall which also operate at the micro-scale. It is important that these issues be considered throughout the thesis, as sampling issues are critical both in setting out the research methodology (Chapter 3) and in interpreting the results of the analyses (Chapters 4 – 7).

Finally, this thesis applies a simple *a priori* objective sampling strategy, based on stratification of plots across a 2 dimensional environmental gradient (presented in Section 3.5.1). After a detailed review of the literature, no other example of an objective model for locating plot studies has been found, though Phillips and Raven (1997) do call for stratified sampling schemes in tropical forest plot studies. Though the sampling scheme adopted in this thesis is simple and fairly basic, it is the first known application of this kind of method to tropical diversity plot establishment.

2.7 Conclusions

This chapter has outlined some of the theories for maintenance of species diversity at the local scale in tropical forests, and provided results of empirical studies related to the spatial variability in species diversity, composition and structure. Despite contradictory findings in many cases, likely due to site-specificity, there is strong evidence that at least a percentage of variability in diversity is brought about by equilibrium related processes, and that environmental factors are important in driving this variability (along with biotic factors). In many cases it is topography that has been attributed or used to explain the spatial variability, but terrain-based characteristics are normally limited to simple elevation, slope and slope position (or landscape unit). This thesis therefore applies rigorous analysis of terrain characteristics through GIS to quantify the role of topography in controlling species diversity, composition and structure over space through niche-partitioning.

Chapter 3

3 Research Strategy and Methods

3.1 Overall research strategy

In order to address the hypothesis and aims outlined in the first chapter, this study combines field-based data collection with desk-based spatial analysis and modelling. The experimental design is to associate field measured tree diversity and structure with carefully selected GIS-derived topographic variables, in order to understand which of these factors, if any, are important in shaping the micro-scale variation in tree diversity and structure.

Two study sites are chosen from proximal but very different tropical environments in order to highlight differences in environmental controls on diversity and structure. The first site, Reserva Tambito situated on the western cordillera of the northern Andes in Colombia is a tropical montane cloud forest (TMCF), with steep topography creating a highly variable environment through the site. The complex topography creates a mosaic of micro-climates, with the physical inputs to the system (water, radiation, nutrients) highly variable around the catchment, and in one way or another are controlled by the topography. Persistent canopy level cloud also provides hydrological and nutrient inputs to the system, and also has many other indirect effects on the ecosystem. The second site, Tiputini Biodiversity Station (TBS) situated in the western Amazon in lowland Ecuador, is a tropical lowland rain forest (LRF) with gentle slopes, almost no elevational gradient but a complex network of small streams running into a main river channel which is of 30m width. Above the canopy the climate and physical inputs are homogenous, but on the ground a great deal of micro-scale variation is found. In this sense the canopy serves as a filter of the energy inputs, partitioning these resources unequally below the canopy. River channels have cut 20-30m deep valleys, and highly dynamic flow levels in the main stream (the River Tiputini) causes widespread and frequent, though not persistent, flooding of large tracts of low lying forest.

These two sites are designed to contrast each other, and provide additional insight into how ecology interplays with topographic variation. In all cases throughout this thesis, each results chapter starts by treating each site independently, but the chapters finish by examining the similarities and dissimilarities in the patterns found at each site, and attempt to extract generalities. All efforts are made to ensure that the same field and desk-based methodologies are adopted in each study site, though fieldwork was not performed at each site during the same period. Fieldwork in Tambito occurred between 1999 and 2001, with fieldwork in TBS starting in 2000 and for the purposes of this thesis finished in 2003. For this reason, some improved field methods were adopted for TBS, though they do not affect the validity of the site-comparisons.

One of the important factors in the field-based experimental design was to ensure that the field-based data is directly comparable with the GIS derived topographic data. This basically means that square plots must be used (for comparison with grid-based raster surfaces), and that the plots must be of a size equal to or an exact multiple of the cell size in the raster based topographic data. Furthermore, the central hypothesis of this study is related to micro-scale variation, and so the field data must capture micro-scale variation.

In the literature a number of plot sizes have been used for ecological studies, including rectangular 0.1Ha plots (Gentry, 1995), square 1Ha. 100m x 100m plots (Pitman, 2000), and also rectangular 25-Ha plots (Valencia et al., 2004) and rectangular 50-Ha plots (Condit et al., 1996). Plot size in all these cases was decided based on the hypotheses being tested, but also depended on the resources at hand. As with any piece of research there are limitations to the amount of data collection that can be feasibly achieved (Phillips et al., 2003), with time and resources always being restrictive in some sense. This thesis is no exception, and so these limitations made it necessary to decide on the best balance between the number of plots studied and the size of each plot. Taking into account the issues of scale and compatibility with cell-based grids, ten plots were established in each study site of size 25m x 25m. This exactly matches one cell in the cartographically derived DEMs for each study site, evading problems of aggregating or downscaling the topographic data for comparison with the plot-based data. Though more plots would have been preferable to add greater statistical significance, and also to allow split-sample validations when comparing modelled variables with measured variables, resource, time and accessibility restrictions have prevented the establishment of more plots.

Originally this thesis was to use aerial imagery to actually measure diversity at the broad-scale. This was aimed at producing a result in itself as a method for monitoring diversity, but was also designed to solve some of the problems of lack of field-based data with which to compare with the GIS data. Despite a considerable investment in field-data collection and image processing, this method was not sufficiently refined, and has been dropped from this thesis as a chapter in itself, and the results are not used to enhance the statistical significance of the correlations between diversity and topographic characteristics. However, some preliminary results were achieved, which show potential for further development. This line of research lacks the scientific rigor for inclusion in the body of the thesis itself, but does merit some tangential mention. For this reason, Appendix 1 presents some of these advances. Further work in this area is being undertaken by others in the HERB research group.

Of most importance in the analysis of topographic characteristics was the digital elevation model (DEM) itself, since all of the topographic characteristics are in some way derived from it. It is evident later in this chapter that a great deal of effort was invested in generating the DEMs for each of the study sites. In the case of Tiputini two DEMs are used throughout the analysis. Despite complicating both the analysis and the interpretation, this decision is justified based on the critical importance of DEM quality on the accuracy of the results. Some discussion and preliminary analysis is presented in this chapter to understand the qualities and associated problems with each DEM. This becomes important in later chapters when interpreting the results.

Also of key importance to this thesis is the selection of terrain characteristics. Given the lack of prior analysis of terrain characteristics in the context of diversity and structure in tropical forests that has been explored in Chapter 2, selection of these variables is made with the objective of covering a broad range of terrain conditions considered potentially important for both diversity and structure. Special attention is made in selecting characteristics that directly affect essential resources for tropical trees such as light, temperature and water, and also factors which may have some indirect effect on other important factors (such as soils, micro-climate). Whilst there is an extensive body of research attempting to map soil characteristics explicitly based on digital elevation models (Gessler et al., 1995; Bui et al., 1999; Ryan et al., 2000; Lookingbill and Urban, 2004), results are variable and often require large calibration and validation datasets which are not available for this study. It is likely that some terrain characteristics capture a degree of soil variability (type and quality), but this indirect relationship is unknown and un-quantified. In any case, some evidence suggests that soil may not be all that important for tropical forest ecology (discussed in Section 2.3.3.4), through direct cycling and the fact that most of the nutrient dynamics take place in the litter and organic layers (i.e. a function of the vegetation and not of the soil) (Vitousek, 1984; Clinebell II et al., 1995; Berendse, 1999). Based on the experimental design of comparing measured diversity and structure with GIS-based terrain analyses, it was deemed better to include numerous terrain characteristics, some of which represent similar terrain conditions and contain degrees of co-linearity. Whilst this co-linearity is problematic to results interpretation later in the thesis, subtle differences in the potential significance of the terrain characteristics themselves sometimes help in isolating the precise causal process. However, in order to ease the analysis, certain terrain characteristics are discussed in greater detail than others, and given greater importance in the interpretations.

This chapter is split into the two major methodological thrusts of this thesis, which were the preparation of terrain-based spatial data and the field-based diversity and structure data collection. This does not necessarily reflect the chronological order in which this research was elaborated, and indeed little of the environmental or spatial data was available when field-work commenced (since the collection of field data began before the thesis formally commenced and required the most significant time and effort of all the aspects of the thesis). For this reason *a priori* sampling strategies were not used in Tambito, and the sampling strategy used in TBS used factors not entirely compatible with the final environmental and terrain variables presented here.

First a brief description of each study site is given, followed by a detailed description of the methodologies adopted to define and calculate the terrain characteristics. Secondly, the chapter addresses the field-based data collection, providing detail on the methodologies used in each study site. On the whole, the same methodologies were used in each study site, but in some cases site-specific conditions necessitated slight differences in methodologies. For this reason, each site is discussed separately. Finally, the methodology for the spatial heterogeneity modelling is presented, as the method is identical for both sites.

3.2 Reserva Tambito

Reserva Tambito, Cauca, Colombia (2^{o} 30'N, 76^{o} 59'E) lies on the western slopes of the Western Cordillera of the northern Andes. It is located within the Choco biogeographic region, identified as one of the major global biodiversity hotspots (see for example Myers et al. (2000)). The altitudinal range is extensive, rising from 1053m to 2860m, with steep slopes (10-70 degrees), and varying altitudinally controlled climates creating a gradient from lower montane cloud forest (LMCF) to upper montane cloud forest (UMCF) in the upper reaches of the catchment (>1700m). Large volumes of epiphytes are found clinging to branches and leaves throughout the catchment (Jarvis, 2000). The total area of the two catchments covers 2150 hectares. The current land-cover within the catchment is mainly primary forest (72% of catchment), with an area of pasture around the Tambito cabin (4% of catchment) and a larger area of surrounding secondary forest (26% of catchment). Tambito has played an important role historically for the region, providing a stop-over for farmers traveling from the coastal regions to the large market in El Tambo, some 30km from Tambito. All that is evident of this history today is a deeply cut path crossing the reserve, and the original cabin site of Tambito where researchers are now accommodated. It is unclear to what extent Tambito was forested in the past, but personal communications with local land-owners indicate that the majority of today's forest is at least 50 years old.

The northerly catchment, termed the Palo Verde, is made up of primary forest, whilst the Tambito catchment has large tracts of primary forest with regions of secondary growth (approximately 15-20 years old) and a small deforested area around the accommodation cabins. The steep and variable topography and the dense understorey make movement around the catchments difficult.

Figure 1 The topographic complexity in Reserva Tambito. Photo taken at 1500m from the main cabins at around 3pm. Cloud presence is typical of the afternoon hours, with the late afternoon often characterised by canopy level cloud presence at all elevations.

3.3 Tiputini Biodiversity Station

Tiputini Biodiversity Station (0^{o} 33'S, 76^{o} 09'W) is located in the Orellana Province of Ecuador. It lies in eastern Amazon, some 110km from the edge of the Andes. The research reserve is located directly opposite Yasuni National Park on the River Tiputini in the important eastern Andean biological hotspot (Myers et al., 2000), with an altitudinal range from just 200 m.a.s.l. to 270 m.a.s.l.

In total, the reserve covers an area of approximately 2400Ha. of primary lowland rainforest. There is a network of streams within the region, ranging from small ephemeral channels to larger permanent channels such as the River Tiputini itself.

Though no record of river levels exists for the region, the River Tiputini at the station has been observed to vary in stage by as much as 15m, causing widespread flooding within the surrounding 'varzea' forest. The reserve contains a range of habitats from those that are never flooded to forest regularly found underwater.

A very detailed description of the Yasuni National Park region as a whole is provided by Pitman (2000), and readers are directed to this work for specifics on the geology, history, culture and biology for the region.

Figure 2 River Tiputini at low flow. During highflow the river exceeds the banks and floods the adjoining forest.

3.4 Generation of biophysical data

3.4.1 Reserva Tambito

The work in Tambito contained in this thesis benefited from prior work performed by researchers (including the author) in Reserva Tambito during the period 1997 to present under the auspices of the HERB project (http://www.kcl.ac.uk/herb) and the Negret Project (http://www.kcl.ac.uk/negret). Rincon-Romero (2001) produced a series of raster grids of biophysical variables for use in hydrological modelling, and some of this same data has been used in this thesis.

3.4.1.1 Meteorological and hydrological monitoring

There are two fully equipped hydrological and meteorological stations at the study site. One of the stations is located in the deforested area (the Campo Plot, 1450masl, Figure 3), whilst the other is located in primary forest on the Cerro El Perro hillside in the Palo Verde catchment (Bosque Plot, 1650masl). Each station is equipped with an array of solar radiation pyranometers (upward and downward facing for determining solar and net solar radiation), temperature probes, rainfall gauges, humidity probes, soil moisture sensors buried at varying depths and wind sensors, in addition to hydrological apparatus whose data are beyond the requirements of this study.

Figure 3 Hydrological and climatological monitoring station at the Campo and Bosque plot, Tambito

The Campo station has provided a total of 4 years worth of data, with occasional periods lacking data. The Bosque station has been more problematic (chiefly due to humidity and energy problems), and the data is highly fragmented over the period 1997 – 2002. The Campo station reports temperatures averaging 18.3 degrees Celsius, with humidity in excess of 90% for much of the time and an annual rainfall at the Campo plot of 3900mm. In addition to this, a six-year manual rainfall record from Tambito has been monitored, and indicates a bi-modal seasonality with October/November and February/March being the wettest months (Figure 4). The dryer season (<300 mm month-1) is from June to September. 80% of the total annual rainfall falls between October and May and only 20% falls between June and September inclusive. The record indicates high sensitivity to El Nino and La Nina (Figure 5). In 1997 (a strong El Nino year), just 20mm of rain fell in the 3 months from June to September.

Mulligan and Jarvis (submitted) used rainfall stations distributed around the catchment to conclude that rainfall linearly increases with elevation at 405 mm per year per 100m elevation. Tambito is located in a highly dynamic environment where climatic conditions change across small distances. In addition to the rainfall inputs, a significant amount of input from cloud interception is also to be expected (Gonzalez, 2000; Jarvis, 2000). Wind speeds are generally low (with hourly averages 2000-2001 less than 0.5 ms^{-1} and five minute averages less than 0.66 ms^{-1}), and only 1.2% of five-minute average values are greater than 3 ms^{-1}. Monthly average solar radiation (1997-2001) varies from 101 Wm^{-2} (January) to 378 Wm^{-2} (July) Hourly average solar radiation is generally low, especially in the afternoons (when cloud cover tends to be more frequent). Monthly average radiation varies from 101 Wm^{-2} (January) to 378 Wm^{-2} (July). Hourly average radiation is generally lower than TBS with a peak at 11am of 540 Wm^{-2}. Values are below 10 Wm^{-2} from 7pm through to 5am.

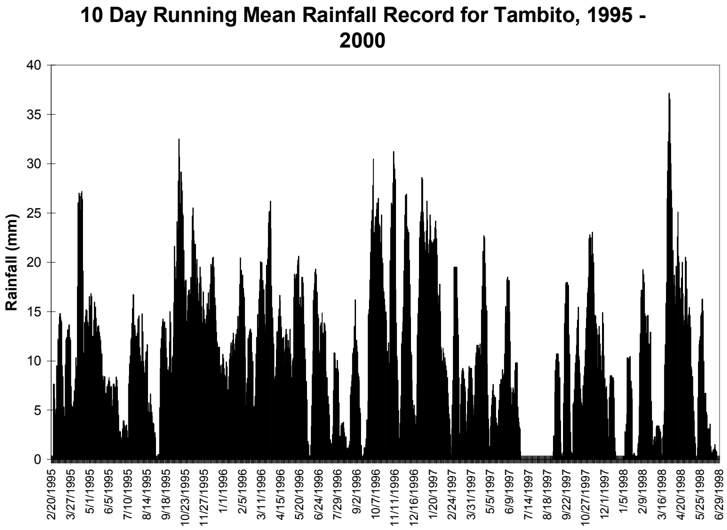


Figure 4 Rainfall (mm) manually measured daily for the Tambito study site, taken at 1450masl in the region around the cabins.

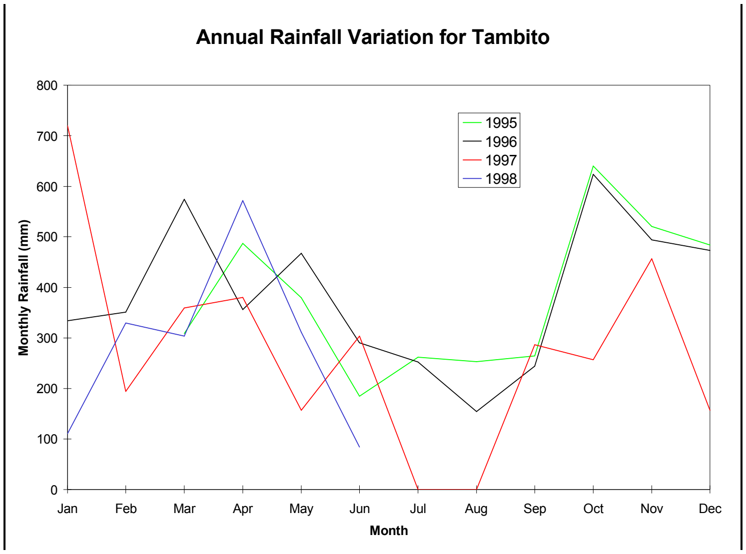


Figure 5 Monthly distribution of rainfall measured manually on a daily basis in the Tambito study site

3.4.1.2 DEM generation

The digital elevation model (DEM) for the study site is the most fundamental physical variable, which is used as a baseline dataset to calculate all terrain characteristics. For Tambito, two potential sources of elevation data were available. These were cartographic map sheets, at 1:25,000 scale and 3 arc-second elevation data from the Shuttle Radar Topography Mission (SRTM). ASTER satellite images were also sought for the study area, to provide a third potential source for a high resolution DEM, but all images as of publication of this thesis contained cloud in and around Tambito.

Topographic data for Tambito was available from three 1:25,000 scale map sheets (sheets 343 I a, b and c) from the Instituto Geografico Agustin Codazzi (IGAC) based in Bogota. Rincon-Romero (2001) digitized contour lines and rivers from these sheets, and made this data available. The contour data on these maps was originally derived from aerial photos, and represents the canopy-top topography rather than the topography at ground level. Furthermore a small patch outside of the Tambito twin-catchments but nevertheless within the region for which there is data lacks contour information due to clouds in the original image. This area is nevertheless outside of the region under investigation in this thesis and no plots are located in this region. This data was re-projected to decimal degrees, and used to produce a DEM with equivalent 25m grid resolution (0.000225 decimal degrees). Arc/Info's TOPOGRID, based on the established algorithms of Hutchinson (1988; 1989), was used to produce the DEM using both contour lines and rivers, using tolerance parameters of 5 for "tolerance 1", representing the density and accuracy of input topographic data, and a horizontal standard error of 1 and vertical standard error of 0. The resultant DEM contains a total of 69,678 cells, covering an area of 7.3km x 5.8km, ranging in elevation from 1086m to 2093m. Slope and aspect were calculated using Arc/Info (which uses the method developed by Burrough (1986)) to visually assess the quality of the DEM, and to provide basic terrain characteristics for use in analysis and modelling outlined later in this thesis. A single scale 3 x 3 window was used in calculating these derivatives as there is little ecological reason why broader scale measures of these variables might influence tree species diversity, structure and composition except through the role of spatial heterogeneity explored in Chapter 6. Figure 6 displays these three basic topographic properties, displayed using hillshading in Landserf to enhance visualisation.

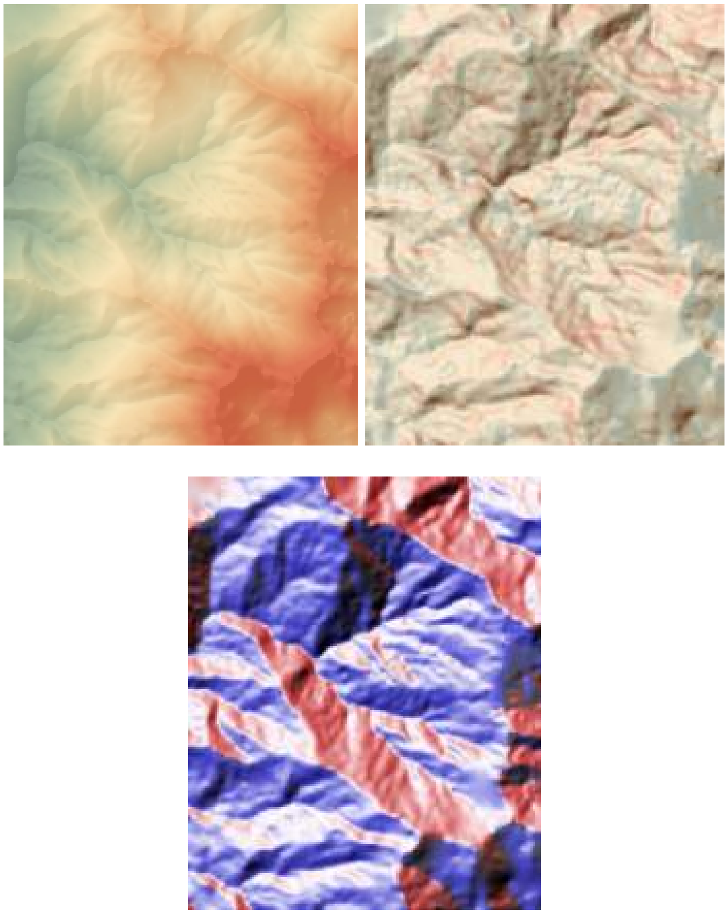


Figure 6 The cartographically derived DEM with 25m cell resolution (left), with the derived slope (center) and aspect (right). Slope varies from 0^{o} (cream) to 58^{o} (red). Aspect is in degrees, ranging from 0^{o} (red) to 90^{o} (white) to 180^{o} (blue) and 270^{o} (white).

SRTM data was also made available for the study region, with cell resolution of 3 arc-seconds (approx. 90m). This was made available by NASA and the USGS late in the process of this PhD in April of 2003. Unfortunately, Tambito contained a large percentage of no data regions (43%) in the SRTM DEM, where steep topography produced strong shadowing, preventing the calculation of elevation due to insufficient textural detail in the original radar images. The SRTM DEM for Tambito is not used in this study, as there is too much missing data (which covered central and important parts of Tambito where plots had been established). Further information on SRTM data for Tambito is also available in Jarvis et al. (2004).

3.4.1.3 Terrain characteristics

Using the cartographically derived DEM (from hereon referred to simply as DEM), a number of terrain characteristics were calculated for comparison with measured diversity and structure from plot studies. These characteristics were selected to represent a broad range of terrain properties which may control structure and diversity through their role in shaping essential resources.

3.4.1.3.1 Potential Solar Radiation Receipt

Section 2.3.3.2 discussed in detail the potential implications of the light environment on tree composition, diversity and structure, stressing the combined role of light quality and quantity. Here a number of light-related factors are presented, capturing both quantity and quality in terms of absolute solar radiation receipt and the intra-annual and diurnal variation. Absolute top of atmosphere radiation is calculated (this section), and two aspect-derived characteristics are presented and their significance on solar radiation thoroughly analysed using measured data (Section 3.4.1.3.2).

A simple radiation model is used to calculate total potential radiation receipt, based on the orbital parameters of the sun, the latitude of the study site and the slope and aspect of the terrain. The solar radiation sub-model of the BENDUM hydrological model reported in Mulligan (1999) was used for the purposes of this study. This model calculates on an hourly basis the potential radiation receipt based on the orbit of the sun at the specified latitude, and the slope and aspect of the ground surface. The hourly time-steps are then aggregated to produce an annual total radiation receipt. The result is a grid of potential solar radiation receipt in the absence of cloud cover or atmospheric attenuation in Wm^{-2}, shown in Figure 7. This "top of atmosphere" radiation receipt should be adjusted to actual solar radiation receipt but insufficient information is available on the spatial distribution of cloud cover in the Tambito catchments to sufficiently grasp the spatial variation in actual radiation receipt through cloud cover variation. For these reasons this study has used unadjusted values of potential receipt. Total potential solar radiation receipt varies spatially in a significant way from 5,600 to 9,600 Wm^{-2}, with north-east facing slopes receiving the least amount, and the greatest radiation receipt on the common gentle-sloping south-west facing hillsides.

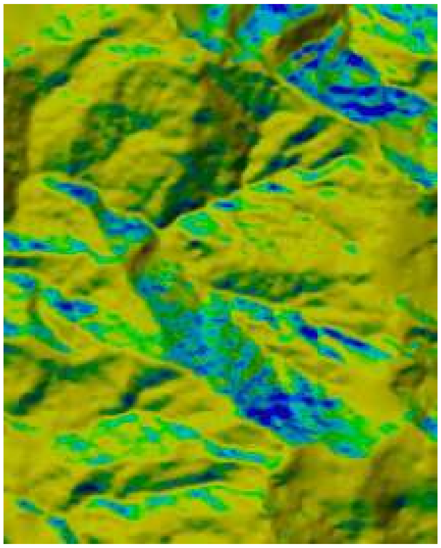


Figure 7 Total potential solar radiation receipt across the Tambito study site. Blue indicates lower receipt (5,600 W/m^2), green intermediate levels (8,400 W/m^2) and yellow high levels (9,600 W/m^2).

3.4.1.3.2 Quantitative Measures of Aspect

Aspect is a critical factor that controls the solar radiation receipt to the land surface. Steep slopes of different aspects may receive quite different levels of solar radiation and this dependence is evident in Figure 7. In Tambito, situated at just 2^{o}N latitude, there is relatively little intra-annual variation in top of atmosphere solar radiation compared with higher latitudes, nevertheless the role of aspect (and slope) is important and some annual variability in radiation receipt exists according to slope and aspect. Section 3.4.1.3.1 applies a solar radiation model to quantify potential light receipt around the catchment, using aspect as one of the key variables. This model does not adjust radiation receipt for atmospheric attenuation by clouds, but provides an overall figure of absolute annual receipt in solar radiation.

However, “top of atmosphere” solar radiation receipt fails to account for two important aspects of solar radiation:

1. Spatial and temporal variation in cloud cover in the twin-catchments of Tambito, which significantly reduces solar radiation receipt at the land-surface
2. Daily and annual variation in solar radiation receipt, brought about by a combination of orbital parameters and temporal variation in cloud cover

The daily and monthly variability in solar radiation receipt is potentially just as important as absolute potential solar radiation receipt, and so two aspect related characteristics are calculated: eastness and northness following Zar (1999):

Equation 1 $$\text{Eastness} = \sin((\text{aspect} * \pi) / 180)$$

$$\text{Northness} = \cos((\text{aspect} * \pi) / 180)$$

For example, northness for an aspect of 360 degrees is 1, for 90 degrees is 0, and 180 degrees is -1.

Understanding the complex role of these two variables on light receipt at the land surface is complicated by the combination of numerous factors. Measured data from an upward pointing pyranometer in the Campo station in Tambito (aspect 7^{o}, northness 0.99, eastness 0.12) is used alongside the modelled solar radiation data and the eastness and northness variables in order to shed some light on the variability of solar radiation at the ground surface, and the significance of northness and eastness. This detailed analysis is important for interpreting relationships found in subsequent chapters between composition, diversity and structure and northness and eastness. Firstly, the role of eastness and northness on top of atmosphere solar radiation is examined, followed by a detailed analysis of their significance in seasonal and diurnal variation in solar radiation receipt. The section finishes by providing some concluding remarks as to the significance of northness and eastness.

Deviation of the actual solar radiation receipt from the modelled solar radiation is not constant, and varies during the year (Figure 8), and depending on the time of day. The modelled solar radiation receipt for the Campo station is uni-modal, with a peak in radiation receipt in the months of May, June and July. However, the measured solar radiation receipt at all times of day is in fact relatively low for May and June, peaking in July and August. Indeed, the greatest deviation from the modelled solar radiation occurs in the months from March – June, coinciding with the wet season. This indicates higher levels of atmospheric attenuation (cloud cover) during these months.

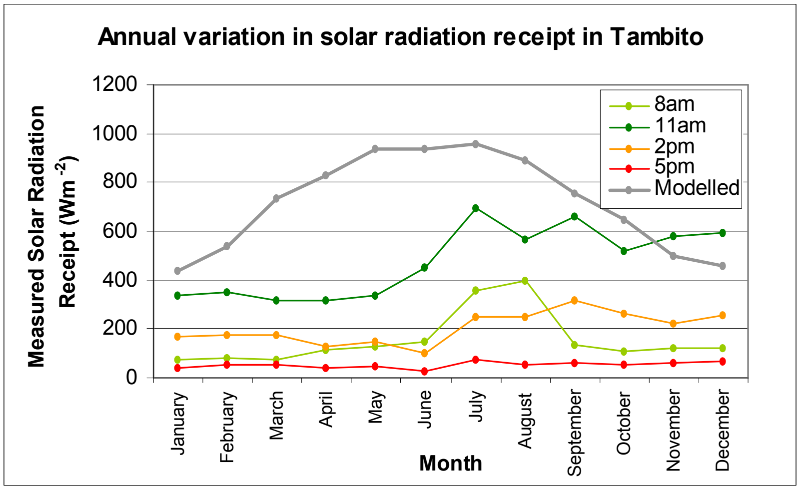


Figure 8 Annual variation in solar radiation receipt at different times of day, using measured data from the Campo station and the average modelled monthly top of atmosphere solar radiation receipt (all hours) for reference.

Relating this annual variation in cloud cover to the northness and eastness variables, the entire Tambito twin catchments are used (i.e. all slopes) to compare northness and eastness with modelled solar radiation receipt. A significant degree of variation in potential solar radiation receipt exists between different degrees of northness, and the higher levels of cloud cover during the months March – June have an important effect. Strongly north facing slopes (positive values in northness) have the highest peaks in potential solar radiation receipt during the summer period (May – July), whilst south facing slopes have the opposite, with the highest potential radiation receipt in the winter period from October – November and lowest receipt May – July (Figure 9). Meanwhile, potential solar radiation receipt varies little on slopes with different degrees of eastness. This has important implications for the northness value, with strongly north facing slopes receiving the greatest amount of potential solar radiation at the same time as atmospheric attenuation is lowest (Figure 8). Inversely, south facing slopes receive the least potential solar radiation in the months with greatest cloud cover. The resultant annual variation in solar radiation receipt is likely to be more pronounced than that shown in Figure 9, with north facing slopes receiving greater solar radiation (contrary to the expectation in the northern hemisphere), and strongly north or south facing slopes also having the greatest range in solar radiation receipt throughout the year.

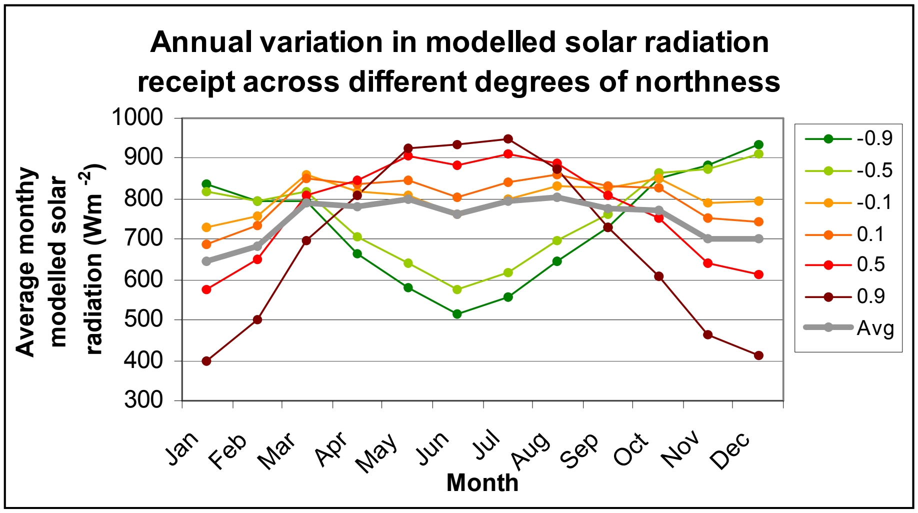


Figure 9 Variation in modelled solar radiation (top of atmosphere) for different degrees of northness throughout the year in Tambito, averaged for all 69,678 pixels.

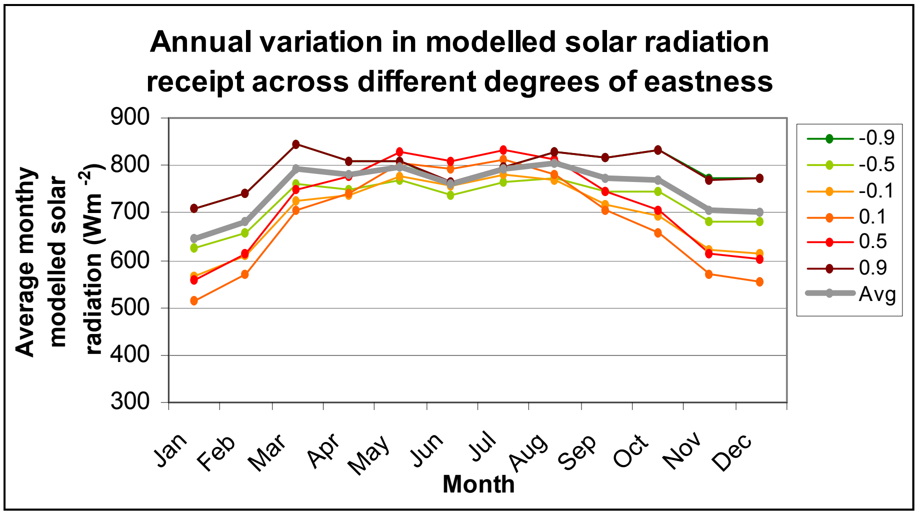


Figure 10 Variation in modelled solar radiation (top of atmosphere) for different degrees of eastness throughout the year in Tambito, averaged for all 69,678 pixels.

Looking at daily variation in radiation receipt, measured solar radiation at the Campo station is compared with the modelled solar radiation receipt for the pixel representing the Campo station (Figure 11). The measured solar radiation receipt at the Campo station peaks at 11am, with an annual average radiation receipt of 560Wm^{-2} at this hour. The afternoon hours have lower than expected solar radiation receipt as a result of build-up of cloud in the catchment, though on average the morning build up of radiation receipt is very well represented by the model (in comparable, not absolute terms), indicating that cloud cover builds up in the afternoon hours. This has important implications for eastness, as east facing slopes (positive values for eastness) receive the greater amount of sun in the morning hours, when atmospheric attenuation is generally lower. Inversely, west-facing slopes tend to receive the greatest radiation receipt in the afternoon hours when cloud cover is higher, potentially resulting in lower radiation.

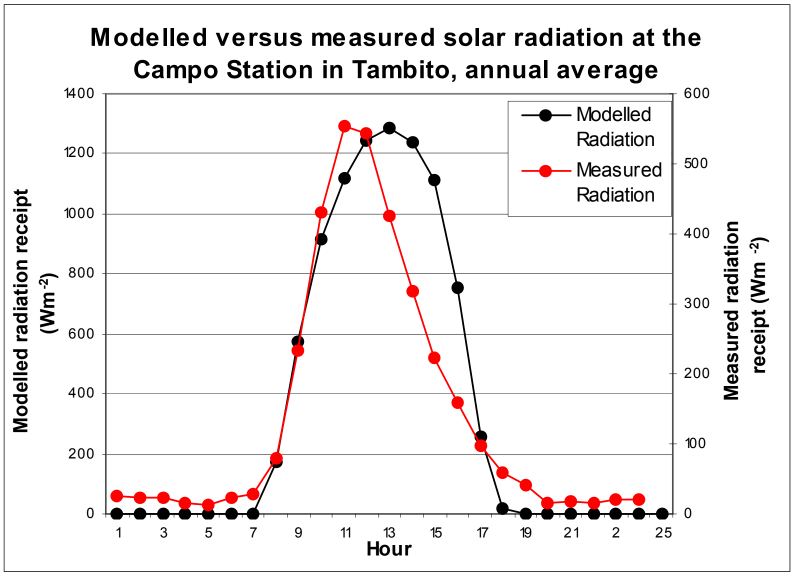


Figure 11 Modelled and measured hourly solar radiation receipt in Tambito, averaging hourly measurements from throughout the year

Combining daily variation in radiation receipt and monthly variation, Figure 12 compares modelled with measured solar radiation for four months through the year, once again just for the Campo plot. As can be seen, the deviation from the modelled radiation receipt is variable throughout the year, with greatest deviation in April in the afternoon hours. In July and especially October little deviation is evident. Examining the absolute values rather than the relative differences, although the peak in modelled potential radiation is generally quite even throughout the year at around 1300Wm^{-2} (ranging from 1210 – 1350Wm^{-2}), the measured solar radiation at this peak varies from 335Wm^{-2} in January (26% of potential) to 720Wm^{-2} in July (58% of potential).

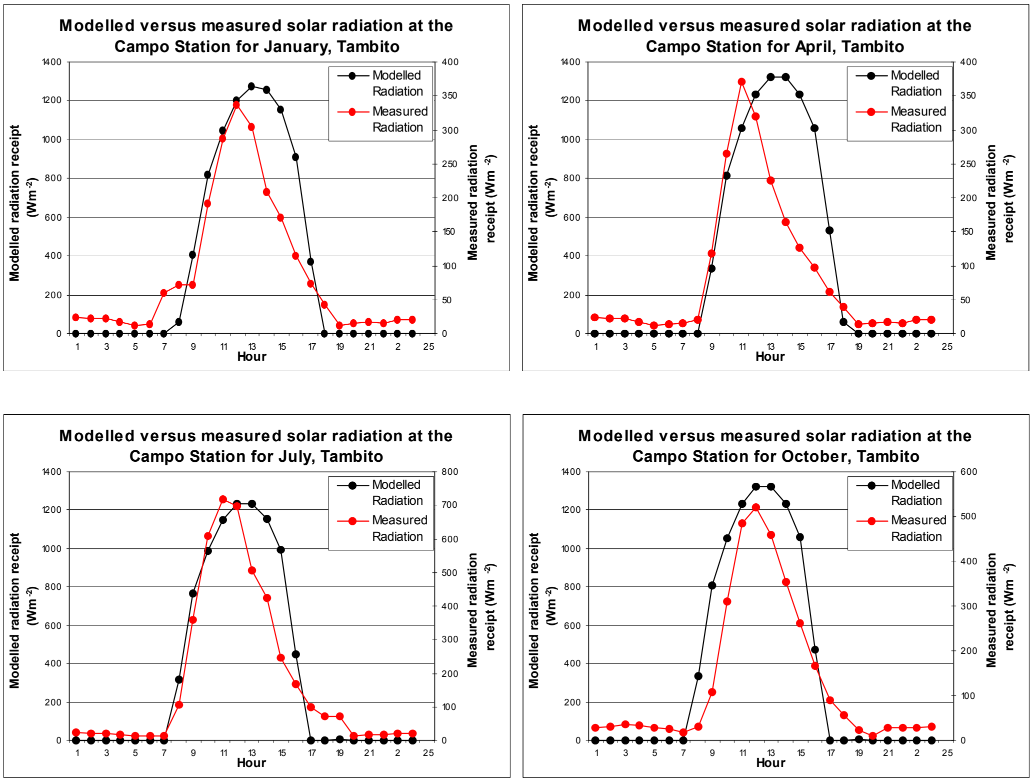


Figure 12 Hourly modelled radiation receipt against measured radiation receipt for the Campo station for four different months, January (top left), April (top right), July (bottom left) and October (bottom right).

These rather complex patterns of solar radiation receipt make the interpretation of the variables solar radiation, northness and eastness difficult. Whilst potential solar radiation receipt is based on a mathematical model, combining slope, aspect, and latitude, significant variations of cloud cover through the year shows that this is unlikely to capture the actual radiation receipt at the ground surface. However, without accurate spatio-temporal information as to the distribution of cloud cover (which incidentally in the field is observed to both drop down from the top of the catchment and flow up the catchment from the Pacific in the afternoon hours), the solar radiation variable cannot be adjusted for actual radiation receipt. For this reason, northness and eastness are used as two other light related variables, which indicate a complex combination of factors.

Northness has been shown to indicate annual variation in radiation receipt, with strongly north facing slopes more likely to receive the greatest amount of solar radiation (greatest potential receipt at same time as the least atmospheric attenuation), depending of course on slope. Strongly north- or strongly south- facing slopes also have the greatest annual variation in radiation receipt, with neutral northness values (approx. 0) having little annual variation.

Eastness is a more complex variable, with less pronounced annual variation in solar radiation across different degrees of eastness, but a potentially strong daily variation. Generally, cloud cover is shown to build up in the afternoon hours, though this deviation of measured from modelled solar radiation is shown to vary depending on the month. However, in general terms east facing slopes are more likely to receive higher solar radiation (average and maximum), whilst west facing slopes likely receive lower radiation levels (average and maximum), depending of course on the slope.

In reality northness and eastness attempt to combine spatial and temporal variation in radiation receipt into single indices but the result is somewhat confused. Nevertheless they are used as terrain characteristics in this study as no other simple means of capturing both spatio-temporal variation in cloud cover and daily or annual variation in potential radiation receipt exists.

It should also be noted that northness and eastness become important in terms of exposure, especially if there are strong and steady winds. Wind speeds for Tambito have long term average hourly values (means of 10-minute readings at the Campo station, intermittently 1997 -2001) of $0.48 ms^{-1}$ with a range of 0 to $2.43\ ms^{-1}$. Means of five-minute averages (of 1-minutes data) give an average of 0.6 m/s and a max of $5 ms^{-1}$. 0% of hourly averages are $>3\ ms^{-1}$ and 1.2% of 5-minute averages are $>3 ms^{-1}$. In the Campo plot, wind direction was dominantly from the south-easterly direction, though this might reflect topographic funnelling as well as the site-specific topographic exposure and the dominant wind direction for the region (combined NE trades and a westerly flow from the Pacific). Indeed, wind direction is likely to vary considerable around the catchment based on topographic funneling and micro-meteorology. Without distributed weather stations around the catchment measuring wind speed and direction it is impossible to accurately map exposure to wind, but it is likely that northness and eastness say little about exposure to wind.

3.4.1.3.3 Mean Curvature

The terrain analysis software *Landserf* (Wood, 2004)) was used to calculate the topographic mean curvature. This is a derivative ranging from negative to positive values, which in simple terms represents the trend in change of slope, negative numbers signifying concave slopes and positive numbers convex slopes. Typically, valleys and toe slopes are concave, and ridges are convex. Competition for light will be more intense in concave slopes, where the topography and the forest canopy produce less surface area for light receipt per unit area in plan form. This effect is discussed in Gale (2000) with relation to gaps, concluding that ridges have greater light receipt and more importantly greater variability in the access to that light (through lateral penetration of the canopy, for example). Curvature is also important for micro-climatic exposure, and especially in Tambito may be strongly related to the exposure to cloud at the forest canopy. It is likely that convex, exposed slopes receive greater cloud presence at the canopy level. This may be important as cloud interception provides an additional nutrient input to cloud forests (Vitousek and Sanford, 1986), and epiphytes tend to concentrate in regions with persistent cloud presence at the forest canopy epiphyte (Nieder et al., 2001). Letts (2003) also argues that persistent leaf wetness is an important factor in the stunting of trees in cloud forests compared to lowland rain forests (through reduced photosynthesis), so greater exposure may also reduce productivity in this way. Finally, curvature may also be strongly associated with soil quality, with highly convex slopes typically being the most leached and nutrient poor (Clark et al., 1998; Clark et al., 1999; Phillips et al., 2003).

The calculation of mean curvature is made using a moving window of user-defined size, with different window sizes capturing variation which occurs at different spatial scales. Nelson (2001) and Wood (1996; 1996) recommends considering multiple scales in terrain analyses, and aggregating multi-scale results into a single map if the most appropriate scale of analysis is not known. For Tambito, the mean curvature was calculated using moving windows of sizes from 3 x 3 cells up to 15 x 15 cells, with a step interval of 2 cells, and the results of each scale aggregated through equal-weighted averaging. There are no precedents of using mean curvature in tropical forest diversity studies, and for this reason the ideal analysis-scale is unknown. The multi-scale approach used here does not limit the analysis to a single scale, though later in the thesis when mean curvature is found to correlate, detailed single-scale comparisons are made for the range of scales from 3x3 to 15x15 cell moving windows. This strategy permits the identification of potential patterns with mean curvature without having to analyse numerous scales, but also allows the identification of the optimal scale when promising correlations are found. It is important to note that small window sizes are likely to be more sensitive to DEM error, and there are means of quantifying this error (Albani et al., 2004), though measurement of error bounds is not applied in this thesis. The final result of multi-scale mean curvature is shown in Figure 13.

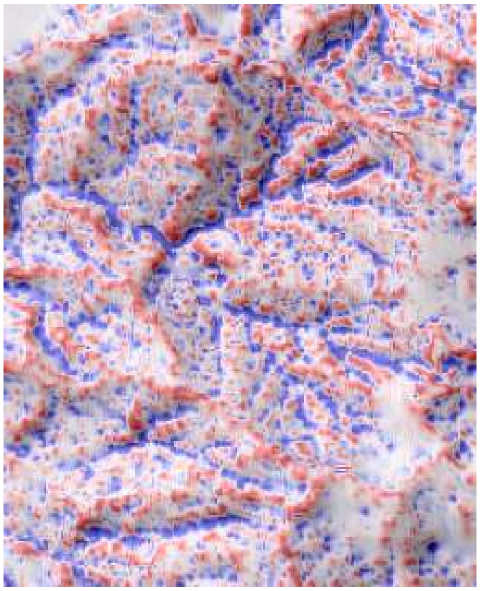


Figure 13 Multi-scale mean curvature for Tambito. Blue signifies concave slopes (-3), white planar slopes with no curvature (0) and red signifies convex slopes (+3).

Numerous other measures of curvature exist, including profile and plan curvature (curvature only in the direction of slope and perpendicular to it), minimum and maximum curvature, and longitudinal and cross-sectional curvature. Rather than complicate the analysis with different measures of curvature, only mean curvature is used here (in addition to toposcale, discussed in section 3.4.1.3.6), though further in depth studies of the role of different types of terrain curvature on composition, diversity and structure would be worthwhile.

3.4.1.3.4 TopModel

The most commonly and popularly used terrain index to indicate soil moisture is the TopModel wetness index (also known as the Compound Topographic Index) (Beven, 1978; Pack et al., 1988; Gessler et al., 1995). Topmodel is calculated using flow directional paths across the landscape to calculate the upslope flow accumulation area for any cell, and combining this with slope to indicate the likely levels of surface overland flow and sub-surface throughflow. Note that it does not take into account absolute nor spatial variation in levels of atmospheric water input. This terrain characteristic is in part indicative of soil-water availability to plants.

The equation for calculating the topmodel wetness index is:

$$\text{Topmodel} = \frac{\ln(\text{Upslope Area})}{\text{Tan}(\text{slope})}$$

Topmodel was calculated using PCRaster, which uses a third-order finite difference method for flow direction and accumulation calculation. Streams and rivers are highlighted as having very high topmodel wetness index values, and ridges and peaks have very low wetness values (Figure 14). It is important to note that the wetness value can change abruptly from one cell to the next, with cells adjoining rivers not necessarily having high levels of wetness. This is important in terms of DEM and GPS positional error, with small errors in positional or elevational error potentially resulting in significant changes in wetness. Furthermore, the topmodel wetness index may not be entirely accurate at the 25m-cell scale in Tambito as fine-scale topographic variation at the ground surface (and sub-pixel topographic variation) is not captured in the DEM, and may be significant in changing flow directions. Further to this, some flow lines appear to be predominantly at 45^o, 90^o, 135^o etc. angles, and this occurs as a result of the D8 algorithm used to define the flow direction in PCRaster. The combination of these potential errors and the abrupt change in wetness that occurs between neighbouring cells urges caution when interpreting results involving topmodel.

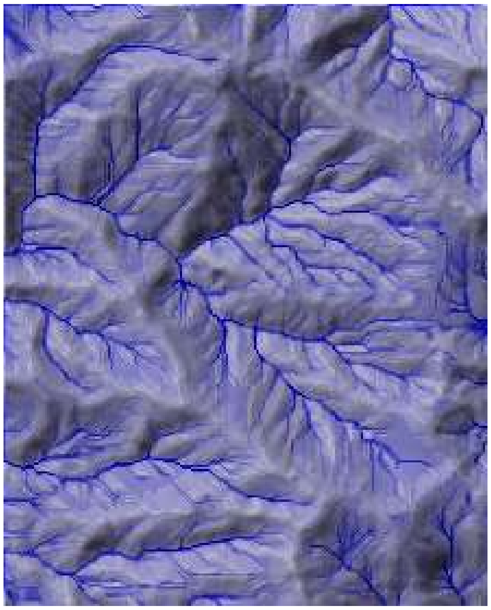


Figure 14 Topmodel wetness index for Tambito, dark blue indicating high wetness values.

3.4.1.3.5 Slope Position

Slope position is a terrain derivative that measures the relative position of a cell from valley floor to ridge. Independent of absolute elevation, this index provides a measure of the position of each cell with respect to landscape features, namely ridges and streams. Slopes close to ridges may be more exposed compared with slopes in valleys where competition for light is likely higher (depending on the steepness of the valley), and the sheltered topography may create warmer and temporally more homogenous micro-climates (depending on wind direction). Proximity to streams may also be important indirectly for presence/absence of seed dispersing species (birds, mammals). In the science of terrain analysis slope position is fairly ambiguous, but numerous tropical diversity studies have used slope position (either approximated or measured in the field) to explain variation in structure, composition and diversity (Webb et al., 1999; Clark and Clark, 2000; Valencia et al., 2004), and for this reason it is used here.

Slope position was calculated using an Arc/Info Arc Macro Language (AML) script provided to the author by David Hatfield of the United States Department of Agriculture (USDA) Forest Service. It is calculated using the following equation:

Equation 2

$$\text{Slope Position} = \frac{(\text{Elevation} - \text{Elevation of nearest valley})}{(\text{Elevation of nearest Ridge} - \text{Elevation of nearest valley})} * 100 + 0.5$$

Values in the output grid range from 0 (valley floor) to 100 (ridgetop). Valleys and ridges are defined through calculation of upslope and downslope flow accumulation respectively (ridges calculated by multiplying the DEM by –1 and analyzing flow accumulation of the resultant grid). As this variable is calculated using an Arc/Info AML flow direction and accumulation is calculated using the basic 8 directional flow method (ESRI, 2001), though it should be noted that better methods for flow accumulation exist using multi-directional proportional flow algorithms (TauDEM/TARDEM for example (Tarboton, 2004), also discussed in Mulligan (2004)).

The AML requires user parameterisation of the flow accumulation threshold beyond which the cell becomes a valley or ridge. In other words, when large limits are used only large valleys and ridges will be identified as such, and small valleys and ridges will be considered somewhere mid-slope. For the purposes of this study a multi-scale approach was used (though the term multi-scale in this case refers to the scale of flow accumulation threshold rather than moving window size), through calculation of slope position using flow accumulation thresholds of 200, 300, 400 and 500. The selection of these thresholds were based on recommendations from the valley/ridge identification AML author (Zimmerman, personal communication). The four resultant maps were then aggregated through averaging, resulting in a single grid of slope-position (Figure 15).

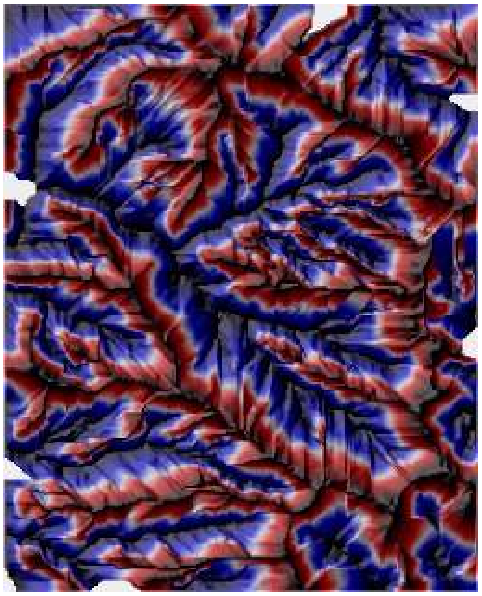


Figure 15 Multi-scale slope position for Tambito. Red signifies cells close to the ridges (100), white signifies mid-slopes (50) and blue signifies cells close to the valley bottom (0).

3.4.1.3.6 Landscape Feature Identification

Characterising a landscape into a range of features captures various aspects of the terrain in one single classification, and these classes may contain distinct environmental processes generating clear patterns in structure and diversity of the forest. Though these classifications are in essence a simplified derivative of many of the variables already discussed (curvature, slope etc.), they capture multiple terrain attributes creating an easily identifiable and interpretable set of landscape classes.

Two topographic feature extraction algorithms were used in this study. The software Landserf produces a landscape feature classification using the algorithms of Wood (1996; 1996; 1998). This uses a moving window of defined size to classify a landscape into ridges, passes, peaks, pits, channels and planar slopes. In this case, a moving window of 5 x 5 cells was used to produce two classifications of the landscape in Tambito; one using the standard method, and the other using an additional network parameter to ensure connectivity of features such as channels and ridges. These classifications are shown in Figure 16. In addition to this single-scale classification, a multi-scale fuzzy feature classification was also used in Landserf, using scales from 3 x 3 cells to 15 x 15 cells. Once again, this range in moving windows is selected relatively subjectively, considered to be representative of meso- to micro- scale topographic variability. This fuzzy feature classification provides membership probabilities to each class, ranging from 1 (signifying membership at all scales) to 0 (no membership at any scale).

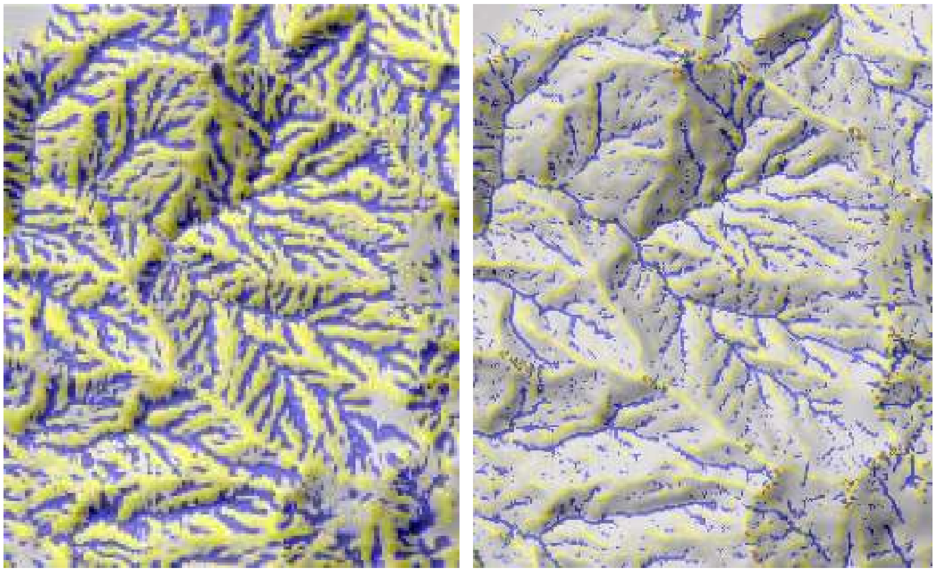


Figure 16 Feature extraction using the Landserf algorithm. The left image shows the classification of features under standard analysis, and the right image shows the same analysis with the addition of network rules. In both cases, the landscape is classified into peaks (red), ridges (yellow), passes (green), planar slopes (grey) and channels (blue).

The second algorithm adopted for landscape characterization uses the method of Zimmerman (2004) to classify into channels, toe slopes, slopes and ridges. This method is based on moving windows that examine the relative elevation of surrounding cells to the central cell (curvature). The method differs slightly from the calculation of curvature. Integration into a single multi-scale measure is achieved by starting with the standardized exposure values of the largest window then adding standardized values from smaller windows only where they exceed the values of the larger scale map. This produces a terrain derivative in itself (termed toposcale throughout this thesis), representing a measure of absolute exposure, closely related to curvature.

To produce a landscape classification, the topographic exposure (toposcale) is then re-classified into four classes, with high positively exposed cells classes as ridges, neutrally exposed cells as slopes, and high negatively exposed (sheltered) cells classified as toe slopes and channels.

In this case, moving windows of sizes from 3 x 3 cells to 15 x 15 cells were used to calculate the topographic exposure, producing a map of topographic exposure between –370 and +330. Cells with values –670 to –150 were classified as channels, -150 to –80 were classified as toe slopes, -80 to +80 as slopes, and +80 to +330 as ridges. These classes were manually selected based on visual inspection of the result, as recommended by Zimmermann (2004). Though subjective, this produces a realistic classification given sufficient field knowledge, though the result is limited in its application to other regions, and indeed in regions containing contrasting topography (lowlands to mountains, for example). The result of this analysis is shown in Figure 17.

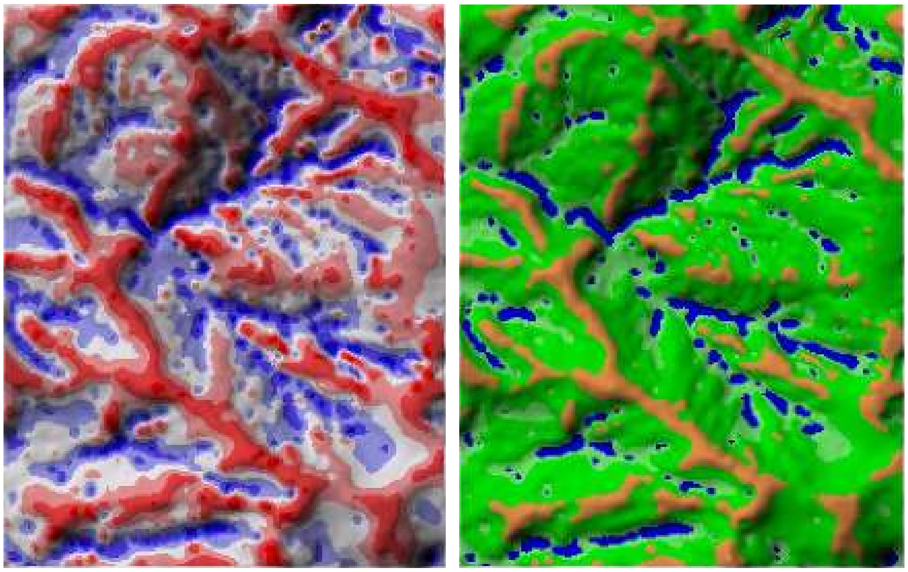


Figure 17 Calculation of "topoclasses" using Zimmerman's method. The left figure represents the toposcale grid (red representing positive values and blue represent negative values), and the right figure shows the reclassification of this grid into channels (blue), toe slopes (light green), slopes (darker green) and ridges (brown).

Visually assessing the topclass classification of Figure 17, it clearly fails to identify the main river channels (Rivers Palo Verde and Tambito) in places, but accurately captures ridges. In conclusion, greater attention should be given to the feature and network feature classifications in the analysis rather than the topoclass variables.

3.4.1.3.7 Terrain characteristic summary

12 terrain characteristics have been produced (nine quantitative, three categorical), and will be used in the analysis. These characteristics represent light related variables (solar radiation, northness, eastness, slope and to some extent toposcale and mean curvature), water availability (topmodel, slope and to some extent elevation),

temperature (elevation), micro-climate (toposcale, mean curvature and to some extent slope and slope position) and landscape unit (feature, network feature and topoclass). Some characteristics are more useful than others, and special attention in the analysis chapters will be given to elevation, slope, mean curvature, topmodel (taking note of the potential problems), the feature and network feature classifications and northness, eastness and solar radiation (the latter three should really be considered together). The potential ecological significance of slope position is less clear and for this reason will receive less attention, despite having been used extensively in some other similar studies (Webb et al., 1999; Clark and Clark, 2000). Furthermore, toposcale is considered to be very similar to mean curvature but less rigorously tested and used as a terrain evaluation method, likewise for its landscape classification variable topoclass.

In subsequent chapters, co-linearity between variables makes interpretation difficult. In the following section this co-linearity is calculated and presented, but it is also useful to show how the different variables are calculated and show in a graphic form the path of derivation for each variable Figure 18.

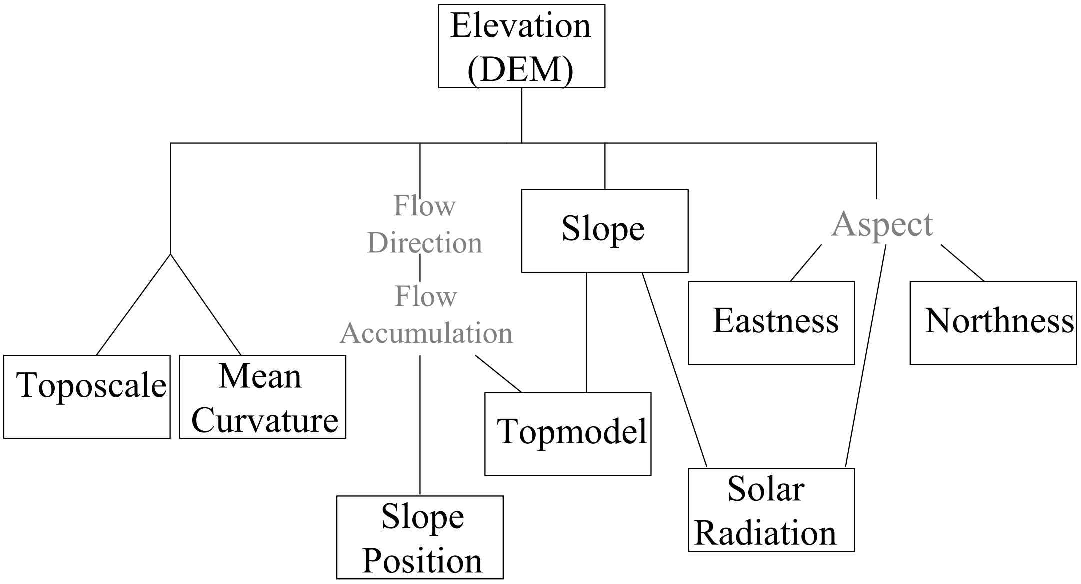


Figure 18 Derivation of each terrain characteristic from the original DEM

3.4.1.3.8 Cross-Correlation Matrix

Many of these characteristics use similar methods and base themselves on the DEM in order to calculate specific properties, and so it is important to examine the cross-correlation of each pair of variables. Table 2 provides a summary of values for each map, and Table 3 shows a cross-correlation matrix between these various terrain properties. In many of the analyses separations are made between continuous variables and the categorical variables (feature, network feature and topoclass).

Variable (unit)	MIN	MAX	MEAN	Standard Deviation
DEM (m)	1144	2903	2022.67	425.46
Slope (degrees)	0.2	57.8	29.85	9.89
Eastness (index)	-1	1	-0.40	0.59
Northness (index)	-1	1	0.04	0.70
Slope Position (index)	0	101	51.08	30.07
Mean Curvature (index)	-2.99	2.96	0.01	0.78
Toposcale (index)	-368	331	-0.47	100.10
Solar Radiation (J/m^2)	5598	9662	8996.55	671.50
TopModel Wetness Index	6.1	20.8	9.00	1.58

Table 2 Summary values for all Tambito continuous terrain characteristics.

Layer	DEM	Slope	Eastness	Northness	Slope Position	Mean Curvature	Toposcale	Solar Radiation	Topmodel
DEM	-	-0.09	0.13	0.05	0.39	0.24	0.28	0.02	-0.08
Slope		-	0.02	0.15	-0.14	-0.09	-0.10	-0.58	-0.33
Eastness			-	0.15	0.00	0.00	0.00	-0.42	-0.03
Northness				-	0.01	0.01	0.00	-0.35	-0.04
Slope Position					-	0.77	0.82	0.09	-0.42
Mean Curvature						-	0.94	0.06	-0.50
Toposcale							-	0.07	-0.46
Solar Radiation								-	0.17
Topmodel									-

Table 3 Cross-correlation matrix between all continuous terrain properties used in the Tambito case study. Values represent the correlation coefficient. Correlation coefficients greater than 0.7 (positive or negative) are highlighted in dark grey, and light grey is used for correlation coefficients of 0.3 to 0.7 (n=69, 678). In reality, most of these correlations are significant (95% level) due to the large number of samples.

The most significant correlations occur between slope position, mean curvature, and toposcale. Toposcale logically negatively correlates with slope position indicating that valleys tend to be found in areas with a low slope position. Toposcale correlates closely with mean curvature, due to their similarity in calculation with only the hierarchical multi-scale method used in toposcale causing a difference in the two results.

3.4.2 Tiputini Biodiversity Station

Field studies in lowland rain forest were made in Tiputini Biodiversity Station. During the process of this study hydrological and meteorological monitoring stations were installed, and some of this data is available for this thesis.

3.4.2.1 Meteorological and hydrological monitoring

A Campbell Scientific automated weather station installed by Boston University has been operating in the station since 1997, though the climate data is intermittent with periods of no data due to technical failures. From Sept. 1997 – March 2003 the logger has a total of 1339 days of data (67% of the time), with Figure 19 showing the period when monitoring was made, and the daily rainfall for these days. For the period of 1997-2004, mean temperature has been 24.8^{o}C, with a daily mean maximum and minimum temperature of 28.3^{o}C and 22.4^{o}C respectively. The lowest temperatures are in June (23.7^{o}C), and the highest temperatures in January (25.8^{o}C). Mean annual rainfall is 2895 mm, with the majority of rainfall occurring between 2pm and 5pm. The greatest rainfall occurs in July (409mm/month), and the least in January (89mm/month). Relative humidity is on average 96.6% (highest in June/July and lowest in December/January). Monthly average radiation varies from 80 Wm^{-2} in June to 189 Wm^{-2} in January. Hourly average radiation is highest at 1200 hours (801

Wm^{-2}) and is less than 5 Wm^{-2} from 8pm through to 6am. Hourly wind speed averages 0.57 ms^{-1}, and is highest when radiation is lowest. Hourly wind speed peaks from 1pm-3pm at 0.81 ms^{-1} and follows a sinusoidal diurnal pattern (matching that of radiation). The highest wind speeds are from the S, SE and NE. Wind direction is usually from the SE (32%) or else NE, E or SE (18% each), 7% of winds are from the SW and less than 5% from all other directions. More detailed analysis of wind speeds are included in Section 3.4.1.3.2.

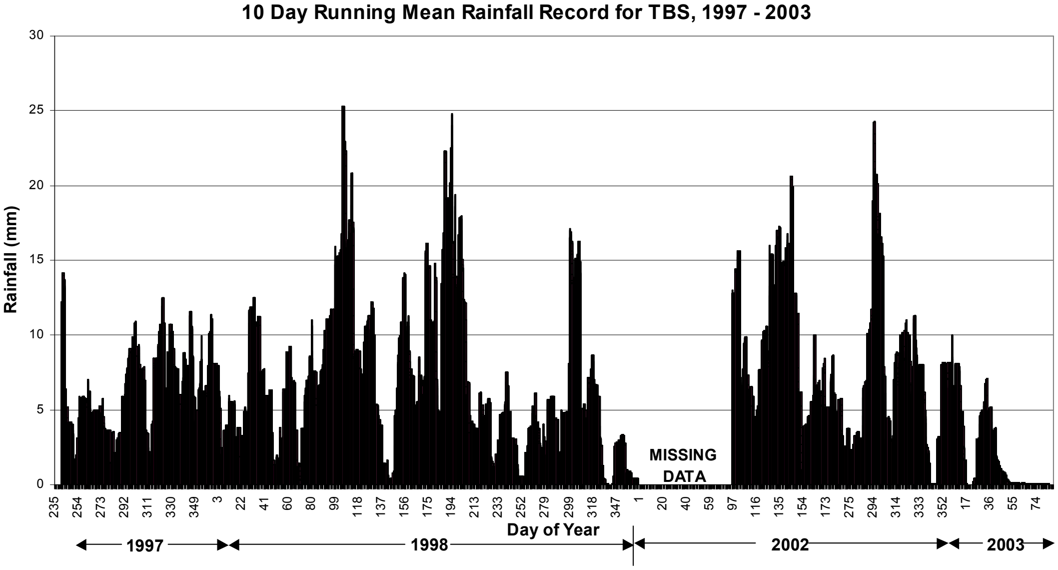


Figure 19 10-day running mean rainfall series for Tiputini Biodiversity Station 1997 – 2003, recorded with the Boston University Campbell Scientific meteorological station installed at the station facilities. Note the missing data from 1999 – 2001.

3.4.2.2 DEM generation

Topography plays a fundamental role in examining relationships between biophysical parameters and tree diversity and structure, but the generation of a DEM for TBS provided a considerable challenge to this study. Prior to this research no DEM was available for the study site, and the topographic landscape made the generation of a representative DEM difficult. Whilst the study site is very flat on the macro-scale, there are complex networks of streams that have created complex micro-scale topographic variation, with some steep-sided valleys of just 10m depth and 30m width, for example. In many cases this ground level topographic variation is not evident in the canopy, causing cartographic maps to overly simplify the topography. For these reasons, different sources of DEM data were sought, with the hope of finding the best representation of small-scale topographic variation, whilst capturing the macro-level differences.

Three potential sources of DEM data were available for the TBS study site. These were 1:50,000 cartography (sheet P111-D4 Zamona Yuturi), the SRTM mission 3-arc second DEM product, and ASTER stereo pair satellite images. DEMs were generated for each of these sources.

The 1:50,000 cartography was scanned and georeferenced using ArcView. Contours (20m interval), rivers and spot heights were then digitized on screen, and the TOPOGRID command in Arc/Info used to produce a 25m DEM using the same parameters as were used in Tambito. The resultant DEM can be seen in Figure 20, along with some basic derivatives (slope and aspect) for assessing DEM quality. As can be seen, the slope is greatest around contour lines, and the interpolation algorithm fails to produce smooth slopes between the contour lines, especially where there are large distances between 20m contour lines. This is a known limitation of many interpolation techniques for DEM generation in flat regions (Hutchinson, 1989), and one that could not be overcome despite numerous attempts using different tolerances.

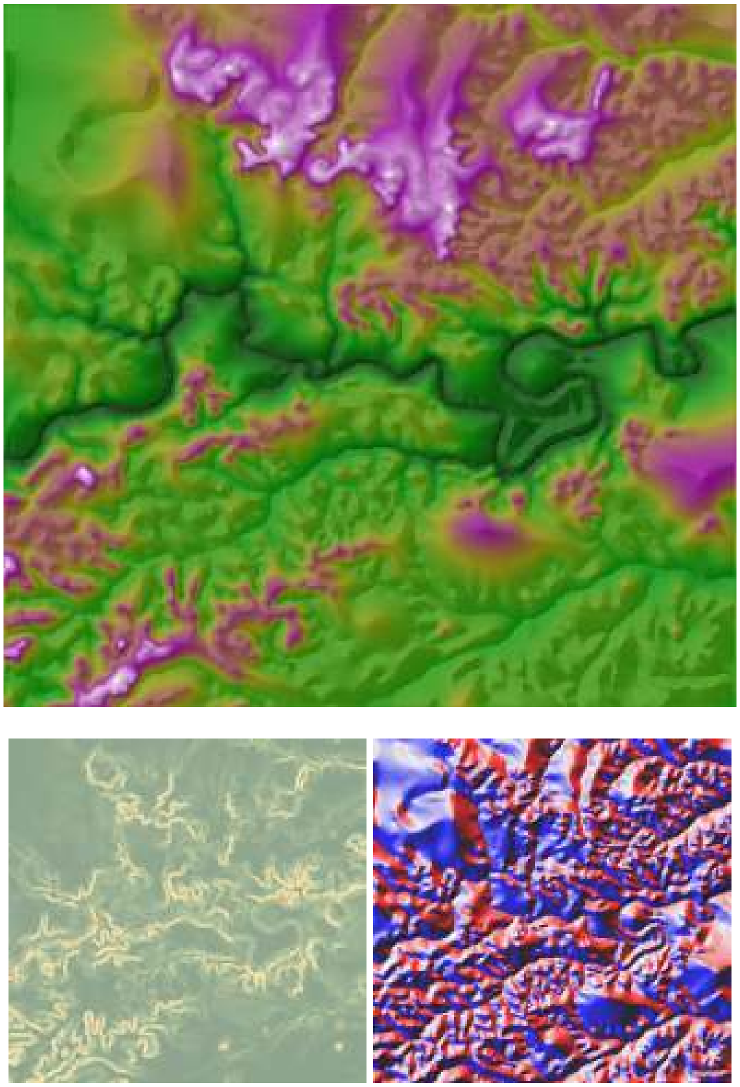


Figure 20 Results of DEM generation using the cartographic maps, producing a 25m grid cell resolution DEM (top), with the derived slope (left) and aspect (right). Slope varies from 0^{o} (light blue) to 31^{o} (red). Aspect is in degrees, ranging from 0^{o} (red) to 90^{o} (white) to 180^{o} (blue) and 270^{o} (white).

SRTM data was made available by NASA in March 2003, providing a 3-arc second DEM for the study area derived from stereo radar data. TBS was extracted from this global dataset, and is displayed in Figure 21 along with derivates (aspect and slope).

The spatial resolution at this equatorial latitude is 92m. None of the no-data cells in the SRTM data which caused problems in Tambito were present in the TBS study site.

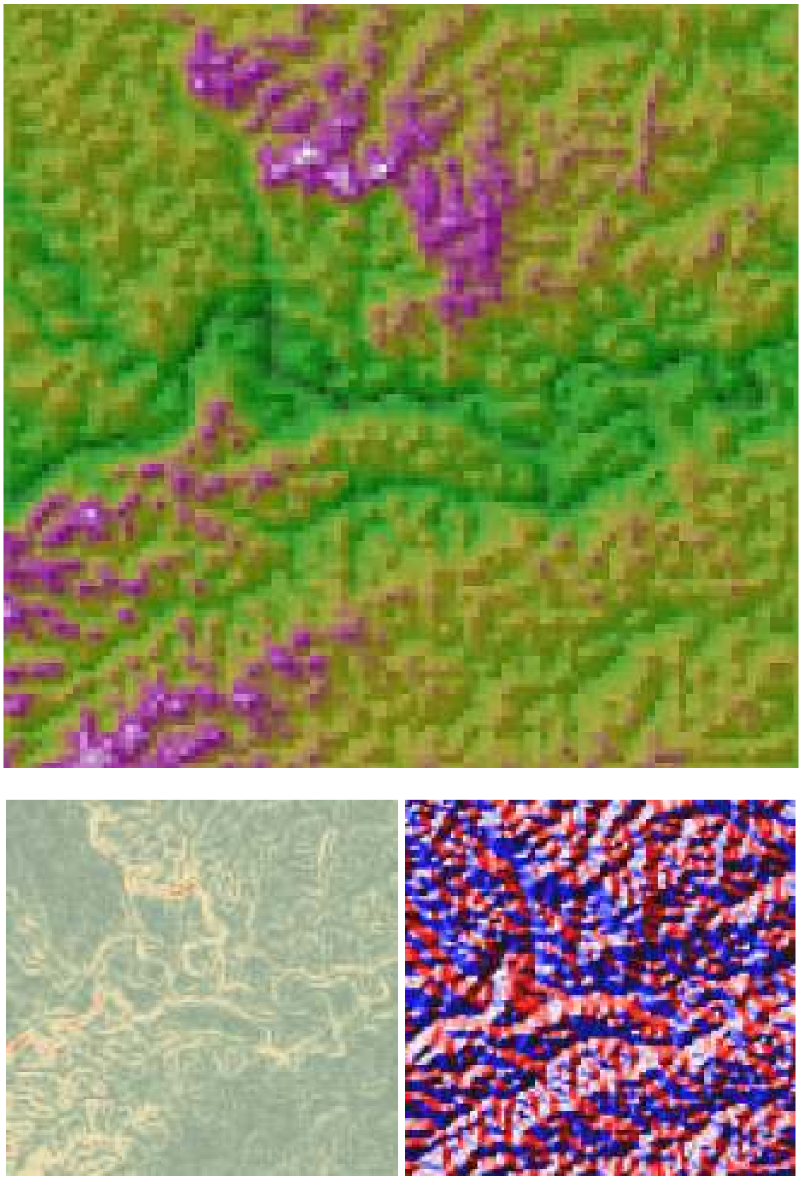


Figure 21 Results of DEM generation using the SRTM satellite derived DEM producing a 100m grid cell resolution DEM (top), with the derived slope (left) and aspect (right). Slope varies from 0° (cream) to 12° (red). Aspect is in degrees, ranging from 0° (red) to 90° (white) to 180° (blue) and 270° (white).

The third and final source for DEM data used in this study was from the ASTER satellite sensor. The ASTER satellite uses two telescopes to acquire stereo pair images in the visible and near-infra-red bands (VNIR) with spatial resolution of 15m. The primary sensor takes vertical images, whilst the backward looking telescope compliments this image with a sideways facing image taken just a few seconds after the vertical image. The stereo pair can then be used to produce high resolution DEMs, with 15m resolution. It is important that no cloud is present in the original image for DEM generation to be successful and since stereo properties are used, DEM production is better in areas of variable topography (where vertical height differences are greater than the horizontal grain of the ASTER image itself – 15m). This is not always the case to TBS. Furthermore care is suggested due to the documented effect of noise in the spectral bands of the stereo-pair relative to the cell to cell height differences in this area (Toutin, 2002).

The ASTER Earth Observing System Data Gateway (EDG) was used to search for cloud free ASTER images covering TBS. Only one suitable image was available with 15% cloud cover from 12th April 2003, which included some light cloud to the north-west of TBS. This ASTER image is shown in Figure 22.

Figure 22 The VNIR ASTER image from 12th April 2003, used to extract a 15m DEM, displayed using bands 2 (red), 3 (infra-red) and 1 (green). Whole image (left) shows heavy cloud cover in the western and south-eastern sector of the image, but TBS is cloud free (right).

The ASTERDEM extension (AsterDTM-V2, 2004) to PCI image processing software was used to automatically extract the DEM without the need for any ground control points or user input. The result is a geopositioned DEM with relative elevation values. These values were converted into metres above sea level using the SRTM data as a calibration set for the entire image (vertical error in SRTM data is claimed to be less than 16m). The resultant DEM of TBS is shown in Figure 23, along with derived slope and aspect.

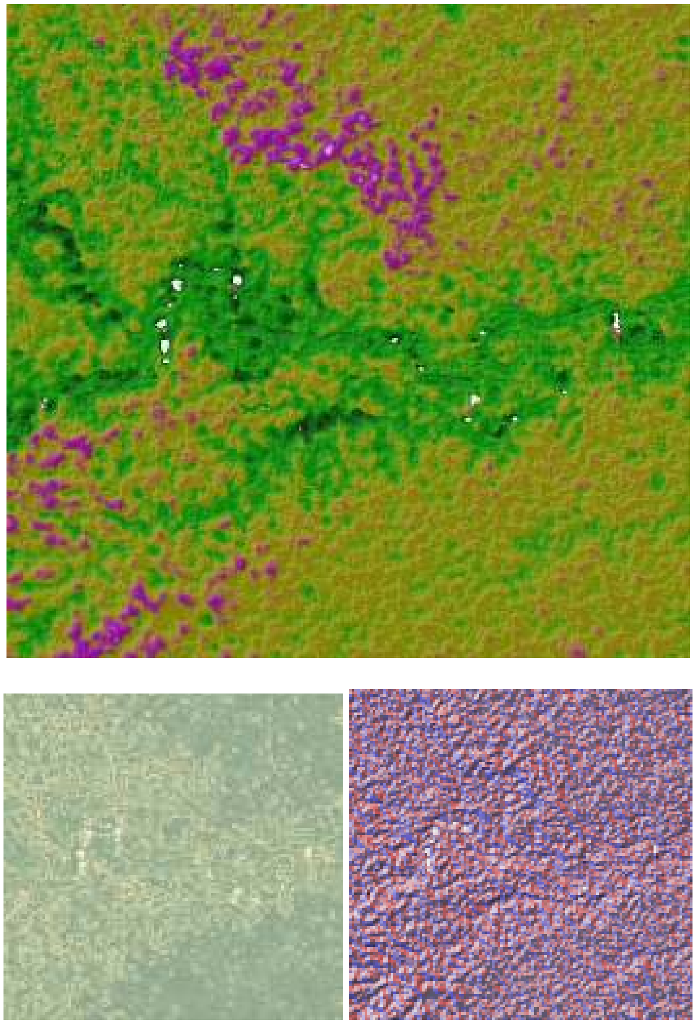


Figure 23 Results of DEM generation using the ASTER satellite image producing a 15m grid cell resolution DEM (top), with the derived slope (left) and aspect (right). Slope varies from 0° (light blue) to 68° (red). Aspect is in degrees, ranging from 0° (red) to 90° (white) to 180° (blue) and 270° (white).

Though the higher spatial resolution of the ASTER DEM is appealing, and the fact that the ASTER DEM captures the general topographic trend of higher elevations in the north-central zone of the DEM, and in a broad sense the river channel, serious questions are raised about the validity of the DEM for capturing the micro-scale topographic variation. The undulating peaks observed in Figure 23 are unlikely to be representative of the true topography, though this DEM is the only one to contain steep slopes that are observed in the field at the micro-scale. Furthermore, the DEM contains 46,000 sinks (of the 396,000 total cells), rendering it hydrologically unsound, and methods for pit removal (in Landserf, for example), fail to adequately correct this problem. For these reasons, and the fact that vertical height differences are not greater than the horizontal grain of the ASTER image in TBS, the ASTER DEM is not used in the analysis, as little confidence can be placed on the quality of the DEM.

Excluding the ASTER DEM, the two DEMs (TOPO and SRTM) capture the general trend of higher altitudes in the northern part of the study area, and south-west of the reserve on the southern side of the Tiputini River. However, the DEMs differ greatly on the fine scale, neither adequately capturing the true micro-scale topographic variation observed in the field. The cartographically derived DEM (hereon referred to as "TOPO DEM") is hydrologically sound, and shows predominantly smooth networks of ridges and valleys, but fails to capture some of the micro-scale topographic variation observed on the ground. The SRTM DEM is also hydrologically sound, but the coarse resolution captures even fewer micro-scale features, representing the study site as topographically homogenous and flat. Both the TOPO DEM and the SRTM DEM likely underestimate the topographic variation. Without a lengthy high precision GPS survey it is impossible to assess which DEM is most representative of the true topography. Both DEMs will be used in the analysis. The TOPO DEM is likely the better quality DEM due to its higher resolution. However, the potential applicability of these analyses in other tropical forested regions is significantly easier using the SRTM DEM, as it has global coverage and is readily available (see for example http://srtm.csi.cgiar.org). Table 4 shows summary statistics for each DEM. The cross-correlation (Pearson's Correlation Coefficient) between the TOPO DEM and the SRTM DEM (calculated after resampling of the TOPO DEM to the coarser resolution of the SRTM DEM (92m) using Arc/Info RESAMPLE) is 0.76, indicating that there are differences between the two. Section 3.7 examines these differences in greater detail.

Layer	Cell Size (m)	No. of Cells	Minimum	Maximum	Mean	Standard Deviation
TOPODEM	25.0	142450	193.7	269.0	227.6	14.54
SRTM DEM	92.6	10400	202.0	278.0	236.5	9.73

Table 4 TBS DEM summary statistics (above) and cross-correlation matrix (below) showing correlation coefficients, n=10,400 (all DEMs were re-sampled to 92m to enable direct comparison).

3.4.2.3 Terrain characteristics

As for Tambito, the same terrain characteristics were calculated for comparison with measured diversity and structure in the plots. Many of the methods were the same as have already been described in Section 3.4.1.3 of this chapter.

3.4.2.3.1 Solar Radiation Receipt

The solar radiation sub-model of the BENDUM hydrological model reported in (Mulligan, 1999) was used on each DEM to calculate the total solar radiation receipt expected for each pixel. Once again, no correction was made for atmospheric attenuation or cloud cover.

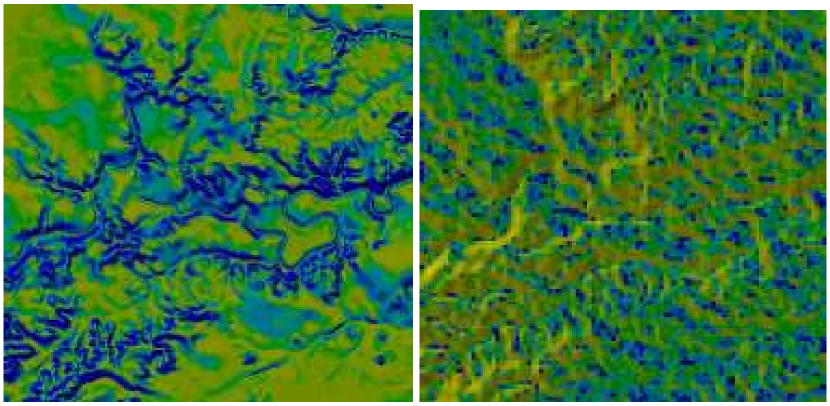


Figure 24 Total potential solar radiation receipt across the TBS study site, using the TOPODEM (left) and SRTM DEM (right). Blue indicates lower receipt, green intermediate and yellow high.

Both the absolute and relative values for the two DEMs vary greatly, with the TOPO DEM being more variable (given the steeper slopes) with radiation receipt ranging from 8657 – 9662 Wm^{-2} and the SRTM DEM having very little variability (9467 – 9662 Wm^{-2}). These differences are brought about by the steeper slopes present in the TOPO DEM.

3.4.2.3.2 Quantitative Measures of Aspect

Aspect was converted to northness and eastness for each of the two DEMs following the same method of Zar (1999) adopted for Tambito. Northness and eastness variables in TBS are relevant in terms of solar radiation receipt and in terms of exposure to wind. Given the low slopes, solar radiation receipt varies little, and indeed northness and eastness variation are likely to have little influence on total solar radiation receipt and the daily and annual variation in this receipt (unlike in Tambito). Data from the Boston University automated weather station and the modelled solar radiation receipt for the cell representing that station is presented for monthly variation (Figure 25) and for daily variation (Figure 26) in solar radiation receipt.

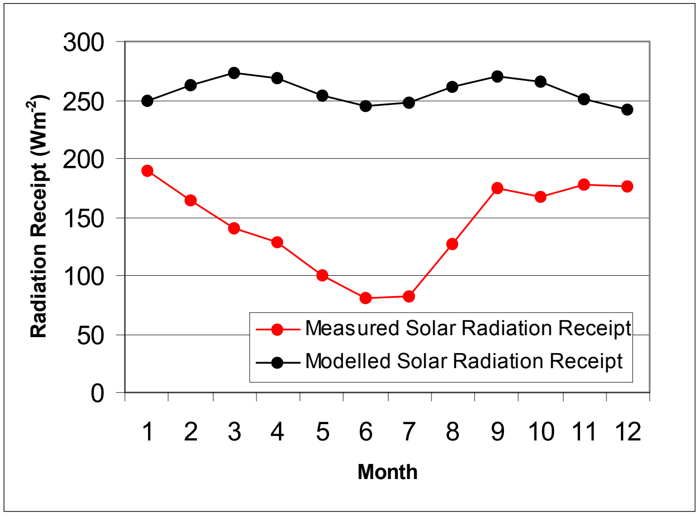


Figure 25 Monthly variability in solar radiation receipt for TBS, showing modelled (BENDUM) and measured receipt for the Boston University AWS. The measured data is averaged for data periods between 1997 – 2004.

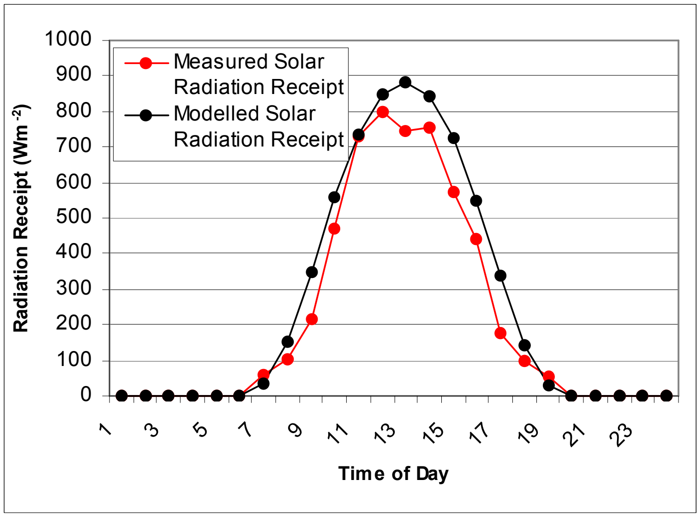


Figure 26 Daily variability in solar radiation receipt for TBS, showing modelled (from the BENDUM model) and measured receipt for the Boston University AWS. The measured data is averaged for data periods between 1997 – 2004.

Though the modelled solar radiation receipt is bi-modal, with greatest potential receipt in March and September, variation in cloud cover produces a uni-modal distribution in actual receipt, with greatest receipt in January, and least receipt in June and July due to increased cloud cover. Daily variation follows much more closely the modelled receipt, with slight lowering in radiation receipt during the early afternoon due to increased cloud cover (12pm – 3pm). Despite this variation, the low slopes and likely homogenous cloud cover over the study site mean that northness and eastness have little relevance for light in TBS.

However, of greater significance in TBS than was the case in Tambito is wind, and northness and eastness measure the exposure to wind. Data from 1997 to 2004 (containing some missing periods) from the Boston University weather station installed in TBS is analysed to show that the average wind speed is 0.51ms^{-1}. The highest windspeeds occur from the SE direction (average 0.57ms^{-1}), and indeed this is the dominant wind direction for 32% of the time. 85% of the time wind blows from the directions of NE, E, SE or S (Figure 27). The highest absolute wind speeds are also in the SE direction, with the maximum windspeed measured at 7ms^{-1} in the SE direction, and over 500 hours of wind above 2.5ms^{-1} in this direction, compared to just 2 hours in the NW direction (Figure 28). After the SE direction, the easterly direction is frequent (dominant direction 17% of the time) and has the highest frequency of high winds (79 occurrences above 2.5ms^{-1}).

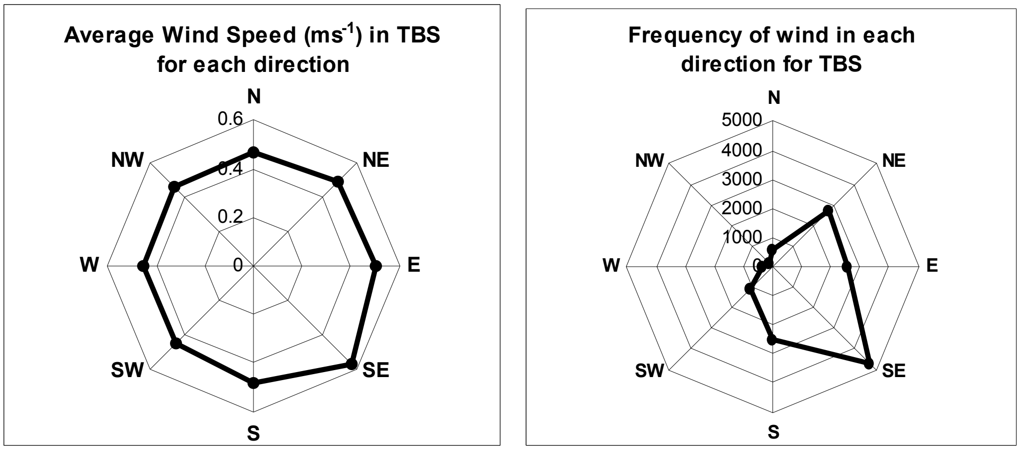


Figure 27 Wind speed and wind directional frequency in TBS based on 7 years (intermittent) of measured wind data from the Boston University automated weather station in TBS.

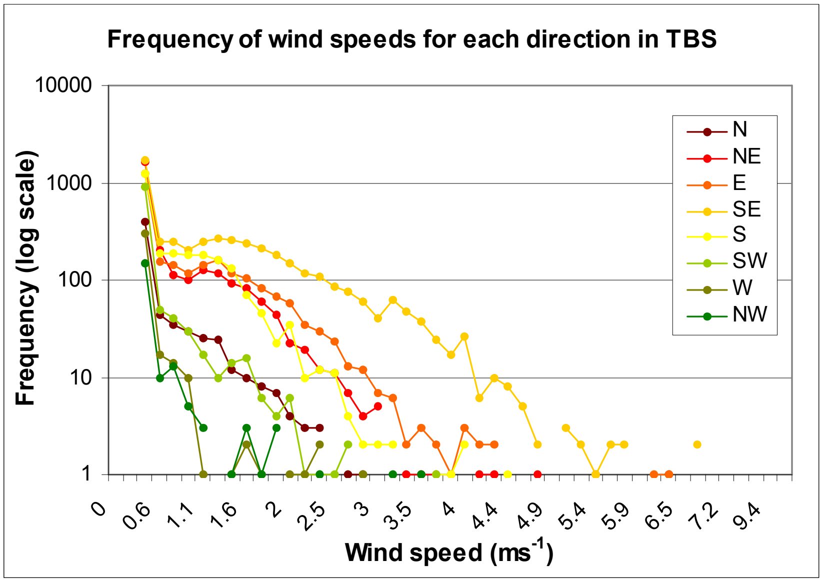


Figure 28 Frequency of wind events for different wind speeds separated for each direction TBS based on 7 years (intermittent) of measured wind data from the Boston University automated weather station in TBS.

The significance of this for eastness and northness is that regions with high – intermediate positive values of eastness (east facing) receive the greatest winds. Northness indicates less in terms of wind direction, though slopes with low northness and with high eastness (i.e. SE facing) are exposed to wind.

3.4.2.3.3 Mean Curvature

Mean curvature was calculated for TBS with the same method adopted for Tambito, using moving windows of sizes 3, 5, 7, 9, 11, 13, and 15 cells for the TOPODEM (25m cell size like Tambito), and 3 and 5 cells for the SRTM DEM, once again to ensure that each result is at the same geographic scale. Limitations in requiring odd sizes of moving window greater than 3 cells explain the use of these window sizes. The results of each scale were aggregated using equal-weighted averaging. The final result of multi-scale mean curvature is shown in Figure 29.

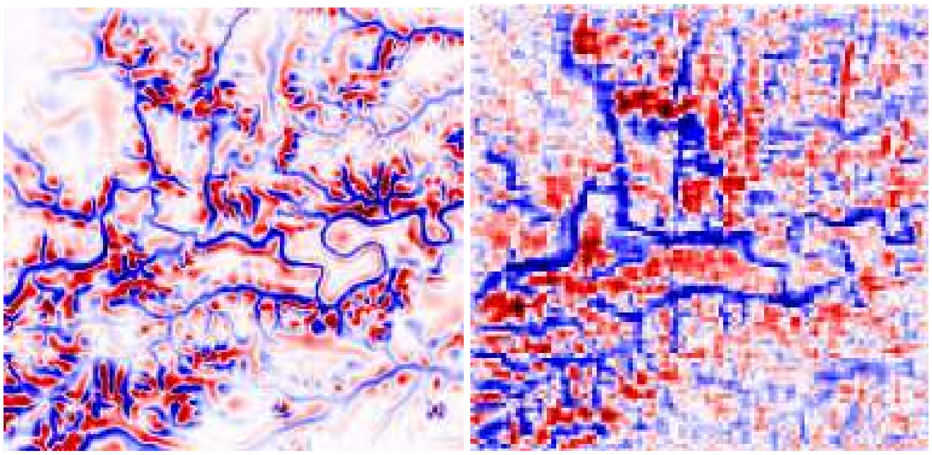


Figure 29 Multi-scale mean curvature for TBS using the TOPODEM (left) and SRTM DEM (right). Blue signifies concave slopes (-3), white planar slopes with no curvature (0) and red signifies convex slopes (+3).

3.4.2.3.4 Topmodel Wetness Index

Topmodel wetness index was calculated for each DEM using the same method as was used for Tambito. However, in the case of TBS TopModel was calculated on the larger DEM area in order to capture more accurately the wetness including the entire catchment. In reality, this was only possible for the SRTM DEM, as this has complete continental coverage, but a region including a large proportion of the lower catchment was included in the calculation for the TOPODEM (55km x 40km). This must be considered a limitation, and potential source of error in the topmodel variable, especially for the TOPO DEM.

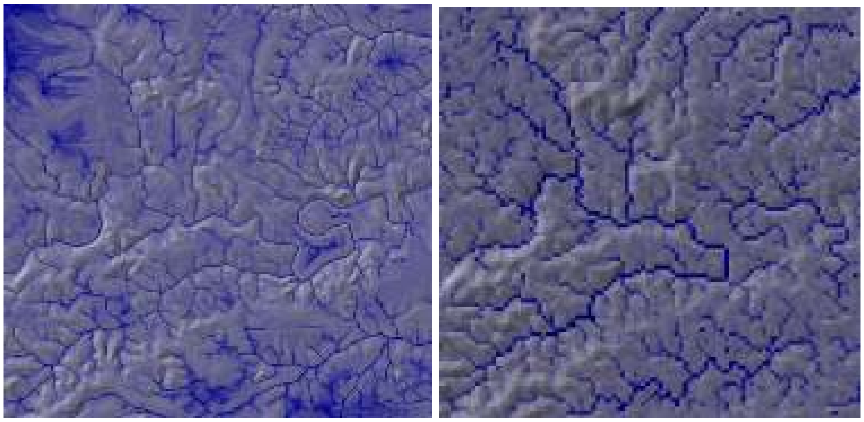


Figure 30 Topmodel wetness index for TBS, using the TOPODEM (left) and SRTM DEM (right), dark blue indicating high wetness values.

The TOPODEM and SRTM DEM both capture the main river channel, although the SRTM DEM loses the continuous flow direction for a short stretch of the river below TBS. This is not important to the result, as all plots are upstream of this, and none are located in the channel itself.

3.4.2.3.5 Slope Position

Slope position was calculated using the same procedure as for Tambito for both of the DEMs (Figure 1). The flow accumulation thresholds varied between DEMs based on the cell size in order to ensure that the results were directly comparable at the same geographic scale, regardless of cell size. The TOPODEM used thresholds of 200, 300, 400 and 500, and the SRTM DEM used thresholds of 54, 81, 108, 135 (smaller thresholds due to the larger cell size). The result for each threshold was aggregated using equal-weighted averaging in all cases.

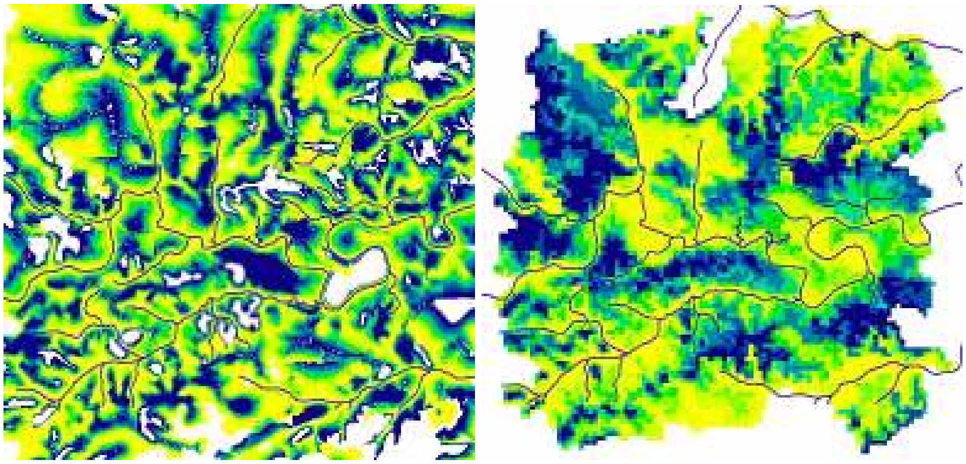


Figure 31 Multi-scale slope position for TBS for the TOPODEM (left) and SRTM DEM (right). Blue signifies cells close to the ridges (100), yellow signifies mid-slopes (50) and green signifies cells close to the valley bottom (0).

3.4.2.3.6 Landscape Feature Identification

Landscape features were identified using the same method as for Tambito, using the algorithm described by (Wood, 2004). A moving window of 7 x 7 cells was used for the TOPODEM and 3 x 3 cells for the SRTM DEM. These classifications are shown in Figure 32. Additionally, multi-scale fuzzy feature memberships were calculated.

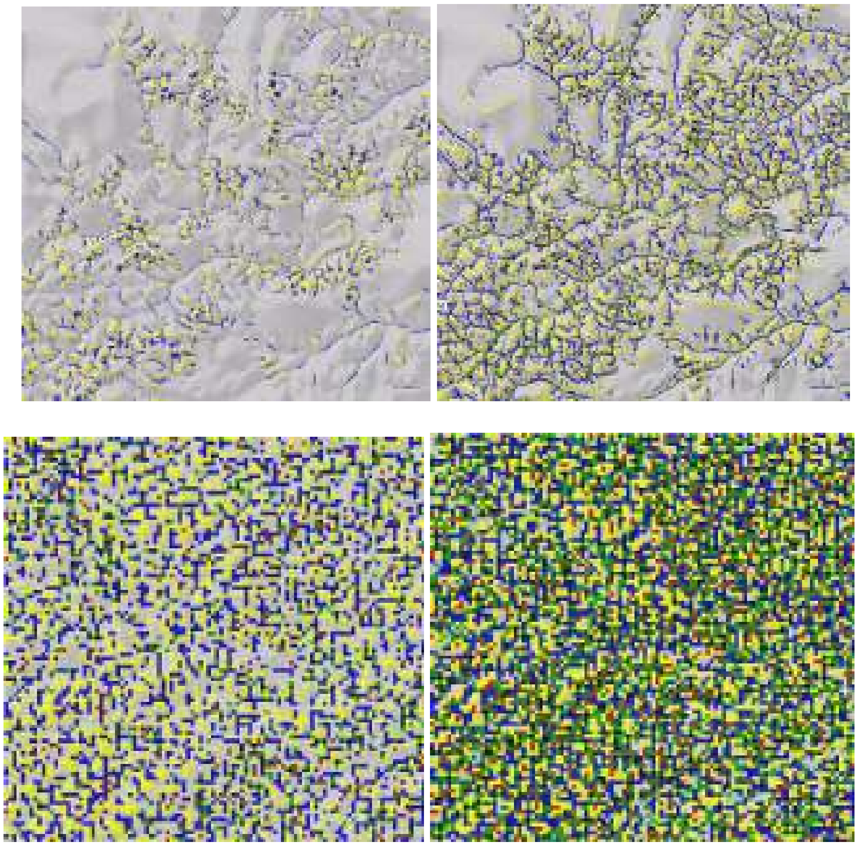


Figure 32 Feature extraction using the Wood's algorithm (2004) using the TOPODEM (top), SRTM DEM (bottom). The left image shows the classification of features under standard analysis, and the right image shows the same analysis with the addition of network rules. In both cases, the landscape is classified into peaks (red), ridges (yellow), passes (green), planar slopes (grey) and channels (blue).

Whilst the TOPO DEM produces a feasible distribution of channels, ridges and some peaks, especially for the network feature classification, the result of the feature and network feature classification for the SRTM DEM appears to reflect little of the actual landscape found in TBS, with not even the main River Tiputini being classified as a channel. This is likely due to the larger cell size, and relatively minor topographic variation present in the DEM.

Zimmerman's (2004) method was also used to identify landscape features, using moving windows of sizes 3, 5, 7, 9, 11, 13, and 15 cells for the TOPODEM, and 3 and 5 cells for the SRTM DEM. Cells with "toposcale" values –670 to –150 were classified as channels, -150 to –80 were classified as toe slopes, -80 to +80 as slopes, and +80 to +330 as ridges. Once again, this subjective selection of limits was made based on visual interpretation of the resultant classification. This is a strong limitation for the quality and applicability of this terrain characteristic in other regions. The result of this analysis is shown in Figure 33.

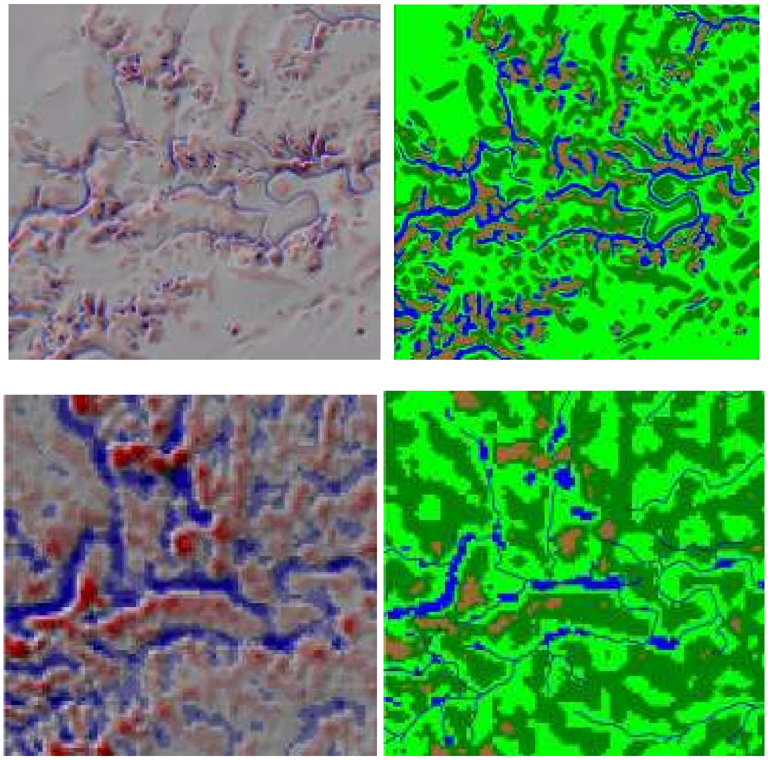


Figure 33 Calculation of "topoclasses" using Zimmerman's method, using the TOPODEM (top), SRTM DEM (bottom). The right figure represents the toposcale grid (red representing positive values and blue represent negative values, and grey represent neutral values), and the left figure shows the reclassification of this grid into channels (blue), toe slopes (light green), slopes (darker green) and ridges (brown).

Once again, the TOPO DEM appears to produce the best landscape classification, and it is important that this be considered in the following analysis chapters. The SRTM DEM classification fails in some sections to capture the main channel.

3.4.2.3.7 Summary of terrain characteristics and DEMs

As for Tambito, 12 terrain characteristics have been produced (nine quantitative, three categorical). These characteristics represent light related variables (solar radiation, northness, eastness, slope and to some extent toposcale and mean curvature), water availability and disturbance (topmodel, slope and to some extent elevation and slope position), temperature (elevation), micro-climate (toposcale, mean curvature, eastness) and landscape unit (feature, network feature and topoclass). Once again extra attention is given to certain characteristics, whilst caution is urged in analyzing toposcale, topoclass and slope position.

Also of importance in TBS are the two DEMs. In almost all terrain characteristics, the TOPO DEM visually performs the best, with the SRTM data producing on the whole realistic looking results, but with a greater cell size that results in a loss of some topographic detail. In conclusion, the TOPO DEM is likely the best DEM in a general sense, though correlations with the SRTM DEM are of significant interest due to its global coverage and potential application in other regions.

3.4.2.3.8 Cross-Correlation Matrix

Table 5 provides a summary of values for each terrain derivative, and Table 6 and Table 7 show cross-correlation matrices between these various terrain properties for each DEM. The correlations are not explicitly discussed in this chapter, though these results are relevant to some of the results interpretation in later chapters.

Variable (unit)	TOPODEM				SRTM DEM			
	MIN	*MAX*	*MEAN*	*STD*	*MIN*	*MAX*	*MEAN*	*STD*
DEM (m)	193.7	270.0	227.5	14.74	202.0	278.0	236.24	9.9
Slope (degrees)	0.0	31.2	3.1	3.41	0.0	10.5	2.08	1.4
Eastness (index)	-1.0	1.0	0.0	0.69	-1.0	1.0	0.03	0.7
Northness (index)	-1.0	1.0	0.0	0.72	-1.0	1.0	0.01	0.7
Slope Position (index)	-48.0	149.0	51.3	35.14	0.0	100.0	47.15	30.0
Mean Curvature (index)	-1.9	2.6	0.0	0.16	-1.0	1.0	0.00	0.2
Toposcale (index)	-661.3	706.2	-0.9	90.36	-198.3	225.1	0.19	55.1
Solar Radiation (*J/m^2*)	8657.0	9662.0	9632.1	51.99	9457.0	9662.0	9646.89	15.6
TopModel Wetness (index)	7.1	25.4	11.6	2.16	8.1	23.4	11.1	1.91

Table 5 Summary values for all TBS terrain characteristics, using both DEMs

	DEM (m)	Slope (degrees)	Eastness (index)	Northness (index)	Slope Position (index)	Mean Curvature (index)	Toposcale (index)	Solar Radiation (mmol/m^2)	TopModel
DEM (m)	-	0.01	0.01	0.04	0.40	0.24	0.40	0.01	-0.21
Slope (degrees)		-	0.03	-0.01	-0.03	0.05	0.04	-0.80	-0.55
Eastness (index)			-	0.00	0.02	0.00	0.00	0.03	-0.03
Northness (index)				-	0.01	0.00	0.01	0.20	0.01
Slope Position (index)					-	0.41	0.61	0.02	-0.32
Mean Curvature (index)						-	0.73	-0.04	-0.33
Toposcale (index)							-	-0.03	-0.32
Solar Radiation (mmol/m^2)								-	0.38
TopModel									-

Table 6 Cross-correlation matrix of terrain characteristics for the TOPO DEM for TBS (n = 143,220)

SRTM DEM	DEM (m)	Slope (degrees)	Eastness (index)	Northness (index)	Slope Position (index)	Mean Curvature (index)	Toposcale (index)	Solar Radiation (J/m^2)	TopModel
DEM (m)	-	0.15	0.01	0.00	0.50	0.43	0.59	-0.12	-0.40
Slope (degrees)		-	-0.05	0.00	0.01	0.08	0.03	-0.77	-0.48
Eastness (index)			-	0.02	0.01	0.00	0.02	0.22	0.02
Northness (index)				-	0.00	0.00	0.00	0.44	0.01
Slope Position (index)					-	0.46	0.61	-0.01	-0.39
Mean Curvature (index)						-	0.34	-0.05	-0.50
Toposcale (index)							-	-0.04	-0.34
Solar Radiation (J/m^2)								-	0.32
TopModel									-

Table 7 Cross-correlation matrix of terrain characteristics for the SRTM DEM for TBS (n = 10,504).

3.5 Establishment of plots

Tree diversity plots were established in order to examine landscape controlled patterns in diversity and structure, and to provide validation datasets for testing some of the modelling hypotheses. These plots were established using methodologies designed to permit easy comparison with spatial datasets, without compromising the quality of the biological data gathered in the field. Transects such as those used by Gentry (1995) would be of little use to this study, as the plots would cover numerous incomplete pixels in the GIS data. It was important that the same method be used in both field sites, and so given that both field sites had topographic data available at 25m resolution, field plots of 25m x 25m were used in this study. This size represents a fair balance between having sufficient individuals in the sample to provide a realistic figure for the diversity and structure at that point (and not being overly sensitive to the precise positioning of the corners), without limiting the number of different plots that could be established given the time and resource constraints. It was important to have sufficient plots to have statistical significance in the comparisons with environmental data, and so ten plots were established in each field site. Whilst more plots would be preferable, limited time and resources did not permit anymore than 10 plots.

3.5.1 Positioning of plots

Access and field conditions were markedly different between the two field sites, and so there were some minor differences in the field sampling. Poor GPS coverage, steep slopes and a dense understorey made conditions considerably more difficult in Tambito. Though no formal sampling scheme was used, the plots were located in regions geographically distinct, evenly covering the elevational gradient and covering both catchments of Tambito. Existing paths were used to locate six of the ten plots, with the location of the corner decided when a predetermined altitude was reached (measured using an altimeter), and by walking 5m to the right of the path. In some cases the topography made it impossible to establish a plot in that exact position, and so the closest feasible area was used. The remaining four plots were established along paths especially opened for this study, geographically distant from the first six plots. Plots were marked based on tape measurement of 25m x 25m areas on the ground, hence under steep conditions the plan area of the plots might be expected to be less than 625m^2. This is a standard means of demarcating plots in ecological studies (Phillips et al., 2003) though attention should be noted that the plots do not therefore necessarily completely compare to the GIS-based cell size of the DEM in steep environments. A Garmin 12XL was used to locate the geographic position of the center of each plot, using averaging for at least 10 minutes per plot. The dense vegetation and steep topography often interfered with the GPS signal, resulting in horizontal RMS errors of up to 20m. Efforts were made to use differential GPS and take plot coordinates with better GPS equipment, but the signals were to weak for a Trimble ProXL GPS to function. The distribution of these plots around the catchments is shown in Figure 34.

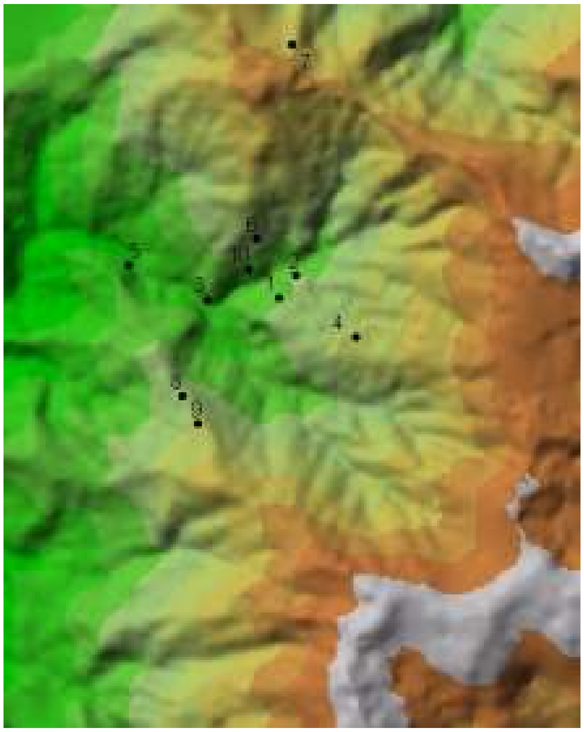


Figure 34 Position of plots in Tambito, positioned in both the Palo Verde and Tambito catchments

Conditions in Tiputini allowed easy access to any point in the study site, due to a thorough system of paths, a cleaner understorey and lower slopes. Under these circumstances, a formal sampling strategy was made using the TOPO DEM (the only DEM available early in the study). The aim of the sampling strategy was to choose a minimum number of unrelated factors, and attempt to locate a plot in each combination of these factors, thereby producing a stratified sampling of the landscape characteristics. Altitude was selected as one of these factors, important for indicating the frequency of flooding from rise in the water level in the river (discussed in Section 3.3)). The 25m TOPO DEM for TBS was classified into four equal area classes (quartiles, Class 1 : 193 – 210m, class 2 : 210 – 220m, class 3 : 220m – 236m and class 4 : 236 – 270m). In this case Class 1 represented areas regularly flooded, with class 2 receiving occasionally floods, and classes 3 and 4 representing terra firma forest where no flooding takes place, based on the observed rise in river level whilst in the field. Equal area classes were used to ensure objectivity, though an alternative method may have been to use subjectively chosen but more meaningful cut-offs between classes.

The other factor chosen was upslope area (also known as flow accumulation), indicative of soil wetness, proximity to river and slope position. This was also classified into four equal area classes (Class 1 : 0 – 3 upslope cells, Class 2 : 3 – 8 upslope cells, Class 3 : 8 – 21 upslope cells, and Class 4 : > 21 upslope cells).

All permutations of these 2 factors with 4 classes were then calculated, producing 16 ‘sampling units’ for TBS shown in Figure 35.

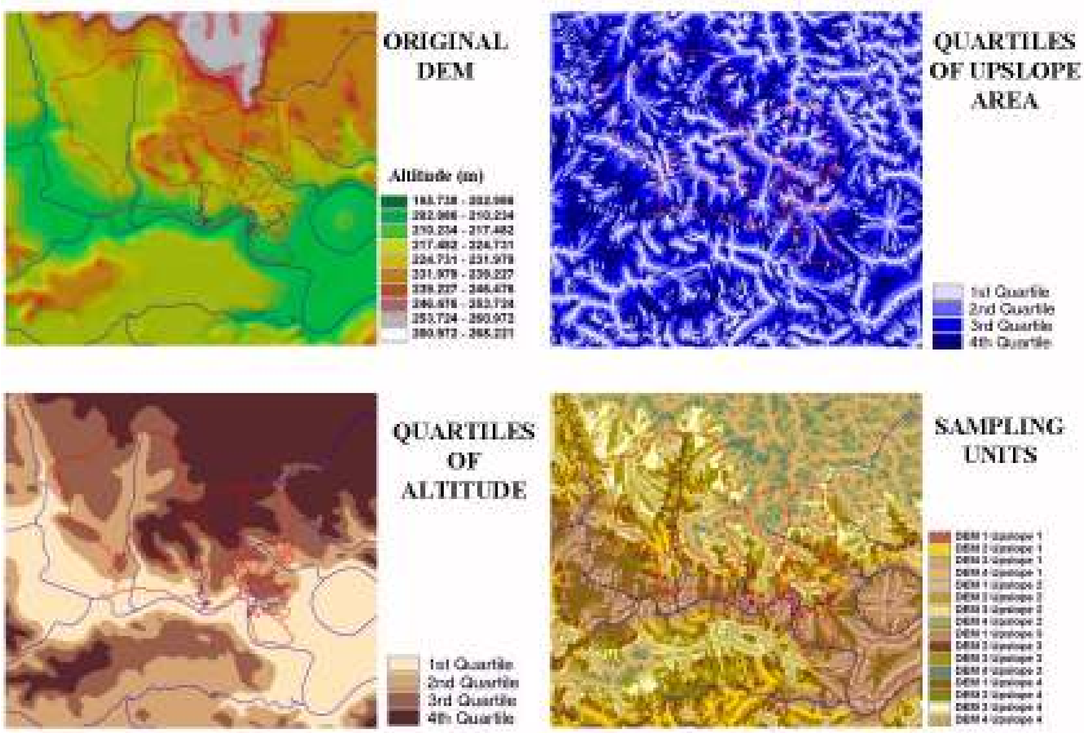


Figure 35 Sampling strategy used to locate ground plots in TBS

Although this sampling strategy could be improved, at the time of field sampling many of the now available terrain characteristics had not been developed. The need for stratified sampling schemes for plot establishment was raised by Phillips et al. (2003) and this is the first known use of this type of *a priori* environmentally based sampling site determination.

Plots were located at pre-defined locations so that 10 of the 16 sampling units were represented (Table 8). Care was also taken to ensure that the plots covered the full geographic coverage of the station. In each case the NW corner of each cell in the GIS data was located using a Trimble Pro XL GPS in the field, and the plot marked out to represent exactly one cell in the GIS. Inevitably GPS error (+/- approximately 10m) caused deviation from the pre-determined plot location, though this was actually minimal (average deviation from the exact plot corner of 3m).

In addition to the 25m x 25m plots, an additional 1-Ha plot was studied, taking advantage of an already established plot of Nigel Pitman (Pitman, 2000), though the data from this plot is not presented in this thesis due to incomparability. The geographic distribution of the plots is shown in Figure 36.

Plot	DEM Class	Upslope Class	Sampling Unit
1	1	1	1
2	3	3	11
3	2	4	14
4	1	2	5
5	1	4	13
6	2	3	10
7	2	2	6
8	4	2	8
9	4	3	12
10	4	1	4

Table 8 Sampling strategy units for each of the ten established plot.

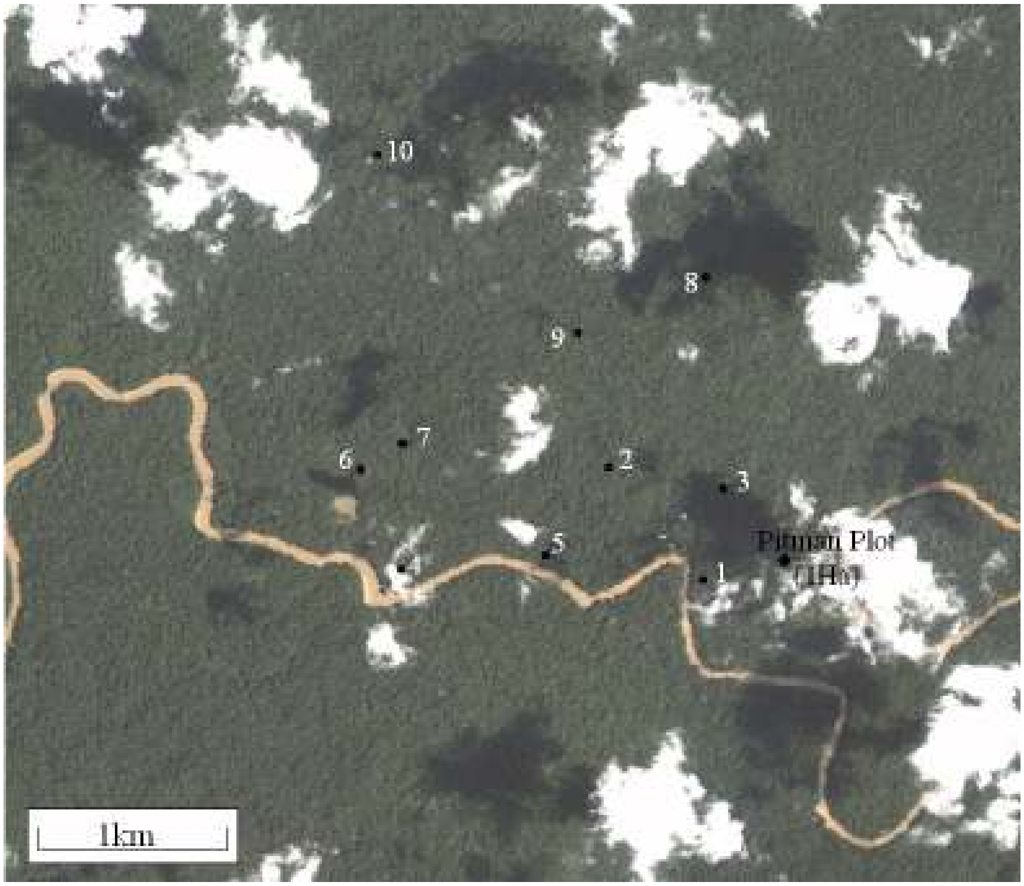


Figure 36 Geographic distribution of the 10 25m x 25m plots established in Tiputini Biodiversity Station.

3.5.2 Plot Descriptions

These short descriptions of the plots are intended only to provide some background should the reader wish to get an idea of plot conditions when individual plots are referenced in the following chapters. To ensure some standardization of the descriptions, they are presented in table form with the most striking features described. This information is based on purely subjective descriptions of conditions observed in the field whilst establishing the plot.

3.5.2.1 Tambito

The plots in Tambito were distributed across a large elevational gradient, encapsulating some very different environmental conditions (Table 9).

Plot	Elevation	Approx. Slope (degrees)	Topography	Understorey	Presence of Cloud	Epiphytism	Frequency of tree falls	Light Levels at ground
1	1651	27	Planar hillside	Light	Medium	Low	Low	Low
2	1684	34	Hillside with ridges	Dense	Medium	Medium	High	High
3	1449	29	Ridge	Dense	High	Medium	High	High
4	1966	24	Planar hillside	Medium	High	Medium	Medium	Medium
5	1299	31	Steep valley bottom	Light	Low	Low	Low	Low
6	1749	33	Hillside with ridges	Medium	Medium	Medium	High	Medium
7	2253	22	Hillside below peak	Dense	High	High	Medium	Low
8	1856	32	Hillside below ridge	Dense	High	High	High	High
9	1950	9	Flat ridge	Light	High	High	Low	Low
10	1600	27	Planar hillside	Medium	Medium	Medium	Medium	Medium

Table 9 Brief description of conditions in the Tambito plots.

3.5.2.2 Tiputini

The plots in Tiputini were visibly less variable than those for Tambito, but still some important characteristics are worth mentioning (Table 10).

Plot	Elevation	Approx Slope (degrees)	Topography	Understorey	Frequency of tree falls	Light Levels at ground	Proximity to River	Flooding Regularity
1	208	2	Flat	Light	Low	Medium	Directly alongside river (7m above normal flow level)	Occasional
2	219	20	Steep hillside	Dense	High	Low	No river closeby	Never
3	210	5	Undulating with small river	Medium	Low	Medium	Small river through plot, but distant from main channel	Occasional
4	201	1	Flat	Medium	Medium	Medium	50m from main river	Regular
5	200	2	Flat with channel in corner	Light	Low	High	Directly alongside main river (3m above normal flow level)	Regular
6	220	5	Planar hillside	Medium	Medium	Medium	200m from main river	Occasional
7	219	10	Undulating with small river	Light	Medium	Medium	500m from main river, but alongside large stream	Occasional
8	262	5	Planar hillside	Light	Low	Medium	Distant from any river	Never
9	238	5	Planar hillside	Light	Medium	Medium	Distant from any river	Never
10	224	8	Undulating	Medium	Medium	Medium	Distant from any river	Never

Table 10 Brief description of conditions in the TBS plots.

3.5.3 Measurement and sampling of individuals

Field data collection in the 25m x 25m plots was essentially the same for both Tiputini Biodiversity Station and Reserva Tambito. Diameter at breast height (DBH) was used to decide which individuals would enter the data collection. All individuals with DBH greater than 5cm were included, chosen to represent all established trees and to exclude saplings. For each individual the following measurements were taken:

- Diameter at breast height (DBH)
- Diameter at base
- X, Y and Z Position in plot
- Height of first branch (approximated)
- Total height of tree (approximated)
- Botanical sample collected

These structural factors were measured based on them being simple and quick to measure in the field. Tree girth (DBH), tree height and basal area (calculated from diameter at base height) are the most basic structural parameters for a tree, and are measured in all studies of structural variation in tropical forests (Federov, 1966;

Proctor et al., 1983; Vasquez and Givnish, 1998; Webb et al., 1999; Clark and Clark, 2000; Ferreira, 2000; Koponen et al., 2004). Height of the first branch is also measured as an indicator of the vertical shape of the canopy, with emergent trees having the first branches high in the canopy, whilst sub-canopy individuals often branch much lower in the trunk relative to the total height.

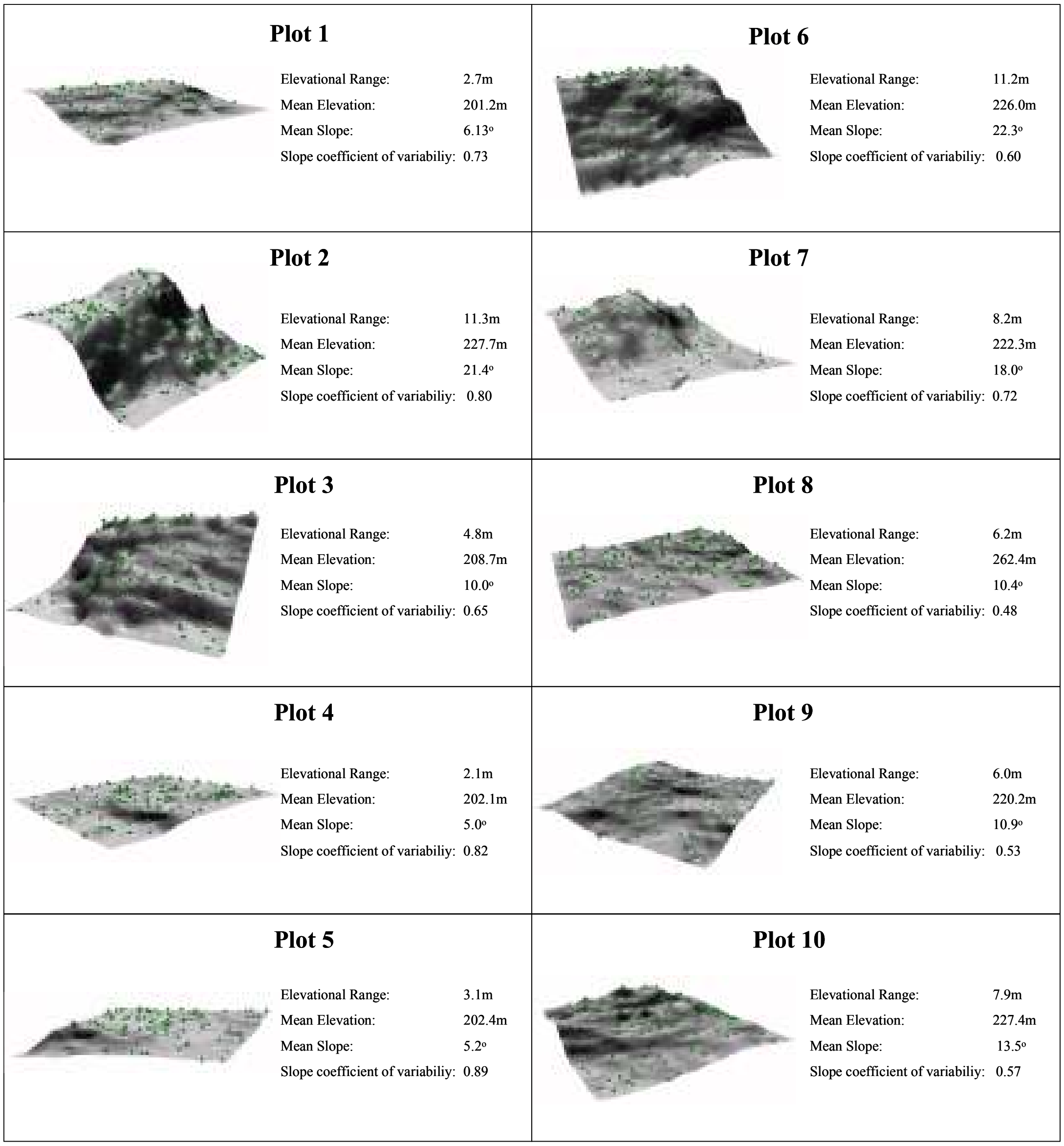
The only difference in data collection between sites was that TBS benefited from the use of a laser rangefinder to provide precise x, y and z coordinates for each tree within the plot (relative to the corner GPS position). The laser rangefinder was also used to measure the height of trees above 10m in TBS. In Tambito, each plot was separated into 25 quadrants of 5m x 5m and each individual was positioned to the quadrant. No data were taken on exact x, y and z positions of each tree, except for 3 plots where the laser rangefinder became available and the plots were revisited (plots 1, 2 and 3). Unfortunately, local political instability from 2002 – present made subsequent visits to Tambito impossible, and so accurate x, y z positions for other plots was not possible.

All tree heights were approximated by the author in all plots and in both sites, except that trees greater than 10m in height were measured using the laser rangefinder in TBS. The laser rangefinder was used as a guide to make the manual approximations, with regular checks on approximations using the rangefinder. Whilst the absolute heights may contain some error, it is expected that the relative heights within and between plots are representative.

Each individual was collected and preserved temporarily in alcohol according to the traditional methods of botanical sample preservation. The samples were then dried for 48 hours at 32°C, and stored as a permanent collection in the Natural History Museum of Popayan (Tambito samples) and the University San Francisco of Quito (TBS samples). Identification of the samples was made to species level whenever possible, though many identifications could be no more precise than genus level. Emphasis was made in distinguishing species, even where the species could not be named. The full taxonomy may not have been ascertained for all individuals, but there is accurate data on whether an individual is of the same species as any other individual.

3.5.4 Production of plot DEMs

The tree position data taken using the laser rangefinder in TBS and for the three plots in Tambito provided x, y and z coordinates of every individual in the plot. This data was used to produce high resolution digital elevation models for each plot. The elevation values in these plot DEMs represent the elevation of the ground surface, as measured by ground based topographic survey using a rangefinder with combined digital compass and inclinometer. Inverse distance weighted interpolation, using the nearest 10 points was used to create 50cm resolution DEMs. Slope was calculated as a derivative. The plot DEMs for the 25m x 25m plots in TBS are shown in Figure 37.



Plot 1

Elevational Range: 2.7m
Mean Elevation: 201.2m
Mean Slope: 6.13°
Slope coefficient of variabiliy: 0.73

Plot 6

Elevational Range: 11.2m
Mean Elevation: 226.0m
Mean Slope: 22.3°
Slope coefficient of variabiliy: 0.60

Plot 2

Elevational Range: 11.3m
Mean Elevation: 227.7m
Mean Slope: 21.4°
Slope coefficient of variabiliy: 0.80

Plot 7

Elevational Range: 8.2m
Mean Elevation: 222.3m
Mean Slope: 18.0°
Slope coefficient of variabiliy: 0.72

Plot 3

Elevational Range: 4.8m
Mean Elevation: 208.7m
Mean Slope: 10.0°
Slope coefficient of variabiliy: 0.65

Plot 8

Elevational Range: 6.2m
Mean Elevation: 262.4m
Mean Slope: 10.4°
Slope coefficient of variabiliy: 0.48

Plot 4

Elevational Range: 2.1m
Mean Elevation: 202.1m
Mean Slope: 5.0°
Slope coefficient of variabiliy: 0.82

Plot 9

Elevational Range: 6.0m
Mean Elevation: 220.2m
Mean Slope: 10.9°
Slope coefficient of variabiliy: 0.53

Plot 5

Elevational Range: 3.1m
Mean Elevation: 202.4m
Mean Slope: 5.2°
Slope coefficient of variabiliy: 0.89

Plot 10

Elevational Range: 7.9m
Mean Elevation: 227.4m
Mean Slope: 13.5°
Slope coefficient of variabiliy: 0.57

Figure 37 High resolution (50cm) plot DEMs for the 25m x 25m diversity and structure plots in TBS, with the green dots representing each tree individuals in the plot (and the original points used to generate the interpolated surfaces).

3.6 Statistical analysis of plot data

3.6.1 Analysis of compositional and structural similarity

The Mantel statistic can be used in its most basic form to examine the degree to which differences in species composition between sites is controlled by distance between the sites. Geneticists have used Mantel tests extensively to measure isolation by distance in populations (Epperson, 2004). In tropical ecology, the Mantel test is extended beyond comparison of composition with distance, to include environmental interactions (Phillips et al., 2003; Almeida et al., 2004), and attempt to understand how environmental factors may shape community composition. The Mantel test itself is a modified version of the Pearson correlation coefficient, differing in that the natural dependence in the distance matrix is taken into account (Potts et al., 2002). The p-value is also calculated differently to determine whether there is significant correlation, using a one-tailed test of a sample of permutations (10,000 in the case of this thesis). In addition to the simple Mantel test, the partial Mantel test examines three-way relationships, normally between geographic distance, environmental distance and species composition or genetic distance, identifying spurious relationships that may occur (i.e. distance only affecting species composition through its co-linearity with environmental distance). Further discussion of the statistical method is provided by Epperson (2004). Whilst some doubt has been expressed as to the validity of partial Mantel tests (Raufaste and Rousset, 2001), Castellano and Balletto (2002) used repeated simulations to show that the partial Mantel test is an accurate means of ascertaining causal relationships. In this study partial Mantel tests were used in addition to the standard Mantel test to search for spurious relationships between significant correlations where variables exhibit some degree of co-linearity.

The Mantel statistic was used to examine the environmental interaction of both composition and structure in the plots, using the software XLStat to calculate Mantel statistics and the associated p-value. For composition, a Jaccard coefficient was calculated based on the presence and absence of species for each plot pair. The Jaccard coefficient is calculated using Equation 3.

Equation 3

$$\text{Jaccard (J)} = \frac{\text{No. Species Common to both plots}}{\text{(No Species in Plot A + No Species in Plot B)}}$$

The Jaccard coefficient is the most widely used compositional similarity measure (Magurran, 2004), and previous studies have used it alongside the Mantel statistics to assess environmental controls on species composition (Tuomisto et al., 2003).

Geographic and environmental distance were also calculated for each plot pair using ten quantitative variables (horizontal distance, elevation, eastness, northness, mean curvature, slope, slope position, solar radiation, toposcale and topmodel). The absolute difference was calculated between the values for each pair of plots, for each variable.

The Jaccard coefficients and geographic and environmental distances were arranged in 10 x 10 similarity matrices, and the Mantel statistic applied. Due to the geographic and environmental distances actually representing dissimilarity, negative Mantel coefficients are expected in the case of positive correlations (as similarity is being compared with *dis*similarity). The p-value was also calculated in XLStat (using 10,000 random permutations), and presented alongside the Mantel coefficient. In the case of Tiputini Biodiversity Station, the Mantel statistic was calculated for characteristics of all both DEMs, hence two separate sets of results are given.

In order to apply the same analysis to the structural data, the Kolmogorov-Smirnov (K-S) test was used to assess the similarity in the cumulative distribuion function for each of the three major structural variables (DBH, tree height and the DBH:Height ratio). The K-S test produces a value representing the similarity of the distributions (based on their mean and standard deviation), that varies between 0 (equal distribution) and 1 (entirely different distributions). For each of the 45 plot pairs, the K-S statistic was applied for each of the three structural variables, and the resultant coefficients arranged in a 10 x 10 dissimilarity matrices. The Mantel statistic was then applied between these matrices and the respective distance matrix of geographic and environmental variables. Due to both these matrices representing dissimilarity, positive Mantel statistics are expected in the case of positive correlation. Likewise for the composition analysis, partial Mantel test were also used to search for potentially spurious relationships, and both DEMs were used for TBS, resulting in two sets of results for each geographic/environmental variable.

3.6.2 Diversity indices

In 1971, Hurlburt contended that "diversity per se does not exist" (quoted in (Peet, 1974), and suggested that ecology abandons the term "diversity". Over 30 years later, diversity is very much a central issue in ecology, and if anything less clarity is available on its meaning.

Magurran (2004, p.101) strongly recommends that a study does not use multiple diversity indices blindly, but carefully selects the appropriate index based on the research questions and the aspect of diversity that is being investigated. Whilst this advice is applicable to many research projects, in the case of the research undertaken in this thesis it would be dangerous to focus on one single aspect of diversity. Firstly, it is unknown what aspects of diversity topography may influence, and secondly, if significant relationships are found between topographic factors and diversity (based on a number of different factors), understanding the type of diversity that correlates best is a requirement in itself, and may help provide explanation as to the processes that are involved in generating that relationship. For this reason, this thesis does not apply Magurran's recommendation, but bases many of the methods for quantifying diversity on her book "Measuring Biological Diversity" (2004). Both diversity and richness measures are used. Richness measures include species richness, genera richness, family richness, and the richness of "plot endemic species" (number of species that were found only in that plot).

In addition to the richness measures, the following diversity indices were calculated for each plot and used in this study:

Shannon $H' = - S . p_i . \ln (p_i)$
Simpson $D = 1 - \sum (p_i)$
Margalef $DMg = (S - 1) / \ln (N)$
Menhinick $DMn = S / N^{0.5}$
Berger-Parker $BP = S_d / N$

Where, S - species richness
N - total number of individuals
N_i - number of individuals in the i-th species
p_i - proportional abundance of the i th species = ni / N

S_d – number of individuals of the most dominant species

The Shannon index is an entropy based measure of evenness, Simpson diversity index (note that 1-D is used here) is also a measure of evenness, whilst Margalef and Menhinick are species richness related indices adjusted for the total number of individuals in the sample (N). Finally, Berger-Parker is a simple and intuitive measure of dominance.

On top of these indices, Renyi's scaleable diversity method is used to produce diversity plots which provide additional information as to the comparability of diversity between plots. Renyi's scaleable diversity index is calculated using the DIVORD 1.5 program (Tothmeresz, 1993) and using the formula:

$$H(\alpha) = \left(\log \sum_{i=1}^{s} p_i^{\alpha} \right) / (1-\alpha)$$

Equation 4

Where α is a scale parameter, which varies from 0 to 3. This index is displayed in a plot with different scale parameters expressed along the x axis, and the diversity in the y axis. This equation is particularly innovative in that the diversity value when the scale parameter is 0 represents the log of species richness, with a scale parameter of 1 it represents the Shannon Index and with 2 it represents the Simpson Index. As α tends to infinity, it represents the inverse Berger-Parker. Typically α varies between 0 and 3. It permits easy interpretation of the diversity between different plots through examination of the relative shapes of the curves. More importantly, in the event of curves crossing it means that one plot is not more diverse than the other, but that it depends entirely on the type of diversity being examined.

Following Magurran's recommendation (2004), special emphasis in this thesis is given to simple species richness and Simpson's Index, for their robustness and simplicity in interpretation. Whilst it would have been advantageous to also include in the analysis a taxonomic diversity index (Desrochers and Anand, 2004) such as the Clarke and Warwick taxonomic distinctiveness index (Clarke and Warwick, 1998), it was deemed impractical due to the level of incompleteness and uncertainty in the species identification.

3.6.3 Structural Variables

Eight structural parameters are analysed in this thesis. These are based on direct measurement of some structural parameters, alongside some derivatives of these variables. Direct measurement was made for stem density (expressed in terms of stemsHa^{-1}), diameter at breast height (DBH) (expressed in cm), diameter at base height (DbaseH) (also expressed in cm), tree height (expressed in m), height to first branch (expressed in m).

Based on these variables, three other variables were calculated; DBH/Height, DBH/DbaseH, and basal area (m^{2}Ha^{-1}). Basal area is calculated based on both the DbaseH and the stem density, and reflects the amount of ground area occupied by tree trunk. The other two variables (DBH/Height, cm m^{-1}, and DBH/DbaseH, cm cm^{-1}) are calculated in order to grasp the degree of investment of resources in different aspects of tree structure. Bruenig and Huang (1990) first used the diameter/height variable to examine resistance to wind, and since Webb et al. (1999) have used DBH/Height to examine structural relationships with topography in American Samoa, with the variable providing clear patterns. Individuals with relatively wide trunks compared to their total height (i.e. a high DBH/Height) seemingly have invested greater resources in augmentation of trunk than in height, possibly indicating amongst other things a response to conditions for greater trunk strength, or in the case of the inverse a search for light. These investments are strategically different: greater investment in height than girth leads to short term gain (of light) but long term weakness (a pioneer strategy), greater investment in girth leads to short term loss of light but greater strength in the long term. The balance between these strategies may vary with the exposure of the site. The DBH/DbaseH variable is designed to measure the degree to which the tree base branches out at the base. Trees with buttress trunks will have significantly lower DBH/DbaseH levels than trees without, and such individuals are likely to have greater stability against tree fall.

Both these indices are likely to reflect both composition (i.e. some species will tend to have wider trunks relative to height than others) as well as morphological responses to site-specific conditions.

3.6.4 Correlation of environmental and topographic variables with diversity

For each site (and each DEM in the case of TBS), the environmental or topographic conditions are correlated with the diversity and structural measures. All diversity measures were used in this analysis (family richness, genera richness, species richness, endemic species richness, Simpson's, Shannon's, Menhinick, Margalef, and Berger-Parker), and in the case of Chapter 5 all structural parameters are also included

(Stem density, DBH, DbaseH, Height, Height of first branch, basal area, DBH/Height, DbaseH/DBH). The environmental and topographic variables are separated into two types of data; quantitative and categorical.

Quantitative variables (elevation, northness, eastness, curvature, slope, slope position, solar radiation, topmodel and toposcale) are subjected Pearson product-moment correlation analyses. In some cases where the data points warrant further study, non-linear regressions are sought, the details of which are discussed specifically in the relevant sections. For each correlation performed, a p-value is calculated in XLStat (using 10,000 random permutations). When significant correlations are found, further tests are performed, the details of which are discussed in the same section.

The categorical variables (landscape classification - feature, network feature and topoclass) could not be analysed in the same way. They were compared to diversity and structural measures using Spearman Rank tests, and the respective p-value calculated. In some cases the fuzzy feature membership was also analysed, comparing the fuzzy membership to a specific class with the diversity or structure using standard Pearson correlations.

In addition to Pearson correlations and linear regressions, multi-variate analyses are also performed to search for combinations of variables that may explain variability in diversity, composition and structure. For these purposes, multiple stepwise linear regression is applied using XLStat. Multiple stepwise linear regression has been used in a number of similar studies to good effect (Clinebell et al., 1995; Heikkinen and Neuvonen, 1997), though caution is taken in interpreting these results as combinations of linear regressions may describe a large degree of variability in data, but reflect little in terms of the causal relations (Fowler et al., 1998). Ideally split sample validation of regression models should be performed, but just the ten plots of data prevent this.

3.7 Examination of DEM quality with respect to ground measured slope and aspect in TBS

Understanding of the quality of the original DEMs and understanding the important role of scale in capturing the topographic variability found on the ground is crucial to permit insightful interpretation of the results in subsequent chapters. This section examines the degree to which the coarse-scale DEMs of the region in TBS (TOPO and SRTM) represent the topographic conditions found on the ground at the sub-plot scales at which the trees experience them. Whilst exhaustive GPS surveys would be one way of gathering this information, it is unfeasible due to the poor GPS satellite coverage under canopy and the subsequent low accuracy of the GPS derived altitude values.

Understanding the representation of the terrain at different scales is important, and a comparison of the slope and aspect at these two scales will indicate the degree to which scale issues are important in this analysis.

Figure 38 compares values in slope and aspect for the regional DEMs (TOPO and SRTM) against the plot DEMs for the same areas, firstly for plot mean slope and secondly for plot mean aspect (measured using northness and eastness, due to the circular nature of aspect).

In all cases there is considerable difference between plot-based slope and aspect and the DEM based slope and aspect. For slope the SRTM DEM correlates best but not significantly (Pearson = 0.53, n=10), with the TOPO DEM reflecting little of the slope measured on the ground (Pearson = 0.11, n=10). In both cases, the DEMs are grossly underestimating the slope levels measured at the sub-pixel scale. Some limitations in the validity of this analysis is brought about by the difference in slope measure that is being used, as the slope in the DEMs is calculated using the elevation of surrounding cells in a 3 x 3 window, whilst the plot DEMs only take into account the within plot conditions. Furthermore, geopositional inaccuracy for some plots means that part of the plot actually falls in a different cell, with a different slope value.

Aspect derived northness (Figure 40) and eastness (Figure 39) compare even less. Neither the SRTM DEM (eastness Pearson = 0.28, n=10) nor the TOPO DEM (eastness Pearson = 0.14, n=10, northness Pearson = 0.30, n=10) show likeness with ground-measured aspect.

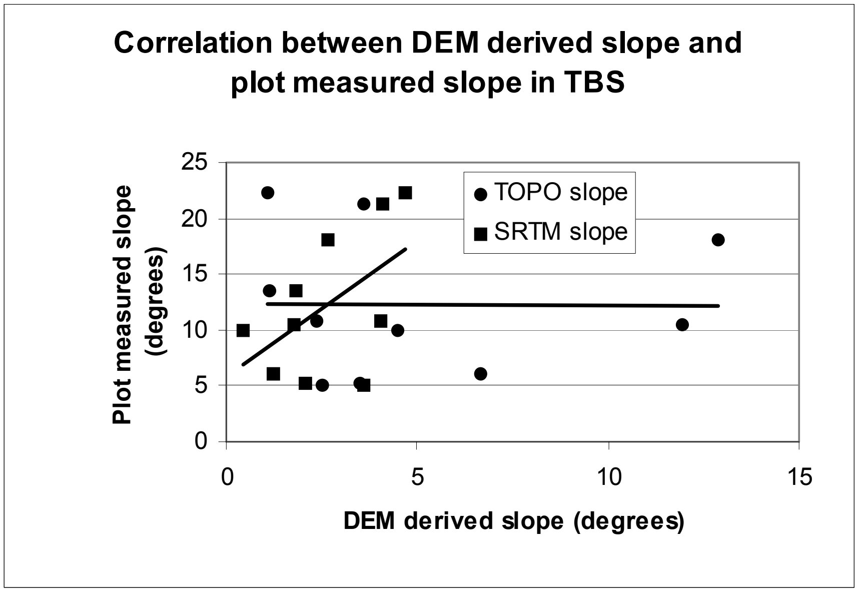


Figure 38 Comparison of DEM derived slopes and the plot measured slopes for the two DEMs in TBS. Slope from the plots was derived as a mean for all pixels.

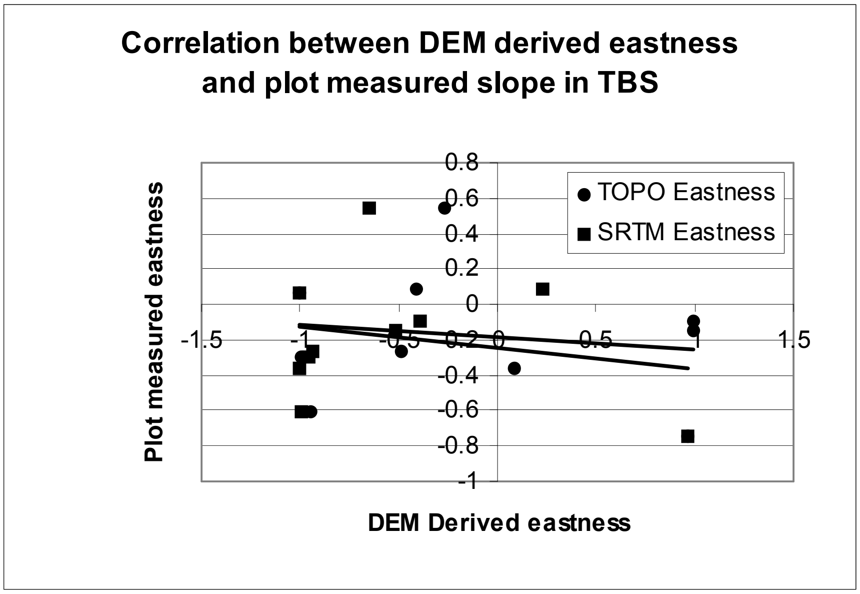


Figure 39 Comparison of DEM derived eastness and the plot measured slopes for the two DEMs in TBS. Eastness of the plots was derived as a mean for all pixels.

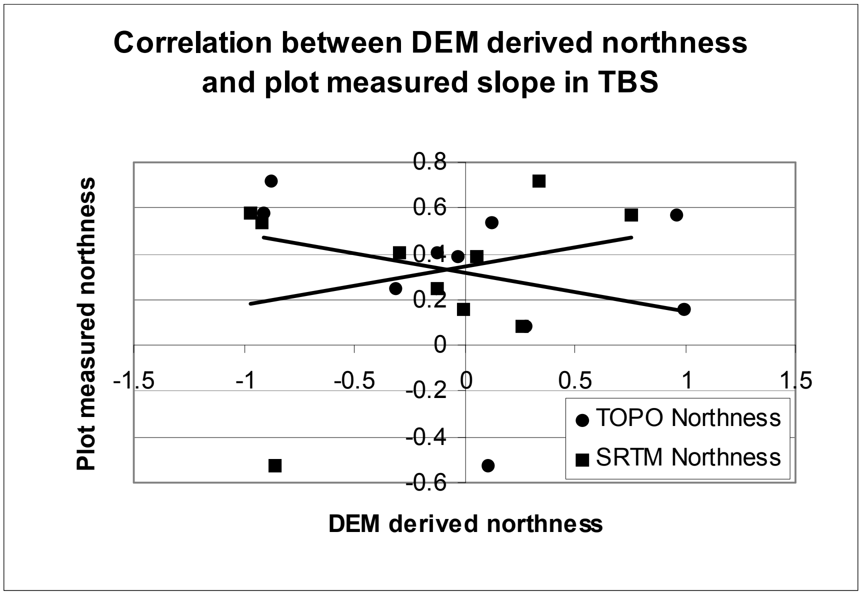


Figure 40 Comparison of DEM derived northness and the plot measured slopes for the two DEMs in TBS. Northness of the plots was derived as a mean for all pixels.

The results of these two analyses indicate that what is measured at one scale (TOPO or SRTM DEMs, for example) does not represent the values of the variable at a finer scale (as measured using the plot DEMs). However, without knowing the relevant scale for describing the variability in diversity, composition and structure of tropical tree species it is not necessarily true that the more information rich scale (plot DEMs) is necessarily better. This is an important point, and one which is considered later in the thesis in the results sections.

Given these disparities between ground-measured topography and its representation in the DEMs, some further analysis is warranted. It is reasonable to assume that each DEM performs better in specific landscapes. Erosion and drainage are likely the most important geomorphic processes in shaping the landscape, and so it is expected that greater small-scale topographic complexity would occur in regions with concave slopes in the lower reaches of the hillside where erosion and streams are more prevalent compared with planar slope segments and convex slope crests. The strength of these processes in lower reaches of the hillside may create complexity which is not captured in DEMs of this resolution, and thus cause the disparities found above. Both DEMs used in this study are derived from tree-top topography, and it is likely that the canopy will smoothen complex topography found on the ground, especially small scale complexity derived from erosion and the generation of gullies.

In order to test this hypothesis, mean profile curvature and slope position are correlated with the coefficient of variability in slope within the plots (a surrogate for topographic complexity). No significant correlation is found with mean curvature nor topmodel, but slope position does show some very significant correlations (Figure 41). The TOPO DEM correlates closest $\text{CoeffVarSlope}_{\text{PLOT}} = -0.003\ \text{SlopePos}_{\text{TOPO}} + 0.86$, $R^2 = 0.84$, $R^2 = 0.79$, n=10), followed by the SRTM DEM ($\text{CoeffVarSlope}_{\text{PLOT}} = -0.004\ \text{SlopePos}_{\text{SRTM}} + 0.85$, $R^2 = 0.47$, n=10). In all cases the trend is for greater ground measured complexity in topography in areas close to the valley bottom. It would be logical therefore to conclude that the DEMs we are using are likely to provide better representation of the ground surface in areas higher in the hillside where erosion and water flow concentration is lower. This is, however, not supported by the data (Table 11), with in most cases higher percentage errors in higher slopes.

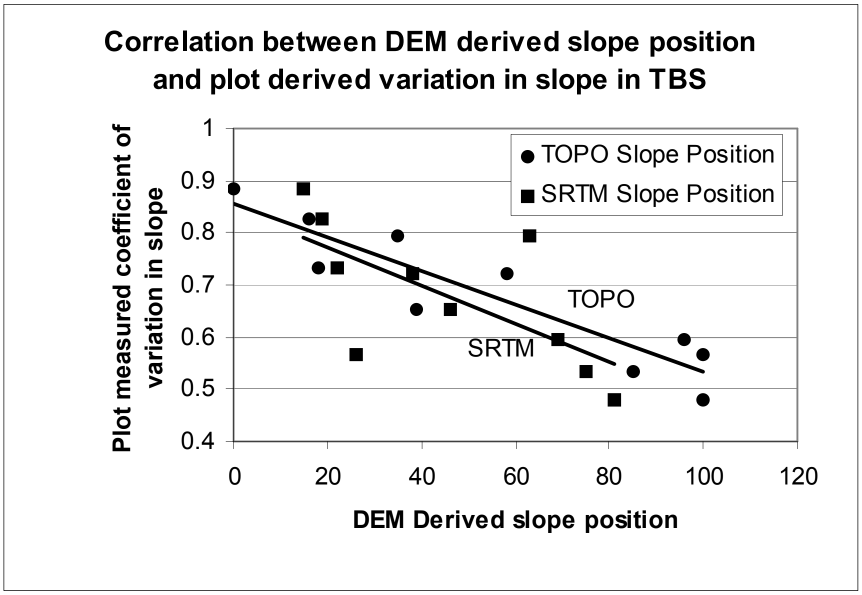
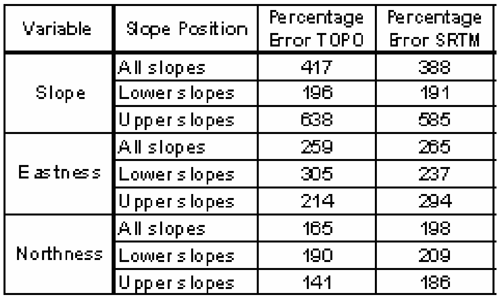


Figure 41 Scatterplot of ground-based measurement of topographic complexity (using the coefficient of variability in slope as a surrogate) against DEM derived slope position.

These findings also indicate that broader scale features such as those used to define slope position (calculated through flow accumulation routines) are sound in the DEMs (best represented in TOPO), but more local topographic features such as curvature, slope and aspect are less representative (worst representation in TOPO, where the interpolation methods produce the greatest amount of smoothing).



Variable	Slope Position	Percentage Error TOPO	Percentage Error SRTM
Slope	All slopes	417	388
	Lower slopes	196	191
	Upper slopes	638	585
Eastness	All slopes	259	265
	Lower slopes	305	237
	Upper slopes	214	294
Northness	All slopes	165	198
	Lower slopes	190	209
	Upper slopes	141	186

Table 11 Error in DEM representation of plot topography for all slopes, as well as for upper and lower slopes defined using the slope position variable.

Without further field-based research it is impossible to further quantify the errors and scale issues in the DEMs, nor understand under what conditions they are more accurate. The conclusion of this analysis is that the DEMs are not representing very well local conditions (sub-25m pixel) like slope and aspect (though obvious methodological aspects in the comparison lower the statistical validity of this observation), with different DEMs performing better for different variables. This may be important in later in-depth analyses with respect to the diversity and structure in the forests. It is also important to note the relationship between slope position and topographic complexity.

3.8 Heterogeneity Modelling

There are few examples of models that quantify spatial heterogeneity of environmental variables that are explicitly designed for application to biological systems. Spatial environmental heterogeneity within the context of this study refers to the diversity of environments within a certain local spatial extent. Translating this concept into a raster grid like all the terrain variables is best done by considering it the variability of pixel values in cells surrounding a single central cell. This type of analysis is often called kernel estimation (Wand and Jones, 1995) moving-window analysis (Fotheringham et al., 1996), convolution filtering (Lillesand and Kiefer, 1999), or focal calculations (Tomlin, 1993). In order to quantify spatial heterogeneity, three main factors must be considered:

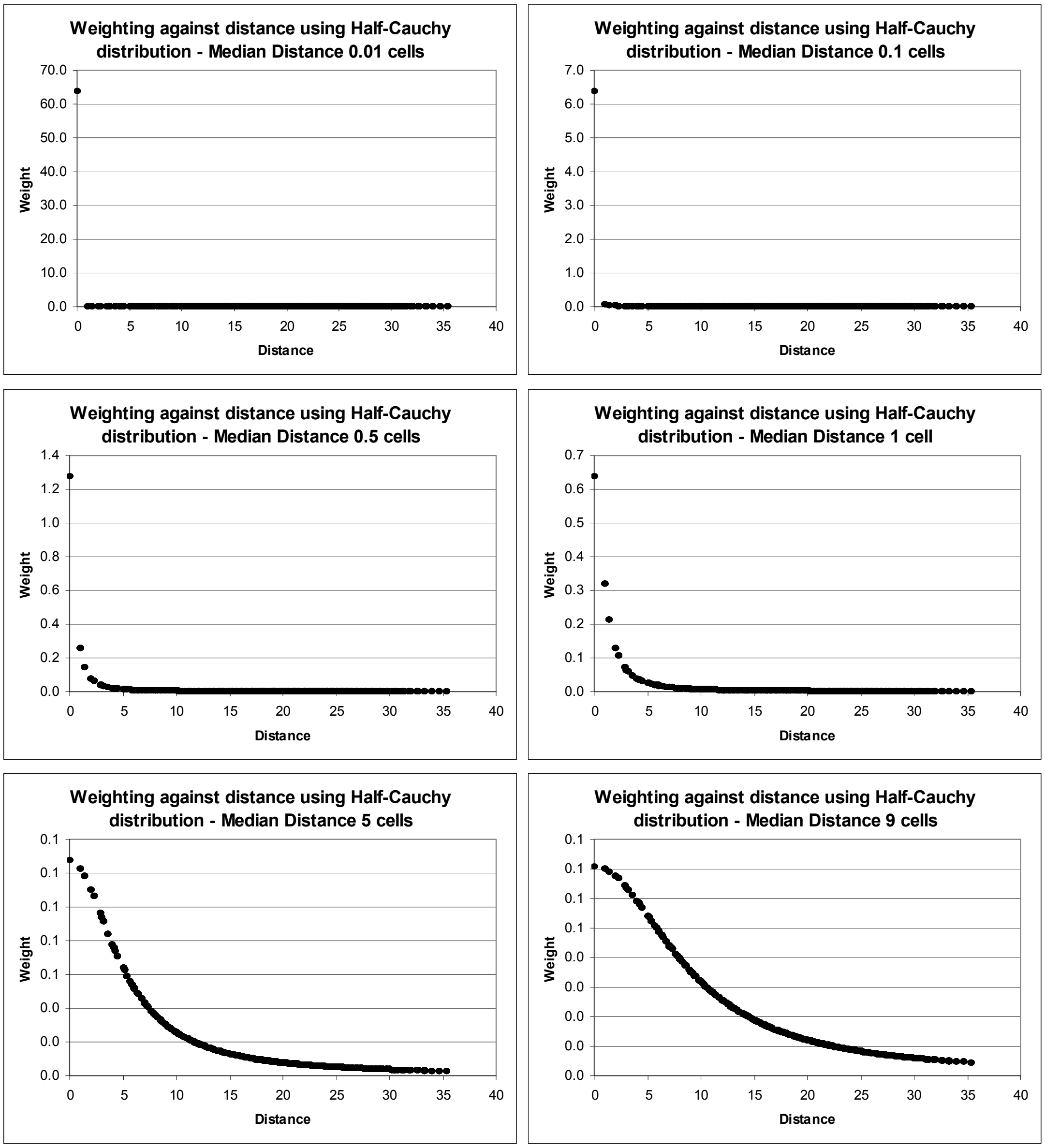
1. The spatial function for weighting (geographic weighting) with respect to distance from the central cell (the shape of the kernel)

2. The size of the search window surrounding each cell (the radius is often called the bandwidth)
3. The equation for actually quantifying the heterogeneity given the array of values for surrounding cells

Given the lack of previous studies that adopt this kind of spatial analysis for tropical ecology, there was no basis on which to select an equation to accurately represent the average spatial function of neighbourhood interactions (such as seed dispersal, competition etc.). Literature in the realm of genetics does provide some indication of a likely equation based on analyses of the probability of pollen transfer. The spatial function of pollen-transfer is likely to be similar to that of seed dispersal due to their similarity in physical processes, both having wind and animal (and insect to a lesser extent for seeds) dispersal mechanisms. Shaw (1995), Xu and Ridout (2001), and Paradis et al. (2002) used the radial half-Cauchy distribution for modeling pollen transfer, preferring this distribution to others for its characteristic long tail. The half-Cauchy distribution also provides a very flexible equation that permits simple adjustment of its shape through manipulation of the median distance variable. Provided the lack of data on actual probabilities and distances of seed dispersal for the average tropical tree, and a lack of data on the spatial nature of competition or other relevant biotic processes, the median distance variable provides an easy way of incorporating multi-scale analyses to cover all potential scales at which these processes may occur. The half-Cauchy curve is produced using the following formula:

Equation 5 $W (r) = (2 / \pi b) 1 / [1 + (r / b)2]$

Where W(r) is the probability of interaction with a neighbouring cell, b is the median distance of interaction and r is the distance from the central cell. When the median distance is set to 0 the weighting for surrounding cells is also 0, increasing the median distance variable produces higher weighting to surrounding cells. Figure 42 shows the shape of the distance-weighting curve for different median distances, ranging from 0.01 to 9 cells. For the analysis, a total of 16 kernels were used with median distances of 0.01, 0.05, 0.1, 0.2, 0.3, 0.5, 0.8, 1, 2, 3, 4, 5, 6, 7, 8, and 9. This multi-scale approach is advantageous due to the lack of knowledge on the spatial function of neighbourhood interactions.


Weighting against distance using Half-Cauchy distribution - Median Distance 0.01 cells

Weighting against distance using Half-Cauchy distribution - Median Distance 0.1 cells

Weighting against distance using Half-Cauchy distribution - Median Distance 0.5 cells

Weighting against distance using Half-Cauchy distribution - Median Distance 1 cell

Weighting against distance using Half-Cauchy distribution - Median Distance 5 cells

Weighting against distance using Half-Cauchy distribution - Median Distance 9 cells

Figure 42 Distance weighting from the Half-Cauchy curve for different median distances from 0.01 cells (top-left) to 9 cells (bottom-right).

In reality the curves shown in Figure 42 are 3-dimensional, and so for some clarity Figure 43 shows an example half-Cauchy kernel with median distance set to 1 cell.

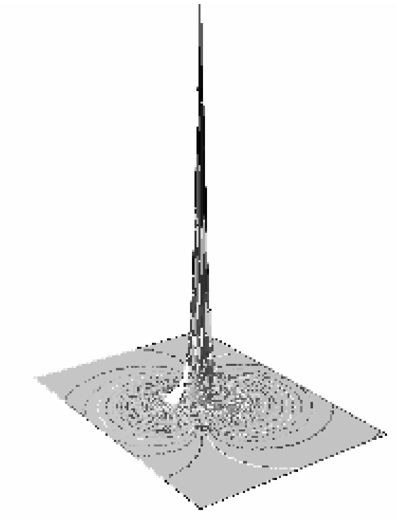


Figure 43 3-dimensional representation of the half-Cauchy spatial function, with the height of the surface representing the weighting.

The spatial function used here is uniform in all directions, though this could have been adjusted to provide higher weighting in specific directions, such as in the dominant wind direction with respect to wind-based seed dispersal. In Tambito this would not be valid, as topographic funneling likely create different wind directions around the catchment (and there is insufficient data to fully analyse and understand wind patterns in the twin-catchments). In TBS a more constant wind direction is likely, and indeed has been shown to be south-easterly. The kernel could be adjusted to provide higher weighting in cells upwind, though this is not performed here as it would provide an extra variable and an extra level of complexity on results presentation and interpretation (for TBS the analysis is already complicated by two DEMs, 12 variables and 16 different scales). This is clearly a limitation, and further studies should incorporate wind direction into this model, though other spatial neighbourhood processes such as competition and biotic interactions are not necessarily affected by wind direction.

The size of the search window should be selected based on the distance function used, so that the window covers all cells with a significant weighting that may affect the final result. In reality, the size of the search window must also depend on processing power and the size of the grid that is being analysed, due to the intensive processing required to make a spatial heterogeneity calculation. For this analysis a search window of 50 x 50 cells was used. Even with the highest median distances the potential effect of cells outside this 50 x 50 cell kernel was calculated to be insignificant (<5% change in result when search window increased to 200 cells for test runs in Tambito and TBS). The selection of the search window was therefore set at of 50 x 50 cells. This avoided computational limitations, and also ensures that edge effects do not encroach on any of the plots (in the case of Tambito, Plot 7 is just 70 cells from the border of the DEM).

Definition of heterogeneity is somewhat similar to that of diversity, with no single number capable of describing all aspects of the phenomenon. So as to compare like with like (i.e. diversity vs. heterogeneity) it was important to measure each variable in a similar way. For this reason, the heterogeneity was calculated using the Simpson diversity index. This is similar to the technique that was used effectively by Burnett et al. (1998) to compare geomorphological heterogeneity (aspect, slope, topmodel amongst other variables) with plant species diversity, though in this study a grid based system was used which lacks the fine-scale capacity of the method presented here.

Simpson's index is calculated based on the frequencies of categorical data. Of the 12 terrain characteristics studied here, nine are continuous and just three are categorical.

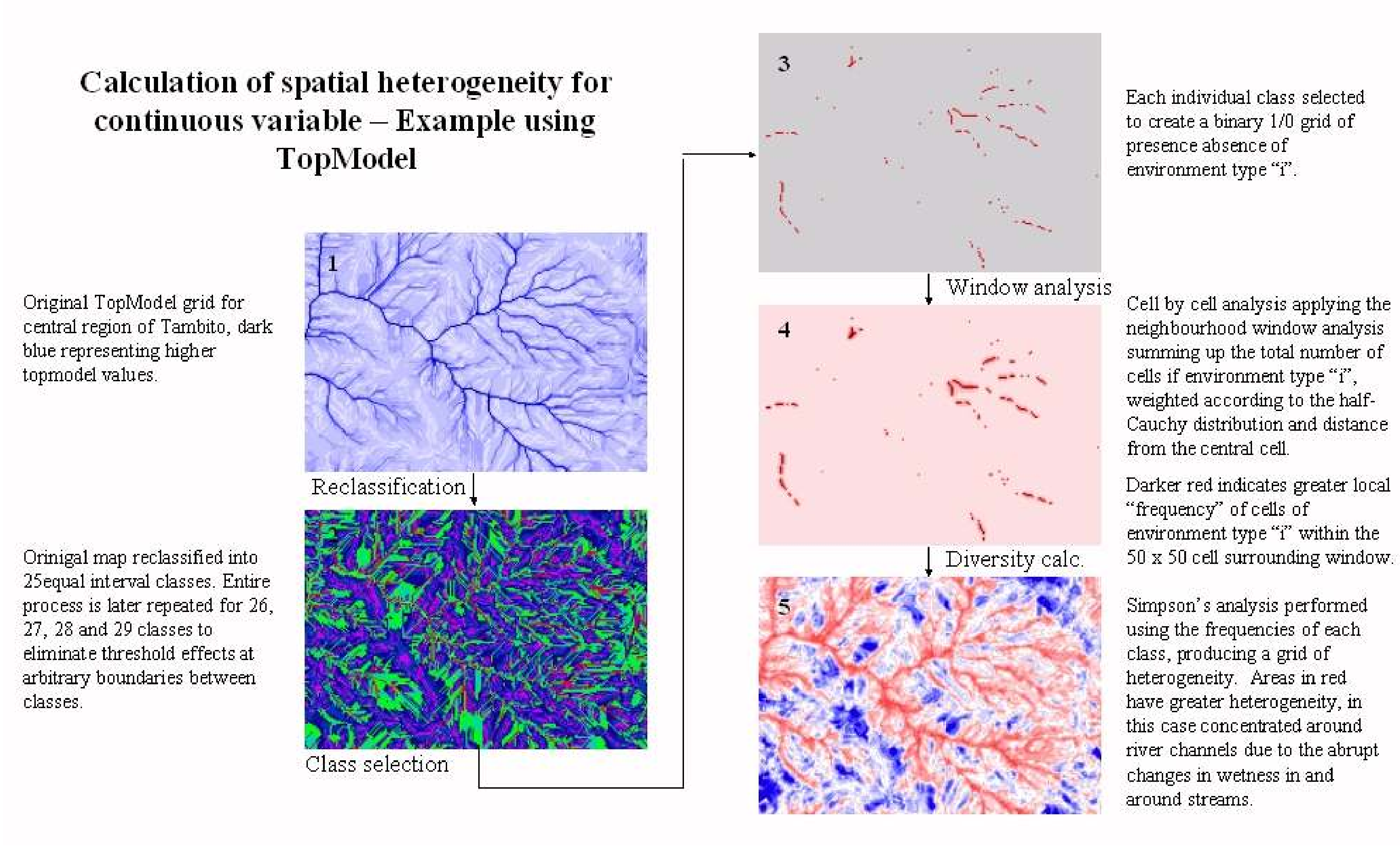
The continuous variables were therefore re-classified into equal interval classes, each class representing environment type ‘i’, thus making it possible to calculate Simpson’s index, where the heterogeneity for the centre cell was calculated using:

Equation 6 $\text{Heterogeneity} = 1 - \Sigma\,(p_i^2)$

The frequencies (p_i) are calculated from the environmental values of all cells in the surrounding 50 x 50 cell region. Individual contributions of each cell to the calculation of these frequencies were weighted by the spatial function. Given this approach, frequency p_i represents the total relative probability of receiving inflowing seeds from an environment of type ‘i’. In practical terms, the frequency (p) is the sum of all distance-weighted cells of environment type ‘i’.

The creation of arbitrary classes creates the problem of threshold effects, where inaccurately higher heterogeneity is found on the interface between two arbitrarily defined classes. To eliminate this threshold effect, the re-classification was repeated five times for each calculation of heterogeneity, splitting the topographic characteristics into 25, 26, 27, 28, and 29 different classes of equal intervals. The final heterogeneity was calculated from the mean of the results of these five iterations. Changing the number of classes changes the geographic location of splits between the classes. These classes were selected based on visual experimentation, and computational limitations. For lower numbers of classes (i.e. 20 – 24), arbitrary boundaries were still observed, whilst greater number of classes vastly increased the time required to run the model.

In reality the calculation described above is fairly simple, and best understood by means of an example analysis shown in Figure 44. The final result is a grid of spatial heterogeneity of each terrain derivative for each of the 16 scales. In general terms, the analyses with low median distances produce complex small-scale distributions of environmental heterogeneity, while higher median distances produce smoother and broader scale measures of heterogeneity.



Calculation of spatial heterogeneity for continuous variable – Example using TopModel

Original TopModel grid for central region of Tambito, dark blue representing higher topmodel values.

Orinigal map reclassified into 25equal interval classes. Entire process is later repeated for 26, 27, 28 and 29 classes to eliminate threshold effects at arbitrary boundaries between classes.

Each individual class selected to create a binary 1/0 grid of presence absence of environment type "i".

Cell by cell analysis applying the neighbourhood window analysis summing up the total number of cells if environment type "i", weighted according to the half-Cauchy distribution and distance from the central cell.

Darker red indicates greater local "frequency" of cells of environment type "i" within the 50 x 50 cell surrounding window.

Simpson's analysis performed using the frequencies of each class, producing a grid of heterogeneity. Areas in red have greater heterogeneity, in this case concentrated around river channels due to the abrupt changes in wetness in and around streams.

Figure 44 Example analysis of spatial heterogeneity for a model environment.

Many other methods could have been used to quantify heterogeneity, including a simple calculation of the surrounding coefficient of variation, absolute surrounding range, non distance-weighted approaches, geostatistical methods (variograms, for example), as well as a similar approach using other diversity indices or richness measures (Burnett et al., 1998; Nelson, 2004). For this study a method was selected which most accurately reflects environmental heterogeneity in a species diversity relevant context, specifically through measuring heterogeneity with an evenness diversity index (Simpson's) for direct comparison with species diversity. Given the lack of previous research determining spatial heterogeneity in terrain characteristics for biological diversity studies, it is difficult to judge if the method adopted here is indeed the best method. It is favourable in terms of measuring heterogeneity in terms of evenness, and permitting the comparison of like with like, though there is also some degree of information loss through the creation of categorical data from continuous surfaces. For the purposes of simplicity in analysis and interpretation, this study only uses the Simpson's index to quantify heterogeneity. Further studies should develop different models and compare results.

These methods for calculating heterogeneity were incorporated into an Arc Macro Language (AML) for use in Arc/Info. Given the high level of processing that these types of spatial analyses require, it was important to automate this analysis. Appendix 2 shows the model used for quantitative variables, and Appendix 3 shows a slightly modified version used for the categorical variables (feature, network feature and topoclass). The method itself is identical, with the only difference of not needing the multiple re-classification into "i" environments.

The heterogeneity at each plot was then extracted from the final grids for each of the 16 scales, and for each topographic variable. This was then correlated with the Simpson's index based on the tree diversity measured within the plot, calculating both the Pearson correlation coefficient and the p-value.

Chapter 4

4 Spatial variation in diversity and composition : Environmental interactions

4.1 Introduction

This chapter makes a basic analysis of spatial variations in diversity within the two study sites, using the plot data along with the basic terrain derivatives described in Chapter 3. The aim of this chapter is to examine the patterns of spatial variation in composition and diversity, and begin to explore these patterns in the context of environmental variation. The analysis is split into two separate sections, firstly examining compositional variation, and secondly examining the variation in richness and diversity.

The central issue being tested in the compositional section is that of habitat association for tropical trees, though attention is brought to the distinction between species level- habitat associations and the compositional level (non-species specific) habitat association being studied here. Numerous studies have recently searched for habitat associations in tropical tree species in a number of different environments, principally in tropical lowland forests (Vormisto et al., 2000; Webb and Peart, 2000; Harms et al., 2001; Vormisto, 2002; Phillips et al., 2003; Tuomisto et al., 2003; Valencia et al., 2004) but also in the elevational gradient of tropical montane forests (Sugden, 1982; Vasquez and Givnish, 1998). In lowlands there is evidence that some association occurs (approximately 20 – 70% depending on the study), but it is also acknowledged that many species are almost randomly distributed across a landscape, with non-equilibrium processes (such as tree fall) controlling a large proportion of the spatial distribution of composition (Harms et al., 2001). In montane regions, studies have found elevation as an important variable associated with composition (Sugden, 1982; Vasquez and Givnish, 1998), but these have generally been broad-scale studies, which have not used micro- and meso- scale terrain variation to search for habitat association. This sections endeavours to statistically test if there is any habitat association in composition present in the plot data based on habitat as measured by the terrain derivatives.

The diversity section moves up one level (from information at the species level to non-species specific diversity), endeavoring to look for spatial patterns in diversity, and test the data to discover whether or not specific topographic conditions favour the generation of high diversity. As discussed in Chapter 2, some of the key drivers of diversity include productivity (often measured using energy or water as a surrogate), soil nutrients (however the relationship may be), and gap dynamics. Different measures of diversity are examined (evenness/dominance and richness) for each plot and compared with the range of terrain derivatives being used in this study to test for association. Where significant relationships are found, further tests are made to understand the physical processes that may be generating the relationship.

Each study site is treated separately at first, but the chapter concludes by integrating the results from each site and discussing the over-arching ecological significance of the findings at both sites. For TBS, both DEMs are used in the study, and for ease of interpretation the results of each analysis for each DEM are presented together.

4.2 Reserva Tambito

4.2.1 Composition

4.2.1.1 General Site Species Composition

The ten 25m x 25m plots established in Tambito contained 1108 individuals, of which 271 different species were identified, distributed in 52 families and 111 genera. Appendix 4 contains a full list of species found in Tambito. Taxonomic identification was made to family level for 99.7% of species, to genus level for 87.6% of species, and to species level for 52.0% of species. It is likely that some species as yet unidentified to genus level will be new genera to the area, and thus the number of different genera is likely an underestimate. Table 12 provides a summary of family composition in Tambito, with Figure 45 and Figure 46 showing the distribution of species and individuals within families.

Family	No. Genera	No. Species	No. Individuals	No. Plots
Actinidaceae	2	2	13	7
Anarcadiaceae	1	1	1	1
Annonaceae	2	3	18	5
Aquifoliaceae	1	4	18	6
Araliaceae	2	3	13	3
Arecaceae	8	15	144	9
Asteraceae	1	1	2	1
Bignoniaceae	1	1	1	1
Bombacaceae	2	3	5	3
Burseraceae	1	6	21	5
Caesalpiniaceae	2	4	4	4
Caprifoliaceae	1	1	4	2
Caricaceae	1	1	1	1
Celastraceae	2	2	8	4
Chletraceae	1	1	1	1
Chloranthaceae	2	2	16	4
Chrysobalanaceae	1	2	2	2
Clusiaceae	3	16	47	10
Cyatheaceae	2	3	38	8
Elaeocarpaceae	1	2	6	4
Euphorbiaceae	7	10	63	9
Fabaceae	1	2	4	3
Flacourtiaceae	2	3	32	5
Hippocrateaceae	1	1	22	5
Hypocastanaceae	1	1	16	4
Icacinaceae	2	2	6	3
Lauraceae	5	28	65	9
Lecythidaceae	2	5	24	6
Marcgraviaceae	1	1	2	1
Melastomataceae	10	33	118	9
Meliaceae	3	8	28	9
Mimosaceae	1	4	9	4
Monimiaceae	2	5	6	5
Moraceae	6	15	34	7
Myristicaceae	2	3	22	6
Myrsinaceae	4	7	21	9
Myrtaceae	3	11	22	9
Ochnaceae	1	1	1	1
Piperaceae	1	2	3	3
Proteaceae	1	1	1	1
Rosaceae	1	3	12	4
Rubiaceae	8	31	201	10
Sabiaceae	1	1	1	1
Sapindaceae	1	2	3	3
Sapotaceae	1	4	12	4
Simaroubaceae	1	1	1	1
Solanaceae	2	3	3	3
Staphyleaceae	1	1	1	1
Styracaceae	1	1	2	1
Theaceae	1	1	1	1
Theophrastaceae	1	1	2	1
Verbenaceae	1	1	2	2
Other	5	5	5	5
TOTAL	**118**	**271**	**1108**	**4.3 (AVG)**

Table 12 Summary of species composition per family in Tambito, including the number of plots where the family was present.

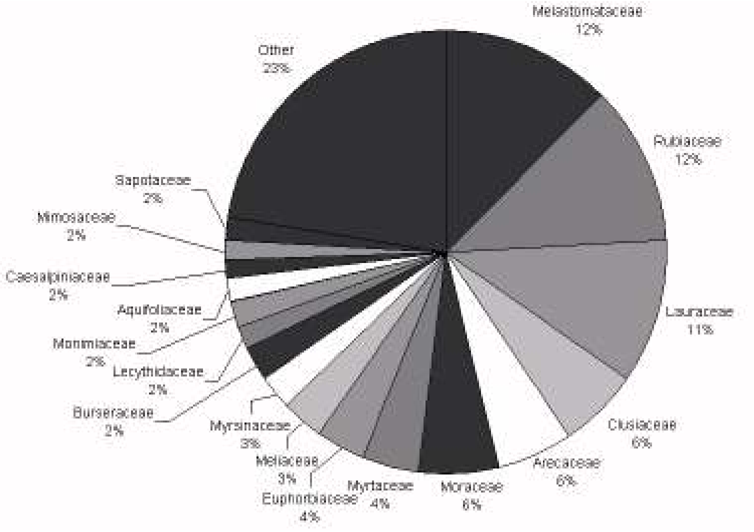


Figure 45 Distribution of species in families in Tambito

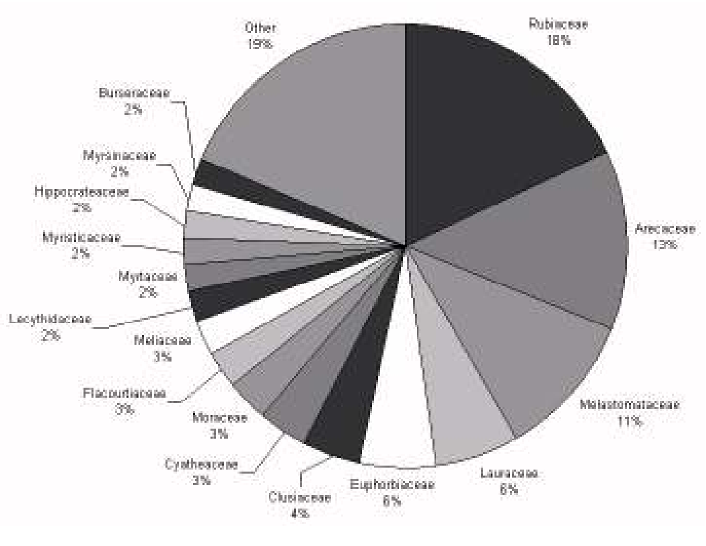


Figure 46 Distribution of individuals in families in Tambito

The most abundant families in terms of individuals are Rubiaceae (201 individuals), Arecaceae (144) and Melastomataceae (118), whilst Melastomataceae is the most species rich family (33), followed closely by Rubiaceae (31) and Lauraceae (28). Over 50% of all species are in just 6 families, and there is only one species present for

18 of the 52 families. The most common species were *Wettinia sp*. (Arecaceae) with 31 individuals in 6 different plots, *Casearia arborea* (L.C. Rich.) Urban (Flacourtiaceae) with 29 individuals in 4 plots, *Cyathea sp1* (Cyatheaceae), a species of tree fern, with 29 individuals in 5 different plots, and an unidentified palm "oja pescado" (Arecaceae) also with 29 individuals and found in only one plot. The average abundance per species was 4.1, and 40.6% of all species having just one individual in the ten plots.

4.2.1.2 Between-Plot Compositional Variability

4.2.1.2.1 General discussion

There was significant variation in composition between-plots in Tambito. Just two families were found in all ten plots (Clusiaceae and Rubiaceae) with 14 of the 52 families (27.0%) occurring in only a single plot. On average each family was present in 4.3 plots. At the species level, the most broadly distributed species were *Hyeronima oblonga* (Tul.) Müll. Arg. (Euphorbiaceae) and *Irarthea sp1* (Arecaceae), which were found in eight plots, with another palm species *Chameadora sp1* (Arecaceae) being found in seven different plots. At the other end of the spectrum, some 188 of the 271 species (69.4%) were found in only one plot.

This does not necessarily signify that a large proportion of species are highly restricted in their distribution, but may simply be a product of the small plot size used here. Given the exceptionally high diversity of species in tropical forests, and the low densities that species tend to have (for example Pitman, 2000) it is unlikely that a 25m x 25m plot captures the full alpha diversity of that particular habitat. For this reason many species “absences” in the plots may indeed be false negatives brought about by the small plot size.

The objective made here with the plots used in this study is that the within-plot habitat is homogenous, whilst the surrounding habitats are heterogeneous. In other words, each plot captures the alpha diversity, whilst comparison between plots examines the beta diversity. In reality it is near impossible to achieve this objective, because habitats vary spatially at very different scales, and that variation is gradual so no clear cut-off is identifiable. Perhaps in highly heterogeneous sites (like Tambito) habitats significantly change over short distances such as 25m (making 25m x 25m plots comply with the objective of the sampling strategy), but in more homogenous sites (like TBS) 25m may only represent a small portion of the actual habitat. Under the latter circumstance, the plot is not representative of the alpha diversity.

Following this logic, for the objective to be achieved it is expected that the number of species within the plot would therefore smoothly increase as greater within-plot space is covered, but that beyond the plot new environments are encountered, thus increasing the accumulation of species.

Species-area curves can be used to examine whether the species richness is saturated or still accumulating as the area inventoried increases. The shape of species-area curves result from a number of factors, making them fairly subjective in terms of interpretation. As greater area is included, it is expected that the number of species will also rise because new environments (*ergo* niches) are being included in the sample. In a heterogeneous environment like Tambito this is particularly the case. Regardless of the inclusion of new niches, space itself is a resource which species compete for, and in particularly diverse ecosystems like tropical forests the number of species is likely to saturate only over very large areas because there are many species and they can be widely distributed. Thus very large plots are usually required, though such plots are very expensive, time-consuming and difficult to inventory in these environments.

Despite these problems associated with the interpretation of species-area curves, they can provide some information, which coupled with other data and analyses provide a clearer picture. Figure 47 shows the species-area curves for Tambito, using the plot quadrants to separate out areas of 5 x 5m, 10 x 10m, 15m x 15m, 20 x 20m and 25m x 25m.

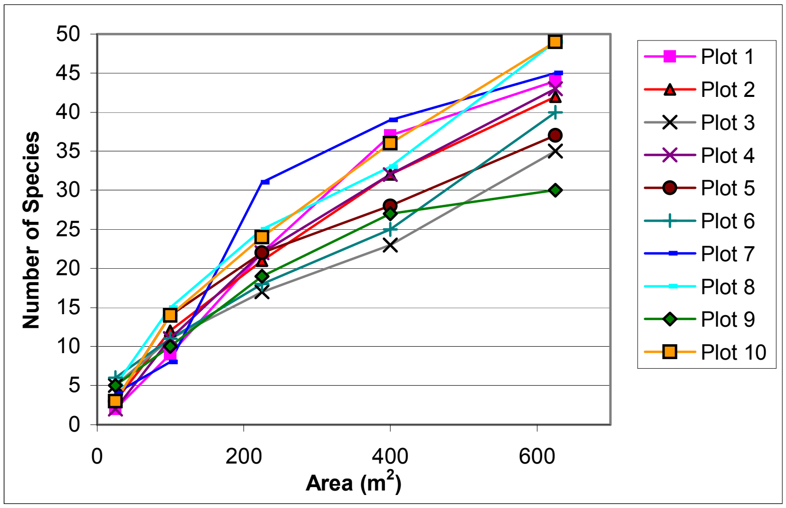
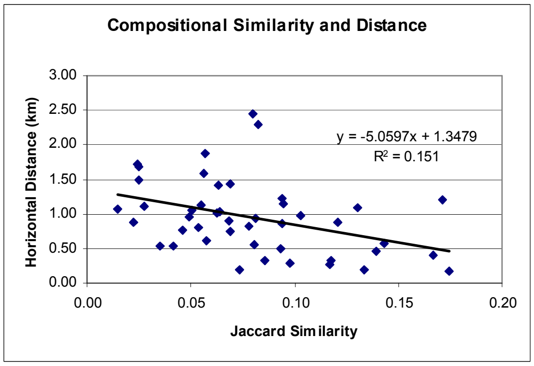


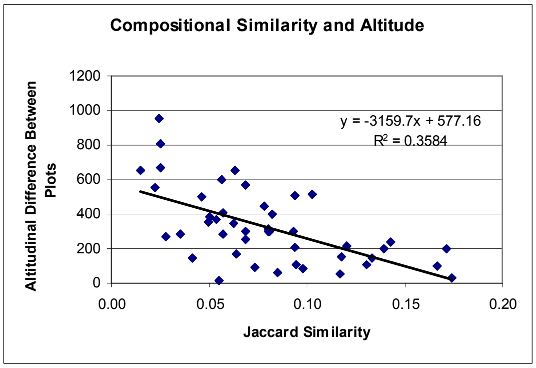
Figure 47 Species-area curves for Tambito, calculated by separating out the quadrants into increasingly sized plots.

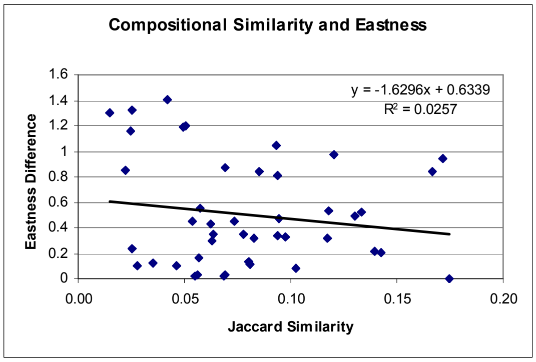
As can be seen in Figure 47, the trend of species accumulation appears to continue beyond the 25m x 25m mark, with little evidence of saturation for any plot. Only plot 9 shows some level of saturation, with just 3 new species being found in the final $225m^2$ of the plot. Given the extremely high levels of diversity present in Tambito, and the reported low densities in tropical tree species (Pitman, 2000), it is expected that $625m^2$ of forest (one plot) will not be particularly representative of the total alpha diversity. Therefore it is impossible to conclude that species are restricted in their distributions to the extent found in the plot data (69.4% of species restricted to one single plot), and this is in part attributable to the small plot-sizes used in the study.

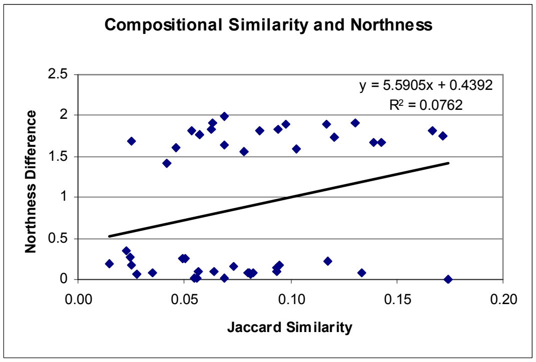
4.2.1.2.2 Single-variate analysis of quantitative environmental variables

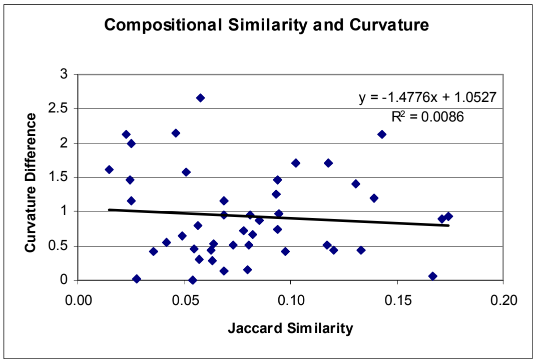
In order to understand the interaction of environment on composition, similarity matrices and statistical analyses using the Mantel test are used. These tests compare between-plot compositional similarity, in this case measured with the Jaccard coefficient and presented in a matrix, with environmental "distance" between the plots, also represented as a similarity (or in this case the inverse – a dissimilarity) matrix. Figure 48 shows scattergrams of compositional similarity against geographic or environment distance for each plot pair (thus 45 points in total). Trendlines are displayed, including the coefficient of correlation. Table 13 then displays the results of the Mantel tests, including the Mantel coefficient, and the one-tailed p-value for 10,000 random permutations.

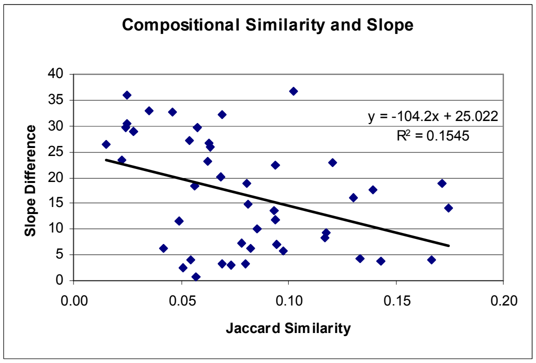

Compositional Similarity and Distance

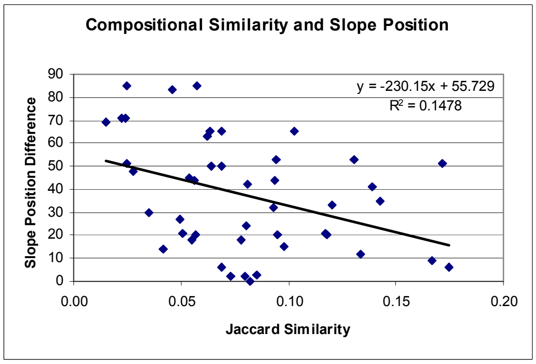

Compositional Similarity and Altitude

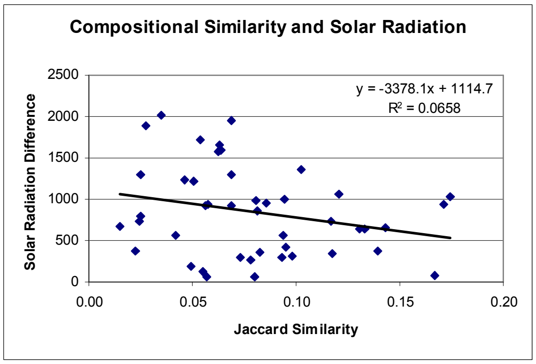

Compositional Similarity and Eastness


Compositional Similarity and Northness


Compositional Similarity and Curvature


Compositional Similarity and Slope


Compositional Similarity and Slope Position


Compositional Similarity and Solar Radiation

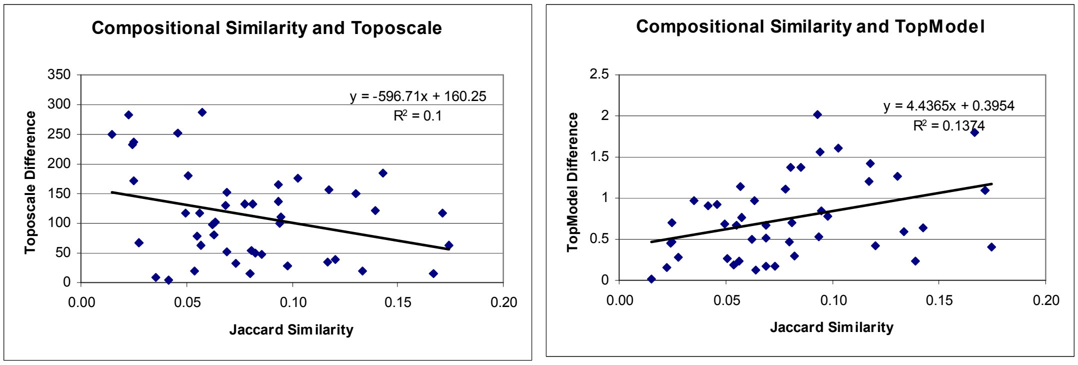


Figure 48 Scatterplots for plot-pairs of compositional similarity (measured with the Jaccard coefficient) and environmental distance (in this case the difference, i.e. dissimilarity) for Tambito.

Variable	Mantel Test	One-tailed p-value	Correlation
Distance	-0.39	0.038	Significant
Altitude	-0.60	0.000	Significant
Eastness	-0.16	0.220	Not-significant
Nothness	0.28	0.088	Not-significant
Curvature	-0.09	0.341	Not-significant
Slope	-0.39	0.003	Significant
Slope Position	-0.38	0.004	Significant
Solar Radiation	-0.26	0.063	Not-significant
Toposcale	-0.32	0.046	Significant
TopModel	0.37	0.032	Significant

Table 13 Summary results of compositional similarity analysis with distance and environmental variables, using Mantel tests and a one-tailed Pearson for Tambito. Note that compositional similarity was compared with environmental dissimilarity (difference), hence negative values in most cases. The northness variable produces very different results due to the heavily skewed distribution of plots in strongly northward and strongly southward facing slopes.

The Mantel tests indicate significant correlation between species composition and topography for six of the ten variables analysed. The highest correlation is for elevation, with slope, distance, slope position and toposcale also having significant correlations to the 95% significance level. The topmodel variable also shows significant correlation, but in the inverse direction (i.e. the greater the compositional difference the more similar the Topmodel values). Least significant variables were aspect related derivatives (northness and eastness) and slope profile curvature.

There are many data points with low degrees of compositional similarity, but also low differences in their topographic conditions, indicating that the variable is not entirely responsible for compositional similarity, but that other factors are at play. However, there are no data points compositionally very similar and environmentally highly different.

Interpreting the results in more depth, it is difficult to ascertain the degree to which distance is important over the other factors, as distance itself correlates relatively closely with elevational difference ($R^2 = 0.31$, $p < 0.0001$, $n = 45$). For this reason a partial Mantel test is performed, using species composition, elevational difference and geographic distance as the third variable. This test concludes that the direct relationship between distance and species composition is in fact spurious (Pearson = -0.1, $p = 0.345$, $n = 45$), and only significant due to the co-linearity with elevational difference.

Similarly, partial Mantel tests performed on each of the correlating variables (slope, slope position, toposcale and topmodel) using elevation as the third distance variable show that none correlate significantly independent of the co-linearity with elevation (Table 14). TopModel is the closest to correlating, with a Mantel statistic of 0.32 (narrowly outside the 95% confidence limit, $p = 0.052$, $n = 45$), but still negatively (i.e. greater compositional similarity between plots with greater Topmodel *difference*).

No plausible explanation can be provided as to the processes behind such a relationship.

Variable A	Variable B	Partial Variable C	Correlation (A,B)	Correlation (B,C)	Correlation (A,C)	Correlation (A,B) | C	p-value
Compositional similarity	Elevation	Distance	-0.60	0.56	-0.39	-0.60	0.00
Compositional similarity	Slope	Elevation	-0.32	0.56	-0.60	0.03	0.47
Compositional similarity	Slope Position	Elevation	-0.39	0.63	-0.60	-0.04	0.45
Compositional similarity	Toposcale	Elevation	-0.38	0.65	-0.60	0.01	0.47
Compositional similarity	TopModel	Elevation	0.37	-0.21	-0.60	0.32	0.05

Table 14 Revised Mantel statistics for correlating variables with compositional similarity in Tambito, applying partial Mantel tests to detect spurious correlations derived from co-linearity between variables.

Evidence of habitat associations with elevation is not a new result for tropical ecology, with numerous examples of species distribution restrictions to elevational zones (Vasquez and Givnish, 1998). However, this analysis has shown a lack of habitat association in composition in many of the other variables. The analysis presented here indicates that habitat association in tropical tree species composition in Tambito is restricted to broad scale factors (temperature gradients for example), rather than local conditions (local slope, curvature, solar radiation receipt etc.), which may still exist but not in a way that is evidenced in our data.

4.2.1.2.3 Multi-variate analysis of quantitative environmental variables

Having identified that elevation alone accounts for a large amount of compositional difference, but that other variables present at least some influence on composition, a multi-variate analysis is performed as a final step in this analysis. Agglomerative Hierarchical Clustering (AHC) is performed using Ward's Method (using XLStat Pro) to produce a dendrogram of plot environmental conditions dissimilarity (Figure 49) and an associated dissimilarity matrix. The dissimilarity matrix is then compared with the compositional similarity matrix (Jaccard Index) using the Mantel statistic. When all 9 environmental variables are used (geographic distance was excluded), the correlation is insignificant at the 95% significance level, though a weak correlation is evident (Mantel R = -0.257, p = 0.07). When the multi-variate analysis is restricted to only those factors already found to be significant (elevation, slope, slope position, toposcale and topmodel), the correlation improves and becomes highly significant to the 99% confidence limit (Mantel R = -0.393, p = 0.006). This is still not as high as the correlation found in the partial Mantel test of elevation (Mantel R = -0.60, p = <0.000), indicating that in reality elevation (and/or distance) are the best predictors of composition (in this case explaining some 36% of compositional variability). Likewise, when multiple stepwise linear regression is applied to the same data, only elevational difference is selected as an explanatory factor, with no other variable explaining more variability in composition with the p-value limit set to 0.10. If elevation alone explains 36% of the variability, clearly other factors are important which are not measured in this study.

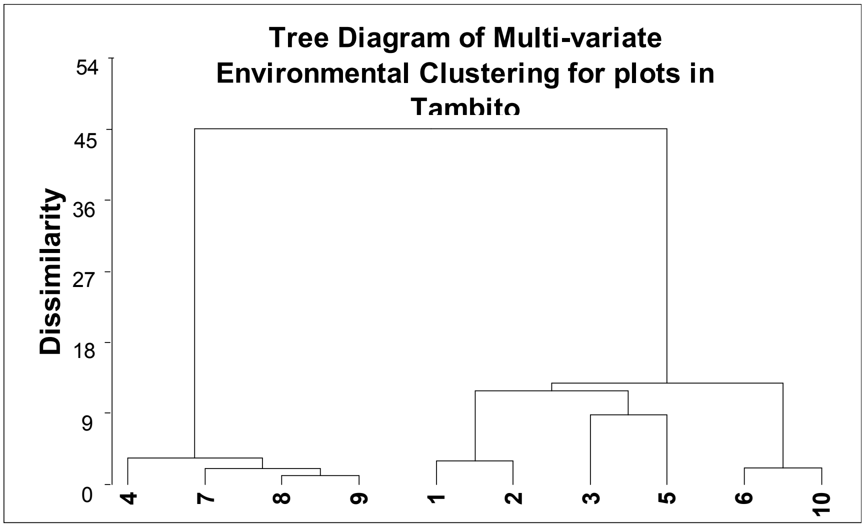


Figure 49 Multi-variate clustering of plots based on all 9 environmental and topographic variables

4.2.1.2.4 Analysis of categorical environmental variables

Mantel tests were only possible for continuous variables, hence the landscape classifications (feature, network feature and topoclass) were not used in these analyses. The degree to which composition is controlled by these landscape classifications is explored using simple tables showing the number of species restricted to specific classes for each of the three variables (Table 15, Table 16, and Table 17). The number of species found to be restricted to a single class is shown. However, many of these species may have been found only in one plot, making it inconclusive whether they are restricted by landscape classification, or are simply rare and have only been captured by one single plot in this study. For this reason, the analysis is also performed only for the 83 species found in more than a single plot.

Feature	No. Plots	No. Species Restricted to feature	No. species restricted to feature only for species distributed in more than 1 plot
Planar	2	163	24
Ridge	7	26	1
Channel	1	24	0
Total		***213***	***25***

Table 15 Number of species associated to specific classes in the "Feature" classification for Tambito.

Network Feature	No. Plots	No. Species Restricted to feature	No. Species Restricted to feature for species distributed in more than 1 plot
Planar	6	141	21
Ridge	4	72	4
Channel	0	0	0
Total		***213***	***25***

Table 16 Number of species associated to specific classes in the "Network Feature" classification for Tambito.

Topoclass	No. Plots	No. Species Restricted to feature	No. Species Restricted to feature for species distributed in more than 1 plot
Slope	5	97	11
Toe Slope	2	35	1
Ridge	3	74	6
Total		***206***	***18***

Table 17 Number of species associated to specific classes in the "topoclass" classification for Tambito.

For all three variables a large proportion of species were restricted to one single landscape class (>76%), but this is more an indication of the fact that 69% of species were only encountered in a single plot. It is impossible to separate out landscape class restriction from low density in these cases. More indicative of habitat association is the proportion of the 83 species found in more than one plot that are restricted to a single landscape class. For this the “feature” classification and the “network feature” classification show the highest levels of habitat association (30% of the 83 species), with the “topoclass” classification showing 22% habitat association. In none of the landscape classes is there a family, which exhibits abnormally higher levels of habitat association.

However these results must be taken with caution, as the few number of data points poorly cover all landscape classes (for example only 1 plot in a channel in the feature classification, no channels in the network feature classification, and no peaks at all in any classification system). Perhaps a clearer way of looking at these results is to note that 70% of the broadly distributed species (i.e. those found in more than 1 plot) were found in different landscape classes, indicating that these terrain derivatives have little explanatory power in terms of composition in Tambito. In any case, this analysis is significantly weakened by the lack of data points, and more plots would greatly enhance the validity of this conclusion.

4.2.2 Diversity

4.2.2.1.1 General discussion

The plot diversity data shows significant between-site variation in diversity in Tambito (Table 18) with species richness varying between 30 and 52 species. On average there were 22 families per plot (ranging from 18 to 27), and 35 genera (ranging from 25 to 46). Prior to discussing in detail the diversity between plots using different indices, the Renyi diversity plots (Figure 72) help in the interpretation of diversity variation between plots.

Plot	No. Individuals	No. Families	No. Genera	No. Species	No. Endemic Species	Simpson's	Shannon's	Margalef	Menhinick	Berger-Parker
1	97	21	34	44	17	0.96	3.45	9.40	4.47	0.12
2	107	24	33	42	16	0.97	3.44	8.77	4.06	0.11
3	118	23	31	35	11	0.93	3.05	7.13	3.22	0.20
4	137	22	34	43	21	0.95	3.31	8.54	3.67	0.16
5	112	19	35	37	23	0.93	3.04	7.63	3.50	0.19
6	87	18	37	40	8	0.97	3.44	8.73	4.29	0.09
7	176	20	40	45	29	0.94	3.24	8.51	3.39	0.16
8	106	28	46	52	26	0.98	3.68	10.94	5.05	0.10
9	75	19	25	30	13	0.96	3.16	6.72	3.46	0.12
10	93	27	34	49	24	0.98	3.64	10.59	5.08	0.08

Table 18 Richness and diversity of plots in Tambito

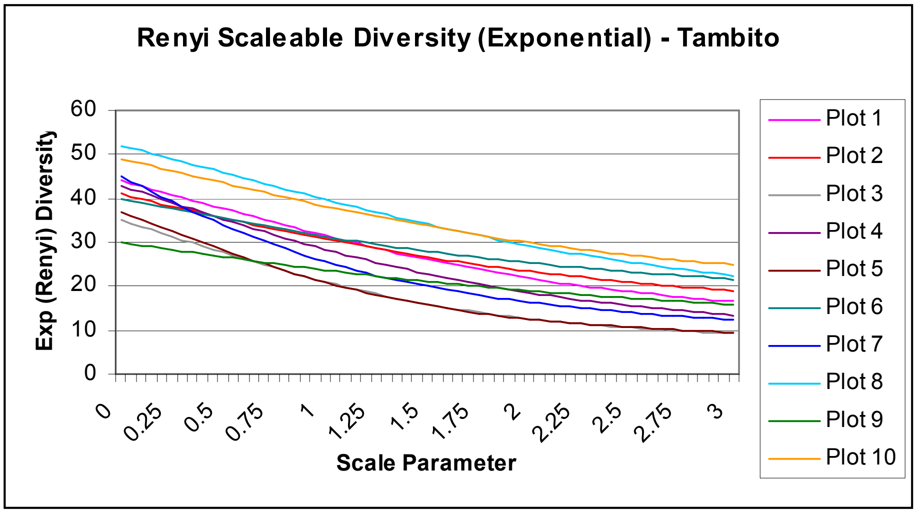


Figure 50 The Renyi scaleable diversity index for Tambito, indicating to what extent plot diversities can be universally compared.

Plots 8 and 10 are the most diverse, with greater richness and evenness in plot 8, but also a higher level of dominance of a single species (Berger-Parker). Although plot 9 has the lowest species richness, plot 5 has the lower "diversity" (Shannon's and Simpson's), and also high levels of dominance of a single species (along with plot 3). This simple comparison merely shows that diversity is not homogenously distributed around the catchment, and that a great deal of variation occurs in species richness, diversity and dominance. The many shapes of the Renyi plots in Figure 72 also show that the structure of diversity is also very different between plots (i.e. non-comparable levels of evenness vs richness). These differences are later found to be important.

4.2.2.1.2 Single-variate analysis of quantitative environmental variables

Taking this analysis forward by comparing the diversity with the environmental variables, Table 19 presents the conditions at each plot, and Table 20 shows the correlation coefficients (and respective p-values) between plot diversity and the environmental variables. In this case only continuous variables are used in the correlation. Later in the chapter the categorical landscape features are compared with diversity.

Plot	Eastness	Northness	Feature	Network Feature	Mean Curvature	Slope (degrees)	Slope Position	Solar Radiation	Toposcale	Topoclass	Topmodel
1	-0.43	0.90	Planar	Planar	-0.13	32.38	54	8434	-12.46	Slope	7.59
2	-0.43	0.90	Ridge	Planar	0.80	46.38	48	7398	51.31	Slope	8.00
3	-0.64	-0.77	Ridge	Ridge	-1.33	50.07	13	8054	-133.38	Toe Slope	7.36
4	-0.56	0.83	Ridge	Ridge	0.37	13.46	78	9419	42.00	Slope	8.97
5	0.76	0.65	Ridge	Ridge	-0.78	43.84	27	8621	-129.46	Toe Slope	8.27
6	0.41	-0.91	Planar	Planar	-0.07	36.43	45	8354	3.23	Slope	9.38
7	-0.40	0.92	Ridge	Planar	0.67	14.10	98	9357	104.00	Ridge	7.82
8	-0.09	1.00	Ridge	Planar	1.33	20.43	98	8998	153.23	Ridge	8.12
9	-0.54	0.84	Ridge	Ridge	0.82	17.46	96	9289	119.77	Ridge	8.29
10	-0.11	-0.99	Channel	Planar	0.38	40.67	33	7706	22.54	Slope	8.79

Table 19 Environmental conditions at each plot in Tambito, derived from the terrain derivatives.

Pearson's Correlation Coefficient	Elevation	Eastness	Northness	Curvature	Slope	Slope Position	Solar Radiation	Topmodel	Toposcale
Family Richness	-0.08	-0.24	-0.07	0.36	0.11	0.00	-0.34	-0.14	0.27
Genera Richness	0.22	0.33	0.15	0.33	-0.22	0.28	0.16	0.06	0.30
Species Richness	0.22	0.05	0.06	0.47	-0.18	0.22	-0.09	0.11	0.39
Endemic Species	0.31	0.08	0.43	0.41	-0.41	0.40	0.33	-0.11	0.34
Simpson's	0.28	-0.04	-0.07	0.70	-0.19	0.31	-0.20	0.45	0.65
Shannon's	0.19	0.01	-0.07	0.62	-0.12	0.23	-0.25	0.32	0.55
Margalef	0.09	0.12	-0.04	0.49	-0.08	0.15	-0.21	0.20	0.39
Menhinick	-0.07	0.20	-0.17	0.45	0.05	0.04	-0.33	0.29	0.35
Berger-Parker	-0.18	-0.10	0.17	-0.62	0.07	-0.21	0.29	-0.49	-0.56

p-value	Elevation	Eastness	Northness	Curvature	Slope	Slope Position	Solar Radiation	Topmodel	Toposcale
Family Richness	0.82	0.50	0.85	0.31	0.76	0.99	0.33	0.70	0.45
Genera Richness	0.54	0.35	0.69	0.36	0.54	0.43	0.66	0.88	0.41
Species Richness	0.55	0.88	0.86	0.17	0.62	0.55	0.81	0.77	0.26
Endemic Species	0.39	0.82	0.22	0.24	0.24	0.25	0.35	0.75	0.34
Simpson's	0.44	0.91	0.86	0.03	0.60	0.38	0.58	0.20	0.04
Shannon's	0.60	0.97	0.85	0.05	0.74	0.53	0.49	0.37	0.10
Margalef	0.80	0.73	0.91	0.15	0.83	0.69	0.56	0.58	0.26
Menhinick	0.84	0.59	0.64	0.20	0.89	0.91	0.35	0.41	0.32
Berger-Parker	0.63	0.79	0.63	0.05	0.84	0.57	0.42	0.15	0.09

Table 20 Pearson's correlation coefficient and the two-tailed p-value between richness and diversity in each plot and the environmental variables for Tambito.

On the whole the plots cover a broad range of environmental conditions, except for the northness variable where the plots are located only strongly north- or strongly south- facing slopes.

Taking elevation as the primary variable (due to its strong co-linearity with many climatic factors), there is no apparent linear relationship with any measure of richness or diversity. However, examining the scatterplot of the data points there is some evidence of a non-linear relationship, with the greatest diversity and lowest levels of Berger-Parker dominance being found in mid-elevations (Figure 51). Applying a polynomial trendline to the data points, we find that Simpson's diversity index correlates significantly (Simpson's = -0.0000002 Elevation^2 + 0.0006 Elevation + 0.44, $R^2 = 0.70$, p = 0.02), with a peak in diversity at 1850m. Similarly, Shannon's diversity peaks at 1800m ($R^2 = 0.46$) and Berger-Parker dominance is also lowest at 1800m ($R^2 = 0.54$). When richness is examined (family, genus, species and endemics) neither linear nor polynomial relationships are evident, and the R^2 are less than 0.1 in all cases (Figure 52).

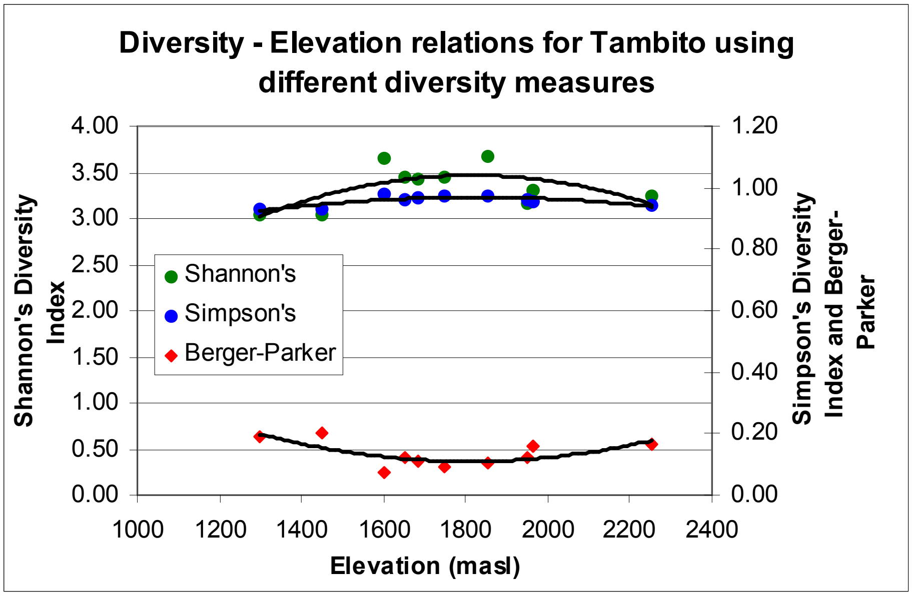


Figure 51 Relationship between plot diversity and elevation in Tambito.

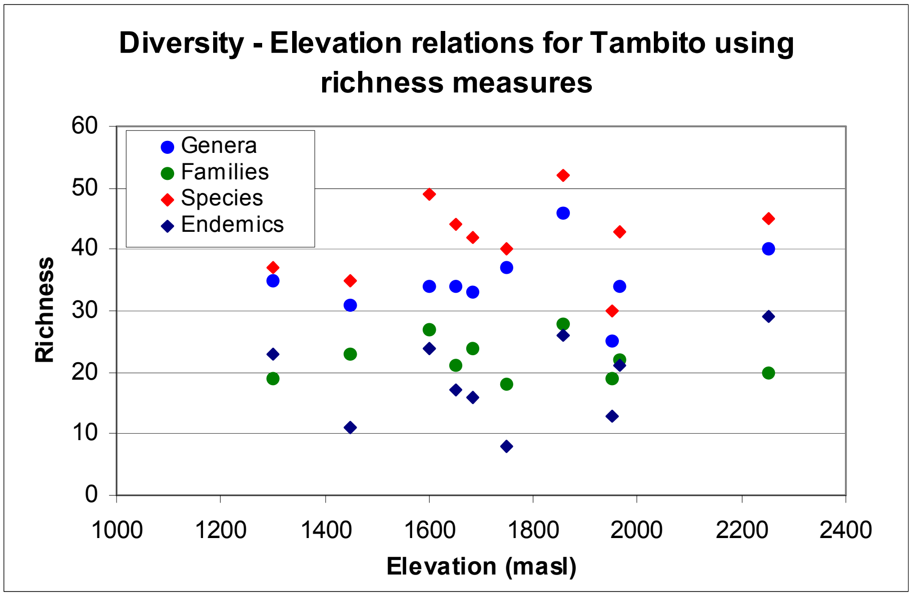


Figure 52 Relationship between plot richness and elevation in Tambito

The mid-elevation diversity peak is further evident in the data when the plots are separated into lower-, mid- and upper- elevation bands, and the average diversity and richness calculated for the plots within each elevational band (Table 21). Though the validity of this analysis is somewhat limited by the few plots found in low and upper elevations and the uneven distribution of plots in each elevational band, there are some clear patterns.

	No. Individuals	No. Families	No. Genera	No. Species	No. Endemic Species	Simpson's	Shannon's	Margalef	Menhinick	Berger-Parker
Lower Elevation Average (1000 - 1500) (2 plots)	115 (3.7)	21 (13.5)	33 (8.6)	36 (3.9)	17 (49.9)	0.93 (0.0)	3.04 (0.1)	7.38 (4.8)	3.36 (5.8)	0.20 (5.7)
Mid Elevation Average (1500 - 1900) (5 plots)	98 (11.2)	23 (16.1)	36.8 (13.3)	45 (13.6)	18.2 (37.5)	0.97 (2.2)	3.53 (7.3)	9.69 (14.6)	4.59 (15.5)	0.10 (47.9)
Upper Elevation Average (1900 - 2300) (3 plots)	129 (39.4)	20 (7.5)	33 (22.9)	39 (20.7)	21 (38.1)	0.95 (0.8)	3.24 (2.3)	7.92 (13.2)	3.51 (4.2)	0.15 (16.7)

Table 21 Average richness and diversity of plots when separated into three elevational bands. In brackets the respective coefficient of variation.

Richness and diversity in all but one case (number of endemics) is greater in the mid-elevations, but there is also evidence that there is greater variability in diversity and richness in the mid- elevations, especially across different richness measures. If this pattern is not simply a result of sampling bias, a number of interpretations could be offered, the theoretical background of which are discussed in Section 2.3.1 of the literature review. Partial Mantel tests have already indicated that the compositional similarity of the plots is strongly controlled by difference in elevation, indicating that species have some habitat associations related to elevation. Elevation *per se* is meaningless in understanding the precise adaptations that species may have to create that association, but it is likely that temperature is an important factor.

One potential interpretation is that mid-elevations have the greatest heterogeneity in elevation (see Chapter 6, also discussed to be of theoretical importance in Lundholm and Larson (2003)), especially in slope, northness and toposcale, and so there is likely to be a greater diversity in topographically induced micro-climates. If indeed temperature is an important factor in controlling species composition, a diversity of micro-climates may duly increase species diversity.

Alternatively, the elevational habitat association in composition identified could mean that the mid-elevations contain the most overlaps of elevationally controlled niches (the mid-domain effect), and thus potentially have the greatest species richness (Colwell and Lees, 2000). More specifically, the mid-elevations are a dynamic zone where species with adaptations to lower temperatures (higher elevations) occur in low abundances, along with species with adaptations to higher temperatures (low elevations). This overlap of species adaptations may create high diversity and low dominance in the mid-elevations.

To illustrate this idea based on Tambito data, a simple exercise is used. Using Excel, species abundances across the elevational gradient are modeled based on normal distributions, calculated based on the mean elevation where the species are found and the degree of adaptability the species has (amplitude). The amplitude is expressed as a standard deviation, with species adapted to very specific elevations having a low standard deviation, and species with wide ranging elevational distribution having high standard deviations. The model then positions 30 hypothetical species along the elevational gradient with mean adaptations at random points in the gradient, with random standard deviations, and calculates for each elevational band the Simpson's diversity index based on abundances for each species, and the Berger-Parker dominance index for the most dominant species. Rapoport's rule (Stevens, 1992) is not applied to this analysis.

An example result from this model is shown in Figure 53, where 30 very differently adapted species occur across the elevational gradient. Despite some points of very low diversity across the gradient which coincide with high dominance of a single species, the general trend is one of less diversity in the extremes, and high diversity at mid-elevations. When 50 random runs are made, and the average diversity per 50m elevational interval is calculated this pattern becomes very clear (Figure 54). As can be seen, a clear peak in diversity occurs in mid-elevations (peaking at 1750m), with the corresponding drop in Berger-Parker dominance. The model used here is highly simplified and fails to take into account many important factors (competition and resources for example). However, it is aimed at providing an example of one possible mechanism that may create a mid-elevation diversity peak, whereby the upper- and lower- extremes of a gradient potentially have less available species to generate high diversity. This is in simple terms an edge effect, and only works under the assumption that there are no other forest species above or below the elevational limits of the analysis.

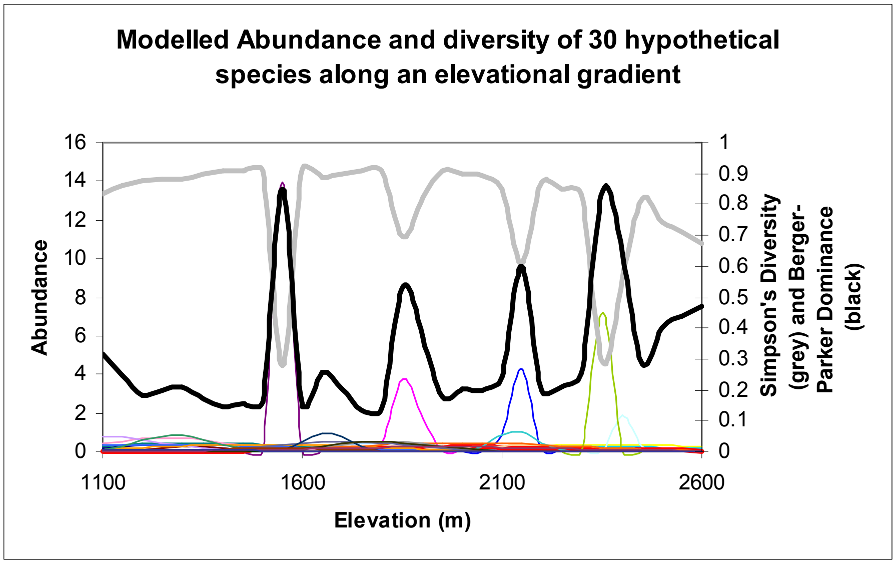


Figure 53 Example of niche model, with 30 hypothetical species with randomly positioned ranges along the elevational gradient. The thick grey line represents the respective Simpson's Diversity Index and the black line the Berger-Parker dominance.

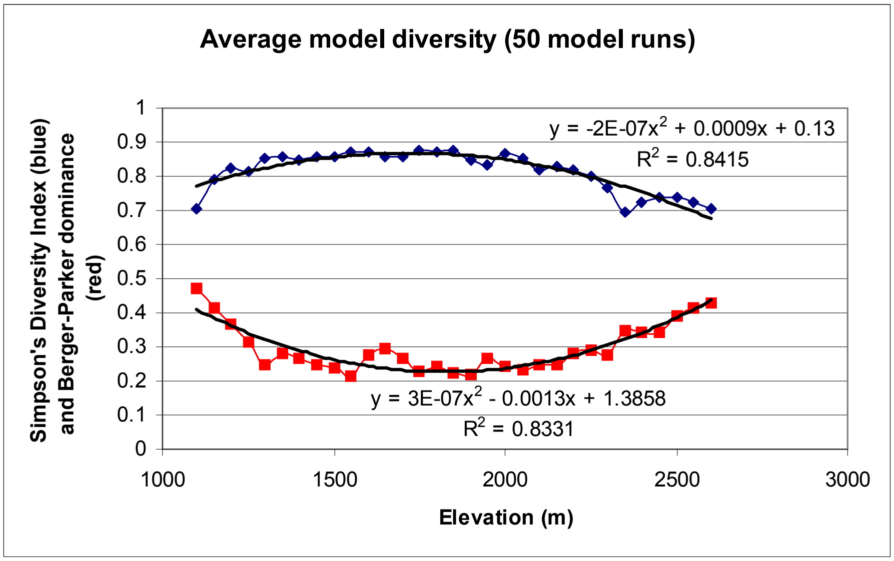


Figure 54 Average pattern of diversity-elevation relations in the simple niche model for Tambito.

Application of this concept to Tambito is complicated somewhat by the fact that the reserve is only a sub-set of the full elevational gradient that stretches from the Pacific (0m) to the high Andes (2,800m within the Tambito region). However, there is little forest cover directly below the reserve, and little area above 2800m. There is contiguous forest down to the Pacific, but this is some 30km to the north of Tambito, and if we assume low distances of seed dispersal it is fair to say that Tambito is cut-off from the lowlands to the Pacific. Therefore, strictly speaking this analysis is covering the entire forested elevational gradient. In other words, it is feasible that low-elevation edge effects on the niche model discussed above are valid, and may explain the low diversity found in the lower plots.

An important factor which the above model fails to account for is space itself, also a variable identified as significant in generating mid-elevation peaks in species richness (Whittaker and Niering, 1975; Rahbek, 1997; Sanders, 2002). Having seen the steep accumulation of species with increasing area (Figure 47), area could be seen as a resource itself (Schoener, 1976), and one which generates higher richness through greater probability of speciation and a larger potential seed pool. Given that elevation is a limiting factor in terms of species range, and assuming that area is a resource, it is important to take into account the surface area of land in elevational bands. In Tambito, mid-elevations (in this case 1600m – 2300m) have the greatest surface area (Figure 55).

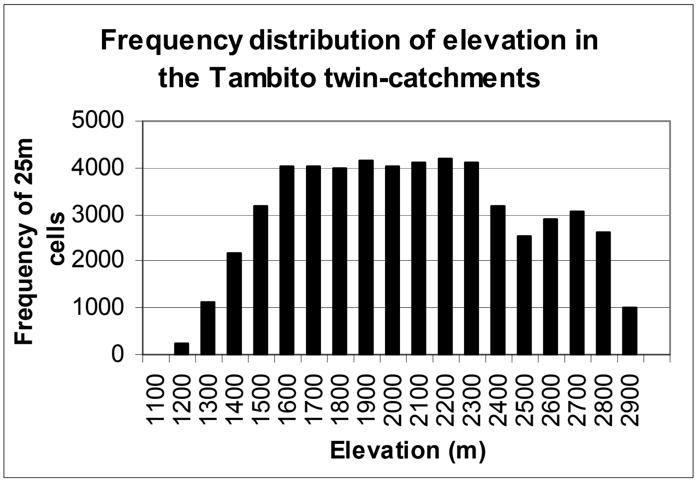


Figure 55 Total area of land across the elevational gradient for the twin-catchments of Tambito, expressed as the frequency of 25m (625m^2) cells per 100m elevational band.

If we assume that elevational bands with greater surface area are also likely to harbor more species, then this further exaggerates the mid-elevational diversity peak in the niche model presented earlier. Furthermore, this area concept also plays an important role in explaining documented patterns of monotonic diversity loss with elevation in long gradients from lowlands to highlands (Terborgh, 1977; Vasquez and Givnish, 1998; Givnish, 1999; Kessler et al., 2001; Grytnes, 2003). Taking a cross-section across Colombia between 2°N and 3°N, 72% of the land surface is below 600m elevation (Figure 56). If the niche model is then adapted to weigh the positioning of the 30 species according to land-surface area (i.e. more species located in low elevations), the edge effect shown in Figure 53 whereby low-elevations have less diversity (and greater dominance) is cancelled out by area, and the trend becomes one of monotonic loss of diversity with elevation (Figure 57). Whilst this is an obvious observation to make (if you place more species in an elevational band then richness is expected to be higher), it illustrates very clearly the balance between the edge effect and land-surface area, and provides one mechanism for explaining the contrasting results of diversity variation across elevational gradients (discussed at length in Rahbek, 1997). In simple terms, assuming that greater area increases the potential species pool, studies with plots located in continuous forest cover from lowlands to highlands will find a gradual loss in diversity with elevation, whilst isolated studies in mid-elevation catchments (like Tambito) are likely to find mid-elevation peaks in diversity (as a result of both edge effects and greater mid-elevation land-surface area in these kinds of catchments).

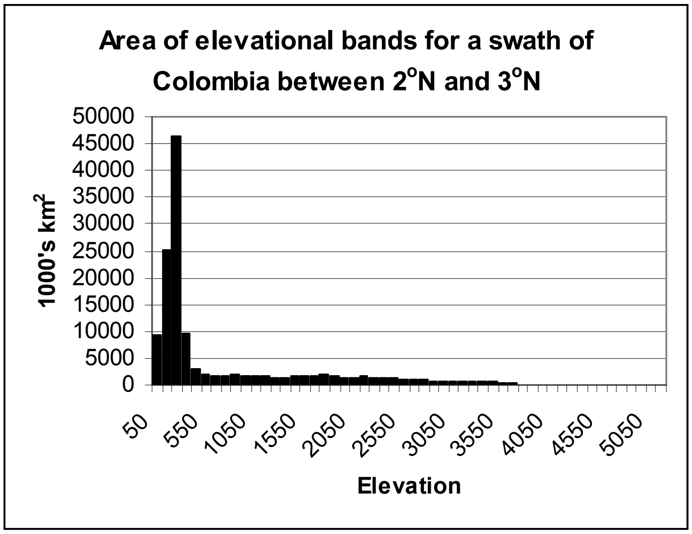


Figure 56 Land-surface area across the elevational gradient for a swath across Colombia between 2°N and 3°N.

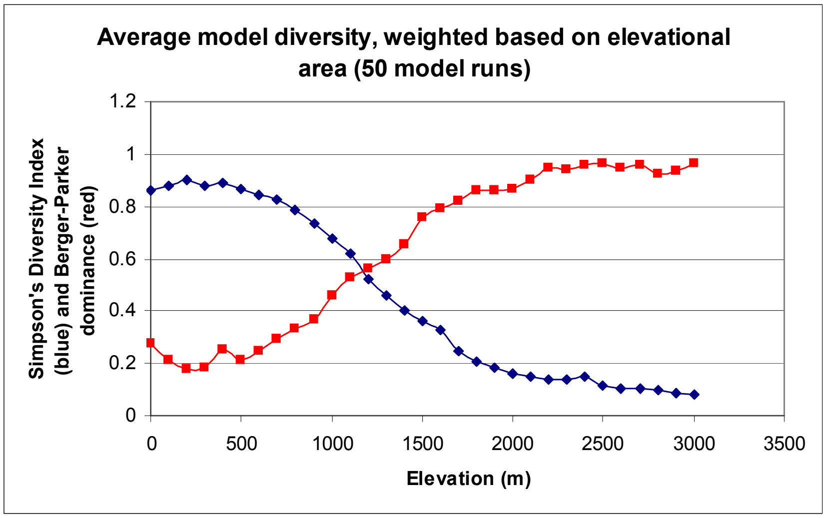


Figure 57 Niche model adjusted for the area concept, with more species located in elevations with greater land surface area, and the elevational gradient extended to range form 0m to 3000m.

Having examined the possible reasons for the mid-elevation peak in diversity, it is also important to look into the high variability in diversity and richness that was found in mid-elevations (high coefficients of variability in Table 21). As shown later in this thesis (Chapter 6), environmental heterogeneity also peaks at mid- elevations, with the greatest heterogeneity coinciding exactly at the same point where the greatest diversity is found (1850m). This may explain the greater variability in diversity and richness in mid-elevations. Rather than discuss and speculate further as to the driving factors behind this mid-elevation peak in diversity (and its variation), this is left to the conclusions where further evidence from TBS is also available for discussion.

Looking at the other environmental variables, few correlations are found, with no visible evidence of non-linear relationships either. Only mean curvature and toposcale (both essentially measuring curvature) showed significant relationships with Simpson's index ($p<0.05$), where the greatest diversity was found in positively curving convex slopes (Figure 58). However, the regression is not entirely convincing, essentially showing that the two least diverse plots happen to be in concave slopes, whilst the other plots have convex slopes and seemingly show little pattern of increased diversity with higher curvature.

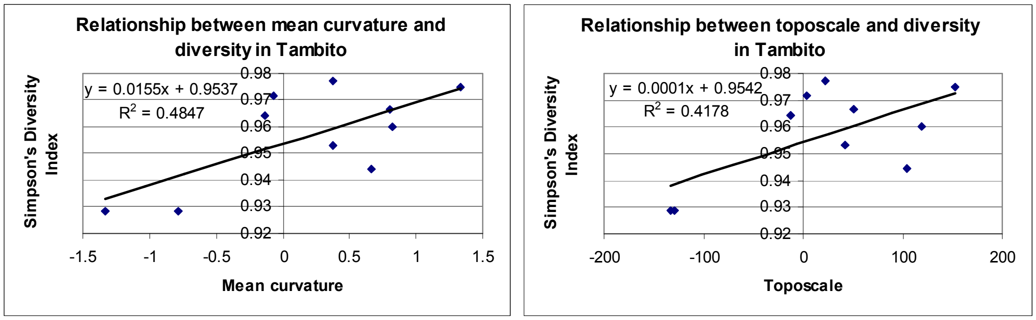


Figure 58 Significant relationships between Simpson's diversity and mean curvature (left) and toposcale (right) for Tambito.

Upon close examination of the data, plot 9 regularly appears as a strong outlier in many relationships, and omission of this plot actually renders a number of highly significant correlations (Table 12). Toposcale, mean curvature and slope position all produce significant correlations with species and genus richness amongst other diversity measures. Strongest is the relationship between species richness and curvature and toposcale (Figure 59).

Pearson's Correlation Coefficient	Elevation	Eastness	Northness	Curvature	Slope	Slope Position	Solar Radiation	Topmodel	Toposcale
Family Richness	0.00	-0.36	0.00	0.49	0.00	0.16	-0.26	-0.14	0.43
Genera Richness	0.52	0.23	0.37	0.66	-0.61	0.77	0.54	0.09	0.72
Species Richness	0.51	-0.14	0.26	0.86	-0.55	0.67	0.19	0.15	0.85
Endemic Species	0.42	0.01	0.52	0.53	-0.57	0.60	0.49	-0.11	0.50
Simpson's	0.27	-0.02	-0.08	0.71	-0.18	0.32	-0.24	0.45	0.67
Shannon's	0.29	-0.06	-0.01	0.76	-0.24	0.40	-0.16	0.34	0.73
Margalef	0.27	-0.01	0.08	0.75	-0.32	0.45	-0.03	0.24	0.72
Menhinick	0.00	0.13	-0.12	0.57	-0.06	0.18	-0.26	0.31	0.50
Berger-Parker	-0.15	-0.13	0.20	-0.62	0.03	-0.17	0.36	-0.49	-0.56

Table 22 Pearson correlation coefficients between plot diversity and richness and environmental variables when plot 9 is omitted from the analysis. Significant correlations ($p<0.05$) are highlighted in grey.

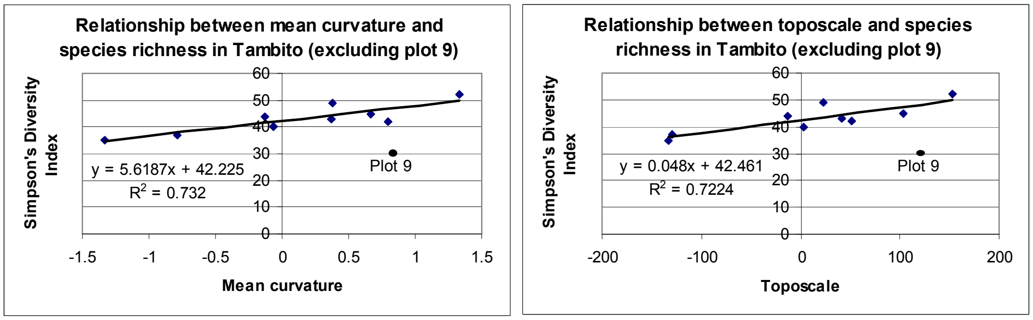


Figure 59 Relationship between species richness and mean curvature (left) and toposcale (right) when plot 9 is omitted from the analysis. The linear relationship and R^2 displayed corresponds to the result without plot 9, though the point is shown in the graph for information.

Omitting plot 9 from the analysis as an outlier is justified based on the conditions experienced in the field. Plot 9 is positioned almost directly on a major ridge (and at the catchment boundary), it was almost flat (slope approximated in the field at 9 degrees) and certainly not convex in terms of curvature (at small spatial scales, though the larger-scale curvature is definitely convex). The widening of the ridge and the small flat and sheltered region in which the plot is located is not identified by the DEM, and therefore the curvature and toposcale values derived from the DEM are not actually representative of the reality found in the field. It is not however justifiable omitting plot 9 from the slope position regression because the slope position is accurately identified as 96, i.e. very close to the ridge.

Having justified the omission of plot 9 from the curvature and toposcale calculations, there is a very strong relationship which has some interesting implications. Furthermore, these patterns are independent of the elevational relationships already discussed. When correlation coefficients are applied to the data for mean curvature at each individual scale (windows of 3, 5, 7, 9, 11, 13 and 15 cells), in all cases, including or omitting plot 9, the highest degree of correlation occurs at mean curvature with a window size of 7 or 9 cells, i.e. a mid-scale measure of mean curvature. The lower correlation at small window sizes may be due to deficiencies in DEM quality at the micro-scale rather than have biological significance, but the effect of curvature on diversity and richness is clearly lower for broader scale measures of curvature (i.e. high window sizes).

Mean Curvature Scale	All Plots		Omitting Plot 9	
	Pearson Richness	Pearson Diversity	Pearson Richness	Pearson Diversity
3	0.41	0.45	0.64	0.44
5	0.55	0.63	0.80	0.62
7	0.58	0.69	0.87	0.69
9	0.57	0.72	0.89	0.73
11	0.51	0.72	0.88	0.73
13	0.44	0.70	0.87	0.72
15	0.37	0.67	0.84	0.70

Table 23 Pearson correlation coefficients for Simpson's diversity and species richness correlations with mean curvature at different scales.

The fact that there is greater diversity on convex slopes could be explained by two possible reasons. One is the topographic exposure, particularly important in cloud forests due to potentially higher levels of cloud presence in exposed regions. Presence of cloud at the canopy provides an extra input of water to the system through cloud interception, which is not necessarily an insignificant amount compared to water input from rainfall (Jarvis, 2000; Mulligan and Jarvis, submitted), but becomes significant in dry months, when cloud interception prevails despite low rainfall. The water contained in clouds has also been found to be richer in nutrients, and so exposed sites may also be richer in nutrients though no studies have made direct measurements of this. However, there is also an argument against this explanation. Increased cloud interception due to exposure also reduces incoming light and temperature, encouraging waterlogging, and increases leaf wetting, thus constricting photosynthesis and respiration. These conditions may favour only a handful of species better adapted to these conditions. The likely effect might be one of high dominance and low richness.

The second possible reason regards access to light, whereby convex slopes potentially have greater light receipt surface area at the canopy level, but also greater probability of direct radiation reaching the ground surface through lateral penetration of the canopy. The variety of angles from which light may be received by the canopy and the sub-canopies and understorey beneath provides a greater number of potential niches for different light-related adaptations. This combination of greater surface area for light receipt per unit area of land, and the resultant diversity in light niches may generate species richness.

There is insufficient data to ascertain which of the two reasons generates the higher diversity observed on convex slopes, though it may indeed be a combination of both factors.

Having isolated this important correlation between richness and curvature, and equally the lack of clear correlation between diversity measures and curvature, this may shed further light on the mid-elevation diversity peaks that have been discussed earlier. Statistically significant mid-elevation diversity peaks were found using diversity measures, but richness measures failed to show the same relationship. Given the strong correlation with curvature, this co-variable may be creating a more complex and variable pattern in richness with elevation, and this effect can be isolated by fitting a polynomial mid-elevation peak trendline to the richness data, and comparing the residual in richness with the curvature for each plot (Figure 60).

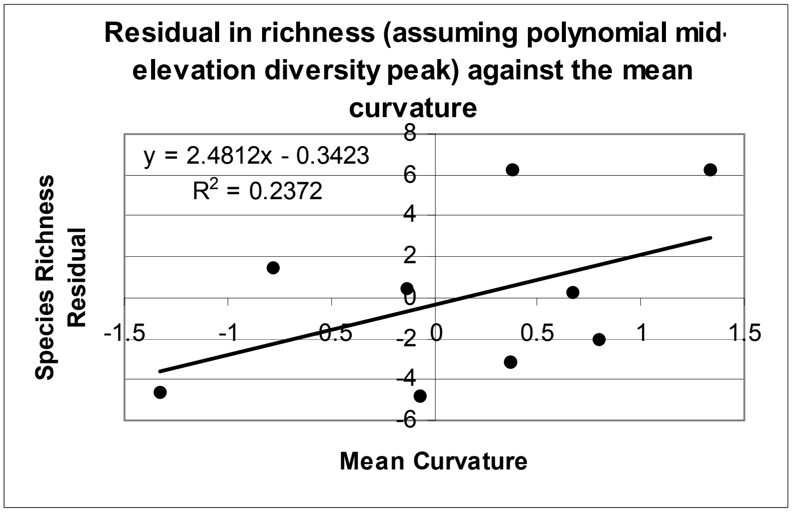


Figure 60 Residual in richness (with respect to a polynomial mid-elevational peak trendline) compared with mean curvature, with the purpose of explaining the variation in richness across the elevational gradient. The residual is calculated based on the actual richness (plot measured) minus the modeled richness (polynomial trendline). Plot 9 is excluded from the analysis for reasons explained earlier.

The relationship between richness residual and curvature is not statistically significant (Pearson = 0.49, p-value 0.18). A weak trend is evident, whereby plots with a positive residual (i.e. greater diversity than expected with the polynomial function) also have convex curvature, and those with a negative residual have concave curvature. However, this is not significant and it cannot be concluded that richness is generated through a simple combination of linearly increasing richness on convex slopes, and a polynomial peak in richness at mid-elevations. Other processes appear to be at play, that are not evident in the data studied here.

4.2.2.1.3 Multi-variate analysis of quantitative environmental variables

It is clear that elevation is important in explaining diversity, but equally curvature and some other factors appear to be important. Analyses are therefore applied that take into account all variables at once to examine to what extent each variable contribute to explaining the variability in diversity. For this, multiple stepwise regression is applied for Simpson's Diversity and richness as the dependent variables, and all nine terrain derivatives as the independent variables. For Simpson's index, just two variables explain 71% of the variability in diversity ($D = 0.0215$ Mean Curvature – 0.0114 Northness $+ 0.95$, $p = 0.01$, $n = 10$). Mean curvature explains 48% of the variability and northness explains a further 22% of the variability. Applying this model to the topographic data produces a clear relationship between modeled and measured diversity (Figure 61), and interestingly the modeled diversity captures the mid-elevation peak already observed (Figure 51). Curvature has already been shown to be important in defining diversity, and some possible reasons for this have also been presented. However, northness alone shows little correlation with diversity when treated alone (Pearson = -0.07), but in combination with curvature does explain some of the variability. This further suggests that solar radiation is indeed important, northness being important in defining the time of year of maximum radiation receipt and the degree of annual fluctuation in radiation receipt. The correlation and the elevational gradient in modeled diversity shown in Figure 61 is expected as the same data went into the model as it is compared against, and this result would be greatly enhanced by a split-sample regression and validation, but with just 10 plots to work with this was impossible.

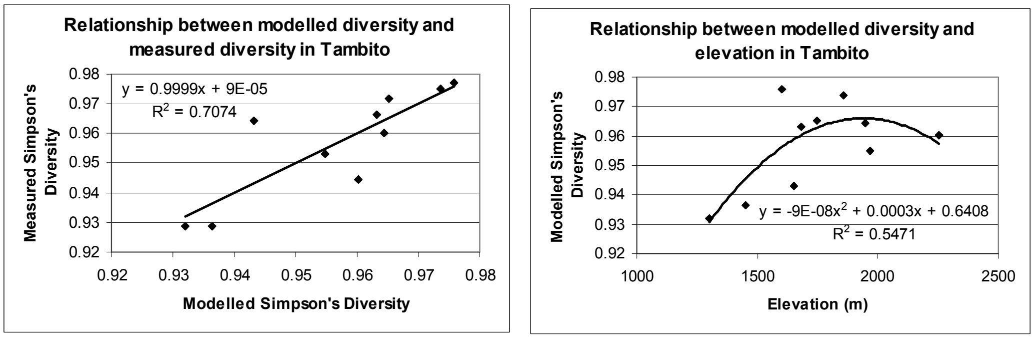


Figure 61 Modelled diversity (calculated using the multiple stepwise regression) correlated against measured diversity (left), and the variation in modeled diversity across the elevational gradient.

When species richness is examined in the multiple stepwise regression, no significant multiple regressions are found on top of the relationships already discussed (Figure 59, for example), both including and excluding plot 9. This in itself is interesting, as strong correlations are found with diversity but few patterns in richness. The Renyi diversity plots have already shown that richness is non-comparable with diversity in most cases, but are to some degree correlated (Pearson = 0.54, p = 0.10, n = 10). These results do show that different interactions occur between environment and richness and environment and diversity, with the topography and environment variables measured in this study affecting evenness/dominance more than they affect absolute species richness.

4.2.2.1.4 Analysis of categorical environmental variables

It would be beneficial to also use the categorical variables to examine possible relationships between the diversity measured in the field and the categorical landscape feature variables. However, there is not a technique available that provides a statistically sound results given the type of data and number of data points. Spearman's rank test is not valid as the landscape features are nominal and not ordinal categories (whilst you can order some variables like valley -> slope, it is questionable as to where a pass might fit in the order). Alternatively, chi-square contingency tests could be applied, but the number of data points (10) means that some boxes in the contingency table will have missing values, invalidating the result. For these reasons the categorical data are not statistically analysed in terms of relationships with diversity.

The multi-scale fuzzy feature classification does however provide a quantitative variable of ridge, channel and planar membership for each plot. Correlations between richness and diversity measures and membership to channel, planar and ridge provide no clear pattern. The fact that greater ridge membership does not necessarily mean greater diversity provides evidence that the categorical variables provide little explanation of diversity patterns.

Greater depth and detail as to the possible explanation of these patterns are left to the conclusions, benefiting from results and discussion from the TBS data.

4.3 Tiputini Biodiversity Station

Having completed the analysis of diversity and compositional patterns in Tambito, the data from TBS is now examined in much the same way.

4.3.1 Composition

4.3.1.1 General Site Species Composition

The ten 25m x 25m plots established in TBS contained 937 individuals, of which 455 different species were identified, distributed in 53 families and 181 genera. Appendix 5 contains a full list of species found in TBS. Taxonomic identification was made to family level for 98.7% of species, to genus level for 76.6% of species, and to species level for 23.1% of species. This significantly lower success rate in terms of species identification is due to the TBS plots having been established after Tambito, leaving less time for post field-work taxonomic identification in the herbarium. As stated before, it is likely that some species as yet unidentified to genus level will be new genera for the plots, and thus the number of different genera is likely an underestimate. Table 24 provides a summary of family composition in Tambito, with Figure 62 and Figure 63 showing the distribution of species and individuals within families.

Family	No. Genera	No. Individuals	No. Species	No. Plots
Anacardiaceae	4	6	6	5
Annonaceae	7	19	16	9
Apocynaceae	4	4	4	3
Aquifoliaceae	1	2	2	1
Araliaceae	1	4	2	3
Arecaceae	7	50	9	9
Bignoniaceae	3	7	4	4
Bixaceae	1	1	1	1
Bombacaceae	4	33	10	10
Boraginaceae	1	2	2	2
Burseraceae	3	22	16	9
Capparaceae	1	1	1	1
Caricaceae	1	2	1	2
Cecropiaceae	3	28	15	9
Celastraceae	1	2	2	2
Chrysobalanaceae	3	26	11	9
Clusiaceae	3	6	5	4
Dichapetalaceae	1	2	2	2
Ebenaceae	1	1	1	1
Elaeocarpaceae	1	10	6	6
Euphorbiaceae	14	24	17	9
Fabaceae	15	173	79	10
Flacourteaceae	9	13	12	8
Humiriaceae	1	2	2	2
Icacinaceae	1	2	2	2
Lauraceae	7	46	33	10
Lecythidaceae	4	22	9	8
Malpighiaceae	1	1	1	1
Melastomataceae	3	16	11	5
Meliaceae	4	42	16	7
Menispermaceae	1	3	2	2
Moraceae	12	111	30	10
Myristicaceae	4	22	14	10
Myrsinaceae	3	6	3	4
Myrtaceae	3	25	24	9
Nyctaginaceae	1	10	3	4
Ochnaceae	1	2	1	2
Olacaceae	1	4	3	3
Piperaceae	1	3	1	1
Polygonaceae	2	8	3	5
Proteaceae	1	1	1	1
Rubiaceae	13	38	24	9
Sapindaceae	2	4	4	3
Sapotaceae	5	30	19	9
Simaroubaceae	1	1	1	1
Staphyliaceae	1	1	1	1
Sterculiaceae	3	7	4	2
Styracaceae	1	1	1	1
Theoprastinaceae	1	1	1	1
Tiliaceae	3	3	3	1
Ulmaceae	2	4	3	3
Violaceae	3	20	4	8
Vochysiaceae	2	3	2	2
Other	4	60	5	3
Total	**181**	**937**	**455**	**AVG (4.6)**

Table 24 Summary of species composition in TBS

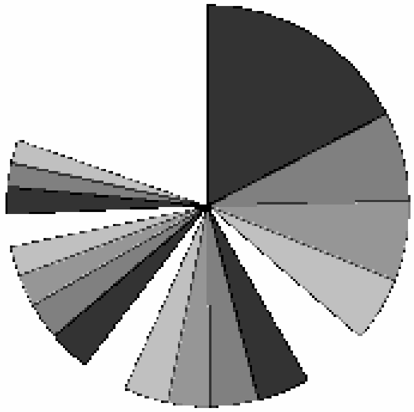


Figure 62 Distribution of species in families in TBS

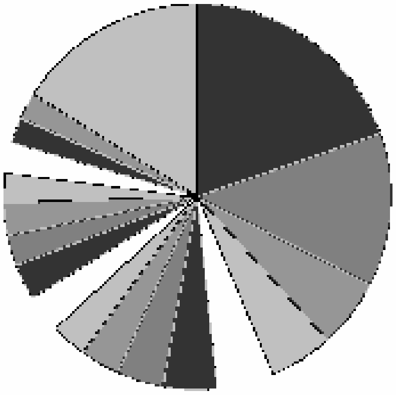


Figure 63 Distribution of individuals in families in TBS

The most abundant families in terms of individuals are Fabaceae (173), Moraceae (111), Arecaceae (50), and Lauraceae (46), with Fabaceae also being the most species rich family (79 species), followed by Lauraceae (33), Moraceae (30) and Myrtaceae (24). Fifty percent of all species are found in seven families, whilst 12 families encountered had just one species present in the plots. The most abundant species were *Sorocea sp.* (Moraceae) with 56 individuals found in just 3 plots, *Browneopsis ucayalina* Huber (Fabaceae) with 37 individuals in 6 plots, *Rinorea viridifolia* Rusby (Violaceae) with 32 individuals found in seven different plots, and *Iriarthea deltoidea* Ruiz & Pavon (Arecaceae) with 25 individuals distributed in seven different plots. Valencia et al. (2004) reports similar family level composition and dominance in these species in a nearby 25-Ha plot in Yasuni (approximately 30km from TBS). The average abundance per species was just 2.1 individuals, and some 309 of the 455 species (68%) having only one individual in the plots.

The taxonomic identification for the TBS collections is less advanced than that of Tambito, and for this reason less species have been classified to date. It is also possible that some collections currently identified as different species will be consolidated into the same species upon further study, so the total number of species may fall. Nevertheless, the plots in TBS contain remarkable levels of diversity.

4.3.1.2 Between-Plot Compositional Variability

4.3.1.2.1 General discussion

Five families were broadly distributed across all plots (Bombacaceae, Fabaceae, Lauraceae, Moraceae, and Myristicaceae), while 12 of the 53 families (22.6%) were found in only one plot. On average a particular family is found in 4.1 plots. At the species level, the most broadly distributed species were *Brownea grandiceps* (Fabaceae), *Rinorea viridifolia*, and *Iriarthea deltoidea* Ruiz & Pavon (Arecaceae) which were found in seven plots, and *Browneopsis ucayalina* (Fabaceae) and *Perebea sp*. (Moraceae) which were found in six different plots. Some 363 of the 455 species (79.8%) were found in only one plot, likely indicating that the 25m x 25m plots only capture a tiny sub-sample of the total diversity to be found in the region.

This is strongly reflected in the species-area curves (Figure 64), where the trend of species accumulation with increasing area is practically linear in all plots. This indicates that the plots are not saturating at a representative value of alpha diversity, and thus the plot richness and diversity is just a sub-sample of the likely alpha diversity in the region.

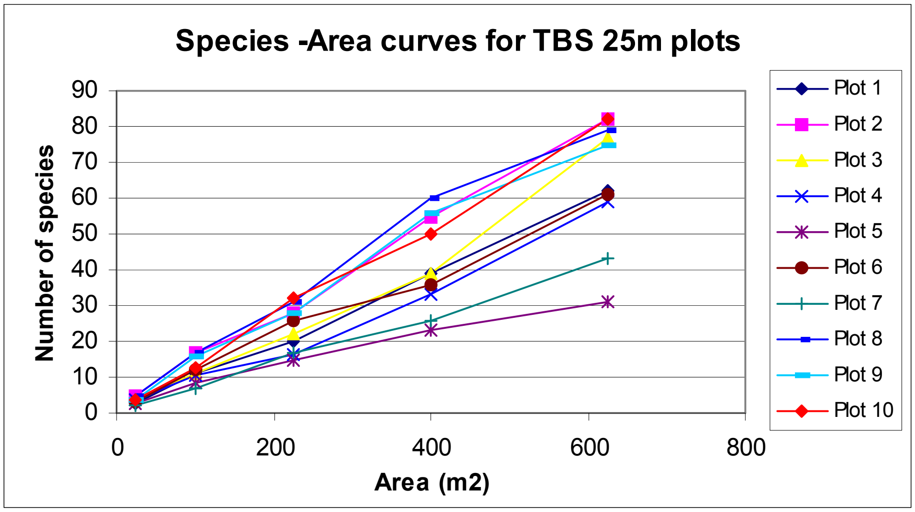
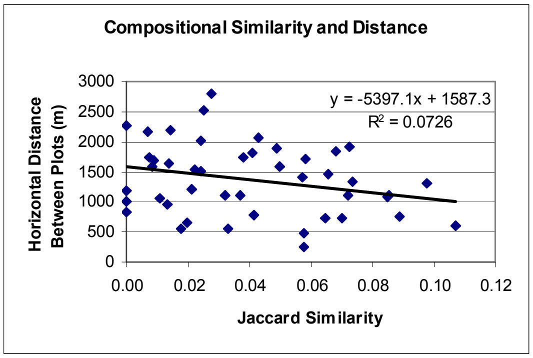
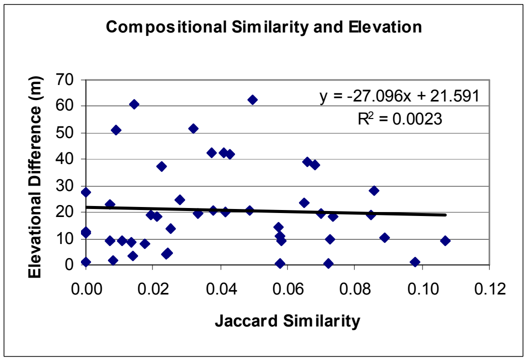


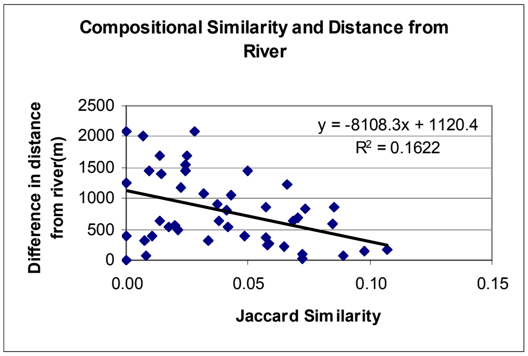
Figure 64 Species-area curves for TBS.

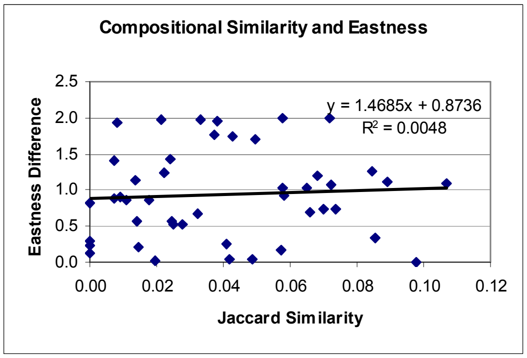
4.3.1.2.2 Single-variate analysis of quantitative environmental variables

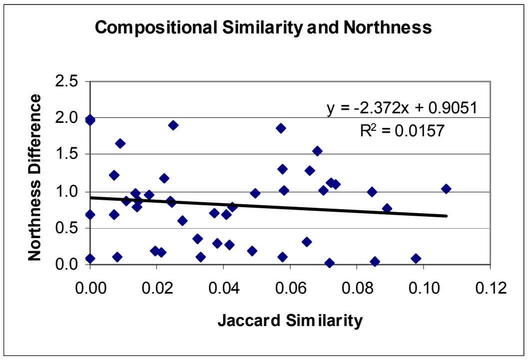
As performed in Tambito, plot compositional similarity is compared with environmental difference using scattergrams and Mantel statistics. This is done using each DEM, so two sets of results are shown (for the TOPODEM Figure 65 and Table 25, and for the SRTM DEM Figure 66 and Table 26). The average elevation value for each plot was collected using GPS, rather than extracted from the DEM. For this reason the same result is achieved regardless of the DEM used. In addition to the terrain derivatives, distance from river was also used as an indicator of potential flood frequency, and also to a certain extent the age of forest. Satellite images over the region show some evidence of past river courses, and indicate that river channels may migrate rapidly in the region. An approximation of the speed of lateral river migration was made based on comparison of historic air photography and recent satellite imagery and approximated at 1-4m per year in flat areas (Mark Mulligan, personal communication). Under this logic, it is more probable that regions far from the main Tiputini River contain older forest and soils.

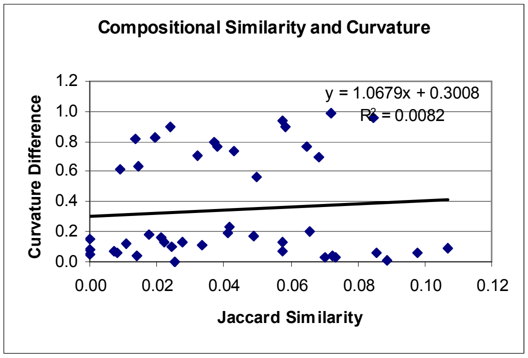

Compositional Similarity and Distance

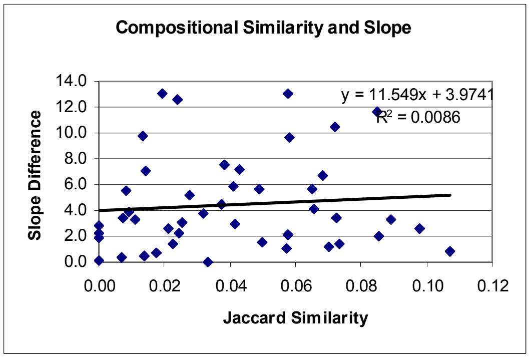

Compositional Similarity and Elevation

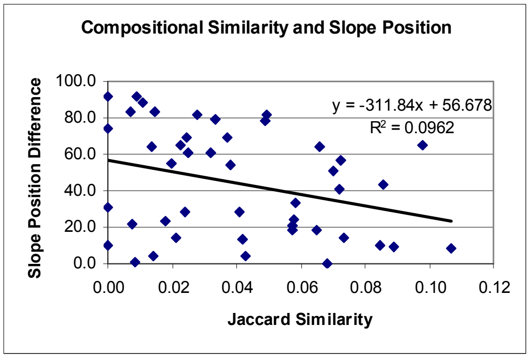

Compositional Similarity and Distance from River


Compositional Similarity and Eastness


Compositional Similarity and Northness


Compositional Similarity and Curvature


Compositional Similarity and Slope


Compositional Similarity and Slope Position

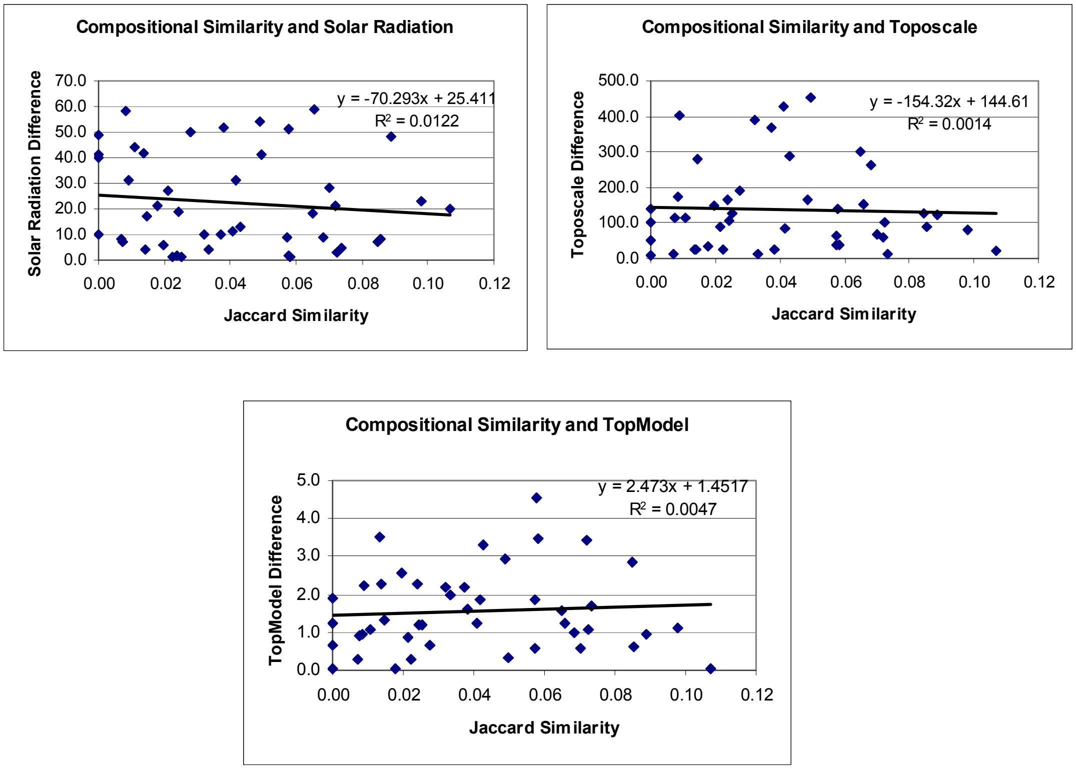
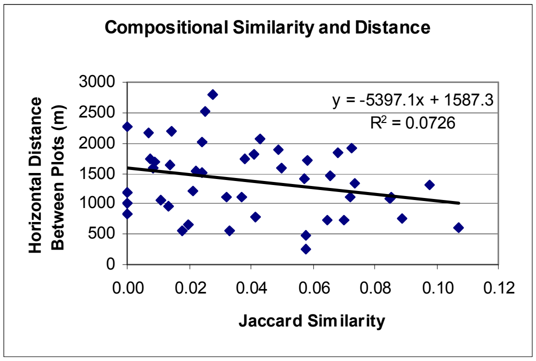


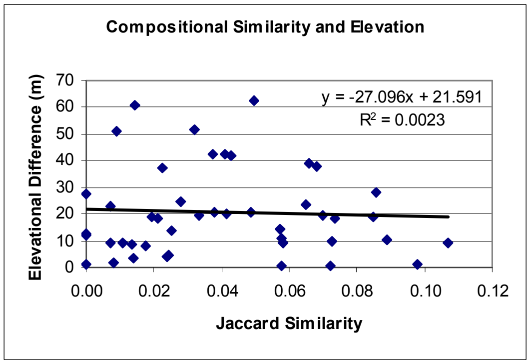
Figure 65 Scatterplots for plot-pairs of compositional similarity (measured with the Jaccard coefficient) and environmental distance (in this case the difference, i.e. dissimilarity) derived from the TOPO DEM.

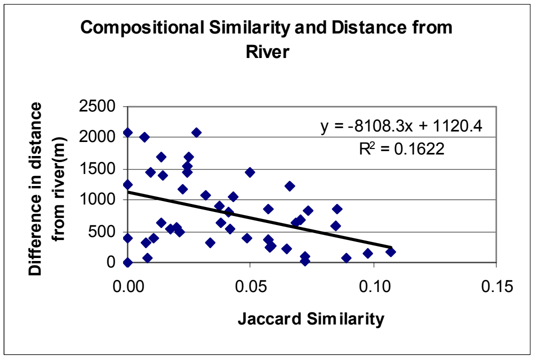
Variable	Mantel Test	One-tailed p-value	Correlation (alpha = 0.05)
Distance	-0.27	0.079	Not-significant
Distance from River	-0.40	0.041	Significant
Altitude	-0.05	0.408	Not-significant
Eastness	0.07	0.370	Not-significant
Northness	-0.13	0.210	Not-significant
Curvature	0.09	0.376	Not-significant
Slope	0.09	0.374	Not-significant
Slope Position	-0.31	0.017	Significant
Solar Radiation	-0.11	0.248	Not-significant
Toposcale	-0.04	0.400	Not-significant
TopModel	0.07	0.407	Not-significant

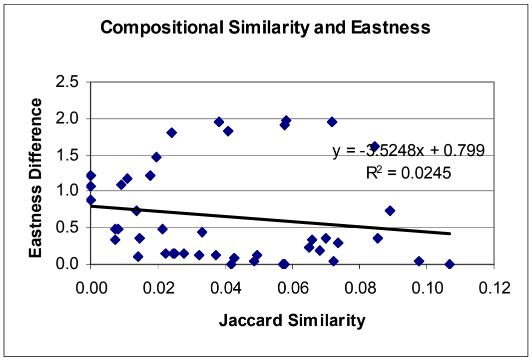
Table 25 Summary results of compositional similarity analysis with distance and environmental variables derived from the TOPO DEM, using Mantel tests and a one-tailed

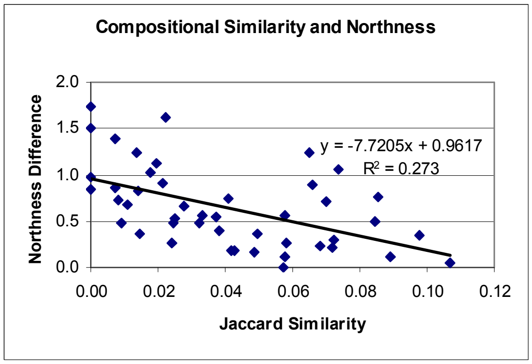
Pearson. Note that compositional similarity was compared with environmental dissimilarity (difference), hence negative values indicate a positive causal relationship.

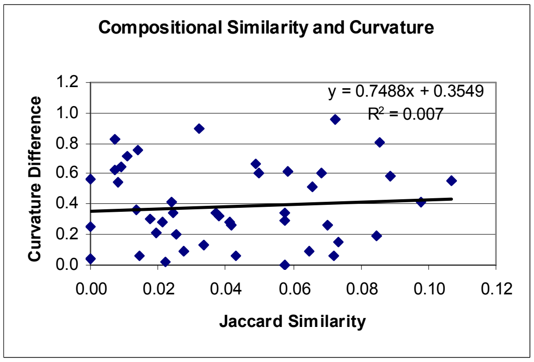


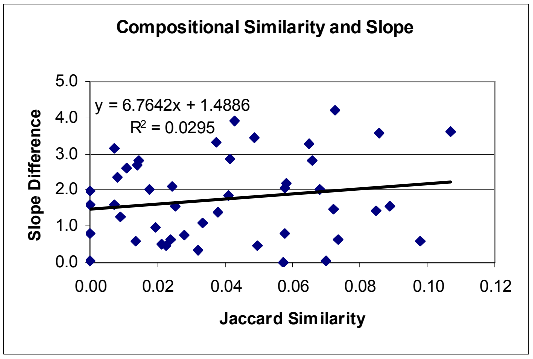


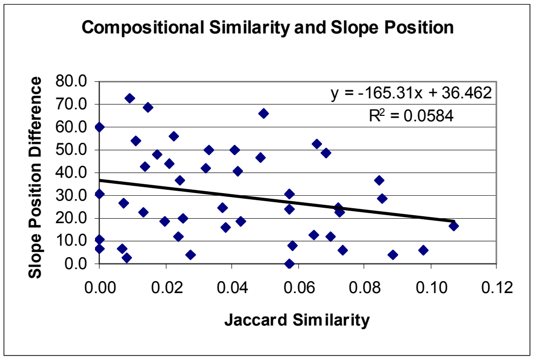












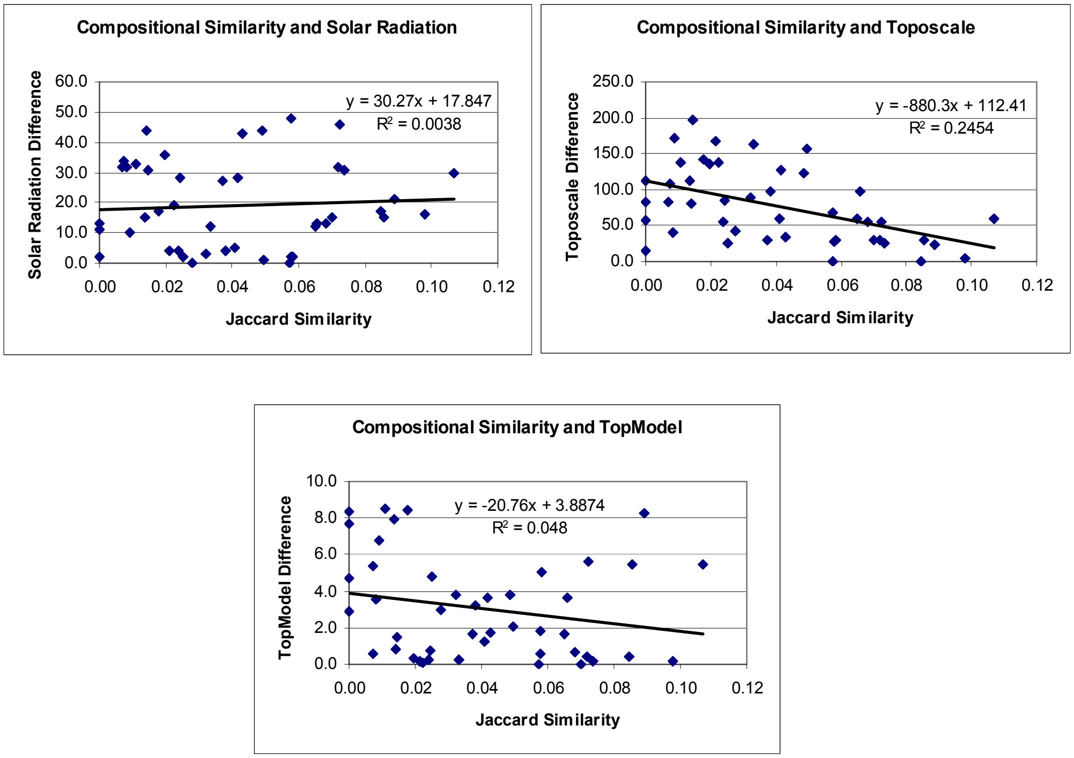


Figure 66 Scatterplots for plot-pairs of compositional similarity (measured with the Jaccard coefficient) and environmental distance (in this case the difference, i.e. dissimilarity) derived from the SRTM DEM.

Variable	Mantel Test	One-tailed p-value	Correlation (alpha = 0.05)
Distance	-0.27	0.092	Not-Significant
Distance from River	-0.40	0.039	Significant
Altitude	-0.05	0.379	Not-Significant
Eastness	-0.16	0.219	Not-Significant
Northness	-0.52	0.007	Significant
Curvature	0.08	0.312	Not-Significant
Slope	0.17	0.130	Not-Significant
Slope Position	-0.24	0.067	Not-Significant
Solar Radiation	0.06	0.417	Not-Significant
Toposcale	-0.50	0.010	Significant
TopModel	-0.22	0.160	Not-Significant

Table 26 Summary results of compositional similarity analysis with distance and environmental variables derived from the SRTM DEM, using Mantel tests and a one-tailed

Pearson. Note that compositional similarity was compared with environmental dissimilarity (difference), hence negative values indicate a positive causal relationship.

The Mantel tests for TBS show significant correlations ($p<0.05$) between environment and composition for distance to river, slope position for the TOPO DEM, and northness and toposcale for the SRTM DEM. Given that no single variable correlates for more than one DEM makes the interpretation of these results problematic and very much dependent upon the data source (see for example the differences in DEM values in Section 3.7 in Chapter 3). Out of 19 correlations between terrain derivatives and composition, four correlate to the 95% confidence limit. At least one of these is expected in a random set of data.

Applying partial Mantel tests on these correlating variables, using distance from river as the third variable indicates that the correlation with slope difference (TOPO DEM) is spurious, but the other two correlations hold (Table 27).

Variable A	Variable B	Partial Variable C	Correlation (A,B)	Correlation (B,C)	Correlation (A,C)	Correlation (A,B) | C	p-value
Compositional similarity	Slope difference (TOPO)	Distance	-0.31	0.49	-0.40	-0.16	0.14
Compositional similarity	Northness (Northness)	Distance	-0.48	0.29	-0.40	-0.44	0.02
Compositional similarity	Toposcale (ASTER)	Distance	-0.47	0.17	-0.40	-0.45	0.01

Table 27 Revised Mantel statistics for correlating variables with compositional similarity in TBS, applying partial Mantel tests to detect spurious correlations derived from co-linearity between variables and the distance from river.

It is interesting to note that Euclidean distance between the plots does not correlate significantly (although a weak trend is evident), but that the difference in the distance to river does correlate. This indicates that broadly-speaking the composition follows a steady gradient from the river-bank to the more "inland" regions. Interpreting this relation is complicated by a number of factors. As already discussed, distance from river is in one sense an indicator of flooding frequency, along with elevation. Regions close to the river are more likely to flood than regions of the same elevation further from the main river channel, although this generalization is complicated by the effect of the network of smaller channels (which during times of high flow become flooded themselves). Though subjective and likely incomplete, an IKONOS image was used to identify the sub-channels within the TBS region (Mark Mulligan, personal communication). The distance of each plot from any type of channel (including the River Tiputini itself) was calculated, and a Mantel test performed on the compositional similarity and the difference in distance from any of these channels (Figure 67).

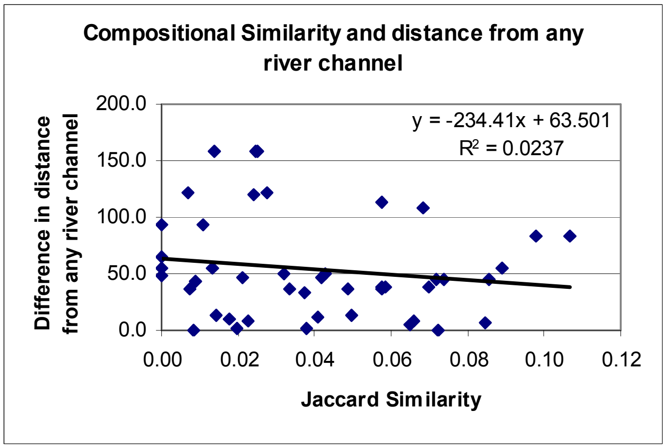


Figure 67 Scatterplot of compositional similarity against the difference in distance from any river channel, using channels identified in an IKONOS image of TBS.

No significant correlation was found between the distance from any river channel (large or small) and compositional similarity (Mantel statistic = -0.154, p = 0.25).

Furthermore, elevation does not correlate significantly with compositional similarity, leading to the conclusion that flooding frequency is not a plausible explanation for the significant correlation between distance from the main river and composition.

In this case, the alternative explanation involves forest age, under the idea that the conditions and forest in those regions further away from the river are in fact “older”. This is plausible, as satellite imagery from the region shows past river courses in the form of oxbow lakes (Figure 68), as well as broader scale re-routing of rivers. If the rivers migrate significantly (supported by Rasanen et al., 1986; Salo et al., 1986), it is probable that the regions closer to the river were more recently river channel than more distant regions.

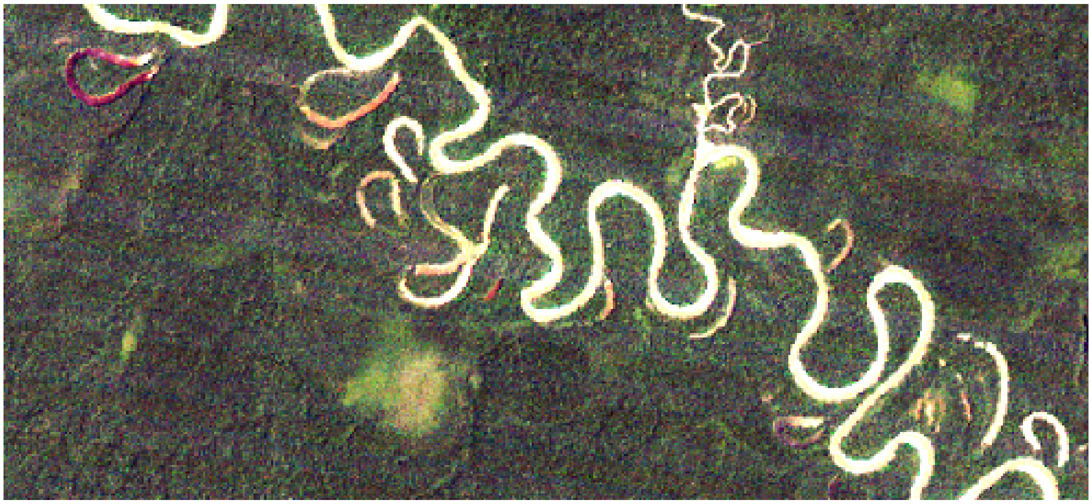


Figure 68 Example of the river migration present in the region, with many oxbow lakes forming where old meanders were cut off. This image is of an area to the south of TBS, taken using LANDSAT TM imagery.

If this is the case, it is unlikely that the compositional pattern is brought about by successional processes, as the time frame involved in river migration is likely to have operated on a longer time-scale, though this cannot be completely excluded from the explanation. However, other indirect and slower effects are likely to be more important. Soils, for instance, are likely to be strongly affected by the time since the site was occupied by a river channel (Huston, 1994). The river is likely to wash away many soil horizons, and subsequently deposit sediments. Once the river moves away from the site, pedogenic processes will commence and the soil will slowly develop. This process of soil evolution will result in differing edaphic conditions (biological, chemical and physical) depending on the time elapsed since the original horizons were washed away by river flow. Given that several studies have shown lowland tropical tree species to have edaphic preferences (for example Clark et al., 1998; Palmiotto et al., 2000; Phillips et al., 2003), the compositional similarity between sites with similar distances from the river may provide indirect evidence that edaphic conditions are important in defining species composition in TBS. Unfortunately no soil data is available for testing this hypothesis, as this thesis is attempting to find readily measurable variables (or surrogates) for explaining the spatial variability in diversity.

Distance to river was not the only variable that correlated with composition. Table 27 confirms that northness (SRTM) and toposcale (SRTM) correlate independently of distance from river.

The significant correlation between the difference in northness (SRTM) and toposcale (SRTM) are only significant for the SRTM DEM, where the cell size limits the accuracy of the terrain characteristic, especially for toposcale. The micro-scale topographic variation is not picked up by SRTM, meaning that the toposcale pixel value over the plot is unlikely to reflect the actual plot conditions. The significance of northness in TBS is somewhat weak, with the low slopes unlikely to produce much variation in solar radiation around the study site, and the dominant wind direction form the south-east and east means that northness is not the strongest indicator of exposure to wind. Furthermore, the correlation with northness shows no correlation at all for other DEMs, providing little confidence in the significance of this result.

4.3.1.2.3 Multi-variate analysis of quantitative environmental variables

Taking a multi-variate approach once more, all nine quantitative terrain and environment variables are subjected to an agglomerative hierarchical clustering analysis for each of the three DEMs, producing a dendrogram of plot similarity (Figure 69, and Figure 70), and an associated multi-variate dissimilarity matrix. The difference in the dendrograms for each DEM is alarming, and is yet another indication that the DEMs themselves are very different and that the analyses for TBS are significantly more subjective due to problems with DEM quality. When the dissimilarity matrix is compared with compositional similarity using the Mantel statistic, no significant correlations are found for either of the DEMs ($\text{Mantel}_{\text{TOPO}}$ = 0.18, and $\text{Mantel}_{\text{SRTM}}$ = 0.22, $p>0.05$ in both cases).

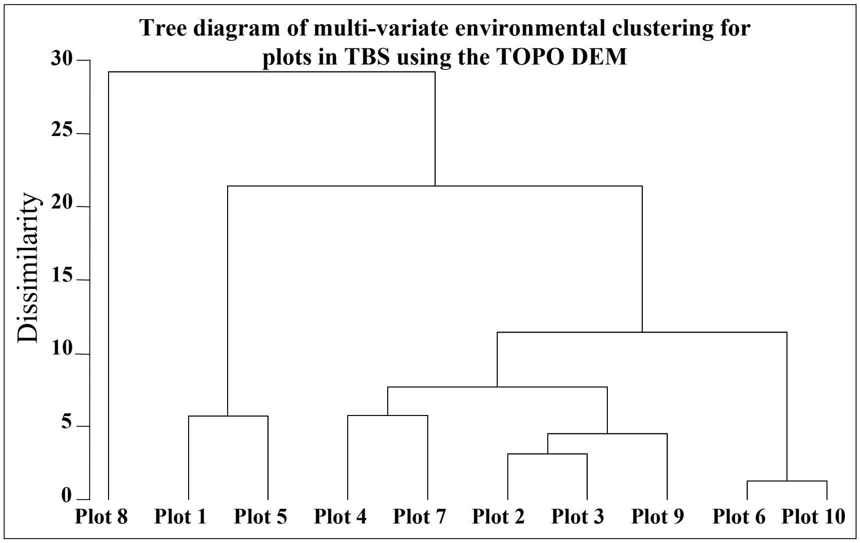


Figure 69 Multi-variate clustering of plots based on all 9 environmental and topographic variables for TBS using the TOPO DEM.

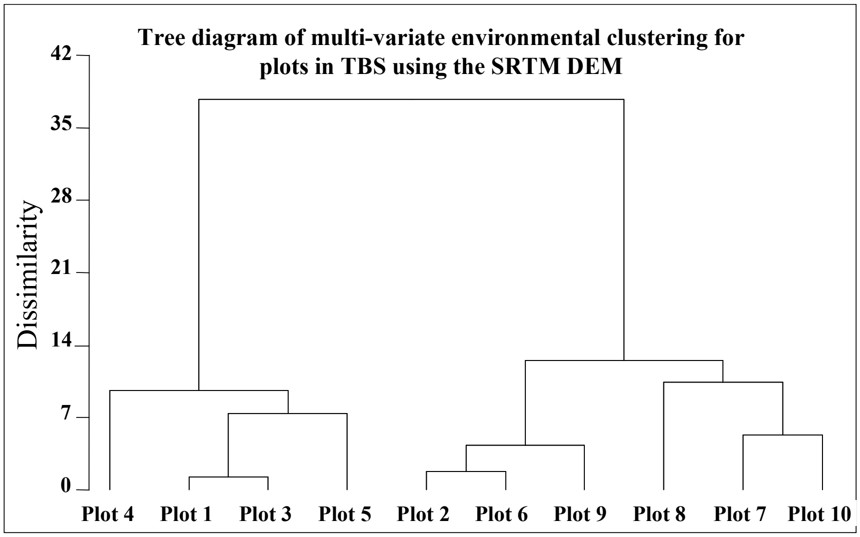


Figure 70 Multi-variate clustering of plots based on all 9 environmental and topographic variables for TBS using the SRTM DEM.

Multiple stepwise linear regressions do however produce some interesting results. When applied to the compositional similarity and environmental difference data for each plot pair, no additional variables outside of distance from river explain the compositional variability when the TOPO DEM is used. However, for the SRTM DEM four variables together explain 52% of the variability in composition, starting with northness (23%), toposcale (a further 13%), distance from river (a further 7%) and elevation (a further 9%) (Jaccard Similarity = 0.076 –0.0189Northness Difference$_{SRTM}$ –0.00026Toposcale Difference$_{SRTM}$ –0.00002Difference in Distance from River + 0.0006Altitudinal difference, R^2 = 0.52, n = 45). When the modeled similarity is plotted against the measured similarity (Figure 71), the greatest errors in predicted compositional similarity occur in modelled high levels of similarity, where there are cases of vast over- and under- estimate of the measured similarity.

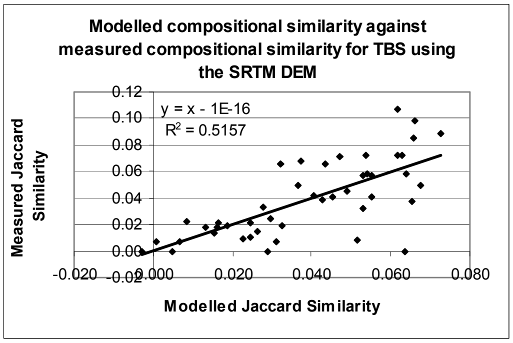


Figure 71 Modelled similarity against the measured similarity applying the results of the multiple stepwise linear regression for the variables of the SRTM DEM.

Extreme caution is urged in trusting the causal significance of the multiple linear regressions, and no concrete conclusions can be derived of these without validation plots.

4.3.1.2.4 Analysis of categorical environmental variables

Finally for the analysis of composition, the restriction of species to landscape classes is analysed using the same methodology presented for Tambito using species distribution restrictions to individual landscape classes (Table 28,Table 29 and Table 30).

Feature	No. Plots	No. Species Restricted to feature	No. species restricted to feature only for species distributed in more than 1 plot
Planar (TOPO)	6	243	30
Planar (SRTM)	5	192	11
Ridge (TOPO)	3	125	3
Ridge (SRTM)	3	133	9
Channel (TOPO)	1	27	0
Channel (SRTM)	2	60	1

Table 28 Number of species associated to specific classes in the "Feature" classification for TBS.

Network Feature	No. Plots	No. Species Restricted to feature	No. Species Restricted to feature for species distributed in more than 1 plot
Planar (TOPO)	3	119	7
Pass (SRTM)	1	44	0
Peak (SRTM)	2	58	1
Ridge (TOPO)	3	125	3
Ridge (SRTM)	4	184	19
Channel (TOPO)	4	133	3
Channel (SRTM)	2	53	0
Pit (SRTM)	1	45	0

Table 29 Number of species associated to specific classes in the "Network Feature" classification for TBS.

Topoclass	No. Plots	No. Species Restricted to feature	No. Species Restricted to feature for species distributed in more than 1 plot
Valley Bottom (TOPO)	1	45	0
Valley Bottom (SRTM)	2	50	5
Toe Slope (TOPO)	4	136	12
Toe Slope (SRTM)	5	217	16
Slope (TOPO)	4	155	7
Slope (SRTM)	3	125	7
Ridge (TOPO)	1	47	0

Table 30 Number of species associated to specific classes in the "topoclass" classification for TBS.

Some 363 of the 455 species were found only in one plot, leaving just 92 species for examination of restriction to a single landscape class. As already discovered for Tambito, very few of these species are shown to be restricted to particular landscape classes. The greatest restriction occurs using the TOPO DEM and the feature classification, with 36% of the 92 species restricted to landscape classes, and the majority are restricted to planar landscapes. The network feature classification shows the least landscape feature association, with the topoclass variable (a derivative of toposcale which has been shown to be significant in defining compositional similarity between plots) showing moderate habitat association in species composition using the SRTM DEM, with 28 of the 92 species showing restrictions in their distributions (30%). In none of these cases was there a single family showing more habitat association than any other.

Though some habitat association is evident, this cannot be considered significant and may simply be a product of the low densities in the species distributions and the related problems associated with the small size of plots used in this study.

4.3.2 Diversity

4.3.2.1.1 General discussion

Once again, significant variation in diversity is found between-plots, with species richness ranging from 31 (plot 5) to an astonishing 82 (plots 2 and 10) (Table 31). On average there were 24 families per plot (ranging from 14 to 28), and 35 genera (ranging from 12 to 49). Similarly for Tambito, Renyi diversity plots are used to aid the discussion on diversity patterns between plots in TBS (Figure 72).

Plot	No. of Individuals	No. Families	No. Genera	No. Species	No. Endemic Species	Simpson's	Shannon's	Margalef	Menhinick	Berger-Parker
1	80	26	36	62	44	0.99	4.01	13.96	6.98	0.06
2	132	24	36	82	44	0.98	4.09	16.75	7.31	0.14
3	95	24	35	77	40	0.99	4.24	16.69	7.90	0.05
4	101	25	29	59	29	0.95	3.60	12.59	5.90	0.21
5	88	14	12	31	15	0.84	2.58	6.70	3.30	0.38
6	90	25	35	61	25	0.98	3.87	13.33	6.43	0.12
7	66	21	33	43	28	0.98	3.56	10.06	5.33	0.09
8	103	28	49	79	49	0.99	4.25	16.86	7.82	0.06
9	95	27	49	75	40	0.99	4.11	16.25	7.69	0.09
10	97	26	34	82	49	0.99	4.31	17.75	8.37	0.06

Table 31 Richness and diversity of plots in TBS

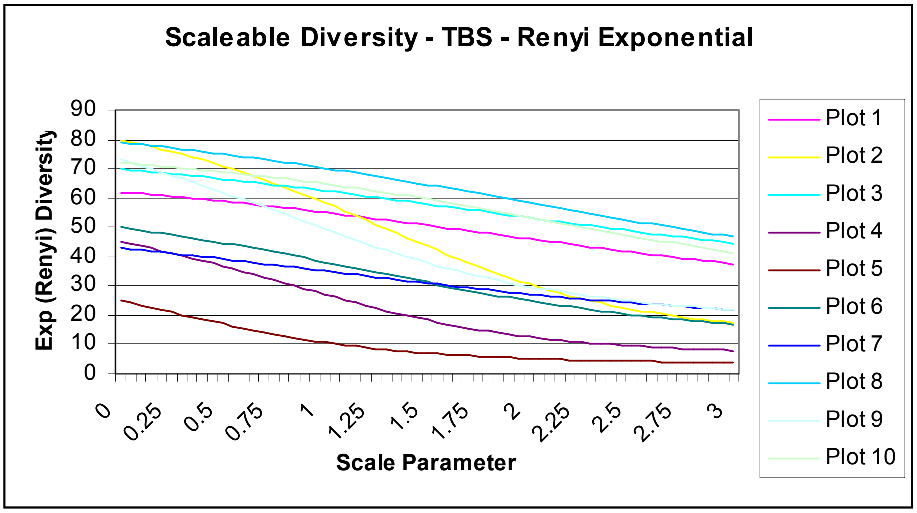


Figure 72 The Renyi scaleable diversity index for TBS, indicating to what extent plot diversities can be universally compared

Plot 5 is the least diverse plot in all aspects by a considerable margin, having high levels of dominance (33 individuals of *Sorocea sp.* (Moraceae)), and very low species richness (31 species). This plot was located immediately next to the main river channel, with strong evidence of regular flooding. Plot 4 is also low in diversity (and is also close to the river where flooding is likely to occur frequently), though it is comparatively more species rich (59 species) than plot 7 (just 43 species). Plot 8 is both the most species rich and the most diverse plot (and is also positioned at the highest elevation), whilst plot 2 has high species richness but relatively low diversity due to high levels of dominance of *Browneopsis ucayalina* (18 individuals). Also worthy of note is plot 9, with high species richness (75 species) but comparably low diversity due to some dominance of *Licania glablanca* (Chrysobolanaceae) (9 individuals). The many shapes of the curves in the Renyi diversity plot shows that not only are there very different levels of diversity around the TBS region, but that also the structure of diversity is also variable (i.e. species richness vs. evenness/dominance is variable).

4.3.2.1.2 Single-variate analysis of quantitative environmental variables

Exploring the potential drivers of this variation in richness and diversity, Table 32 presents the environmental conditions at each plot using each of the DEMs. On the whole the plots cover a complete range of environmental conditions, with a good distribution of points in all the variables, as a result of the more formal sampling strategy that was adopted compared to Tambito (see Chapter 3, Section 3.5.1). There is a great deal of variation between the topographic conditions for each plot depending on the DEM used, so interpretation of the patterns is somewhat confused by DEM quality, and any results must be analysed with caution.

Plot	Altitude (m)	Eastness	Northness	Mean Curvature	Slope	Slope Position	Solar Radiation	TopMod	Toposcale
1	203	-0.95	-0.31	-0.18	6.66	18	9592	11.76	-142.92
2	219	-1.00	-0.03	-0.06	3.62	35	9629	11.40	-50.00
3	210	0.08	1.00	-0.10	4.50	39	9648	11.28	-81.46
4	201	0.99	0.11	0.09	2.49	16	9652	9.57	10.62
5	198	-0.41	-0.91	-0.09	3.49	0	9621	16.26	-75.85
6	220	-0.99	-0.12	0.05	1.06	96	9651	12.37	20.85
7	219	0.96	0.28	-0.11	12.90	58	9639	10.40	-23.85
8	262	0.99	0.13	0.42	11.92	100	9638	9.07	257.46
9	238	-0.27	0.96	0.02	2.38	85	9659	12.47	6.23
10	224	-0.48	-0.87	0.10	1.15	100	9646	11.45	54.92

Plot	Altitude (m)	Eastness	Northness	Mean Curvature	Slope	Slope Position	Solar Radiation	TopMod	Toposcale
1	203	-0.99	-0.13	-0.12	1.25	22	9652	12.75	-120
2	219	-1.00	0.05	0.05	4.10	63	9624	9.07	19
3	210	-1.00	0.00	-0.09	0.46	46	9654	14.55	-185
4	201	-0.51	-0.86	-0.08	3.60	19	9620	9.20	-60
5	198	0.23	-0.97	-0.15	2.06	15	9641	17.47	-149
6	220	-0.95	-0.30	0.09	4.69	69	9608	8.94	158
7	219	0.96	0.26	0.04	2.64	38	9656	9.51	79
8	262	-0.39	-0.92	0.10	1.77	81	9642	9.92	119
9	238	-0.65	0.76	0.05	4.05	75	9639	9.08	59
10	224	-0.94	0.34	0.06	1.81	26	9650	9.89	39

Table 32 Environmental and topographic conditions at each plot in TBS using each DEM (TOPO DEM top, SRTM DEM, below).

Similarly for Tambito, the various richness and diversity measures are correlated with each environmental and topographic variable in the search for patterns in the data. Each analysis is separated for each DEM (Table 33, and Table 34).

Pearson's Correlation Coefficient	Elevation	Eastness	Northness	Curvature	Slope	Slope Position	Solar Radiation	Topmodel	Toposcale
Family Richness	0.57	0.05	0.40	0.47	0.00	0.60	0.26	-0.73	0.44
Genera Richness	0.80	0.13	0.59	0.47	0.25	0.68	0.29	-0.63	0.51
Species Richness	0.54	-0.15	0.33	0.40	-0.18	0.53	0.28	-0.52	0.36
Endemic Species	0.55	-0.05	0.19	0.33	0.14	0.44	-0.05	-0.57	0.33
Simpson's	0.49	0.04	0.48	0.21	0.18	0.60	0.22	-0.74	0.25
Shannon's	0.55	-0.07	0.42	0.32	0.01	0.61	0.24	-0.65	0.32
Margalef	0.55	-0.13	0.36	0.38	-0.15	0.56	0.28	-0.54	0.35
Menhinick	0.55	-0.10	0.38	0.34	-0.08	0.60	0.26	-0.57	0.33
Berger-Parker	-0.51	-0.05	-0.46	-0.18	-0.28	-0.61	-0.13	0.68	-0.25

p-value	Elevation	Eastness	Northness	Curvature	Slope	Slope Position	Solar Radiation	Topmodel	Toposcale
Family Richness	0.08	0.89	0.25	0.17	0.99	0.07	0.47	0.02	0.20
Genera Richness	0.01	0.72	0.07	0.18	0.49	0.03	0.41	0.05	0.13
Species Richness	0.11	0.68	0.34	0.26	0.61	0.12	0.43	0.13	0.30
Endemic Species	0.10	0.88	0.59	0.35	0.71	0.21	0.89	0.09	0.35
Simpson's	0.15	0.92	0.16	0.57	0.63	0.07	0.55	0.01	0.48
Shannon's	0.10	0.85	0.22	0.37	0.98	0.06	0.51	0.04	0.36
Margalef	0.10	0.72	0.31	0.28	0.69	0.09	0.44	0.11	0.31
Menhinick	0.10	0.78	0.27	0.34	0.82	0.07	0.47	0.09	0.35
Berger-Parker	0.13	0.88	0.18	0.62	0.43	0.06	0.72	0.03	0.49

Table 33 Pearson's correlation coefficient and the two-tailed p-value between richness and diversity in each plot and the environmental variables for TBS using the TOPO DEM.

Pearson's Correlation Coefficient	Elevation	Eastness	Northness	Curvature	Slope	Slope Position	Solar Radiation	Topmodel	Toposcale
Family Richness	0.57	-0.60	0.32	0.54	0.10	0.52	-0.10	-0.69	0.43
Genera Richness	0.80	-0.34	0.44	0.66	0.12	0.77	0.04	-0.65	0.54
Species Richness	0.54	-0.74	0.39	0.50	-0.02	0.54	-0.03	-0.47	0.24
Endemic Species	0.55	-0.55	0.38	0.39	-0.29	0.35	0.31	-0.37	0.16
Simpson's	0.49	-0.44	0.55	0.56	-0.03	0.48	0.12	-0.65	0.41
Shannon's	0.55	-0.64	0.50	0.54	-0.08	0.53	0.10	-0.56	0.32
Margalef	0.55	-0.72	0.43	0.51	-0.06	0.53	0.03	-0.48	0.25
Menhinick	0.55	-0.68	0.50	0.50	-0.13	0.50	0.12	-0.48	0.26
Berger-Parker	-0.51	0.37	-0.56	-0.50	0.21	-0.44	-0.32	0.50	-0.34

p-value	Elevation	Eastness	Northness	Curvature	Slope	Slope Position	Solar Radiation	Topmodel	Toposcale
Family Richness	0.08	0.07	0.36	0.11	0.78	0.12	0.77	0.03	0.21
Genera Richness	0.01	0.33	0.20	0.04	0.74	0.01	0.91	0.04	0.10
Species Richness	0.11	0.01	0.27	0.14	0.96	0.11	0.92	0.17	0.50
Endemic Species	0.10	0.10	0.27	0.26	0.42	0.32	0.38	0.29	0.66
Simpson's	0.15	0.20	0.10	0.09	0.94	0.16	0.73	0.04	0.24
Shannon's	0.10	0.05	0.14	0.10	0.82	0.12	0.79	0.09	0.36
Margalef	0.10	0.02	0.21	0.13	0.87	0.12	0.94	0.16	0.49
Menhinick	0.10	0.03	0.14	0.14	0.73	0.15	0.73	0.16	0.47
Berger-Parker	0.13	0.30	0.09	0.14	0.55	0.20	0.37	0.14	0.33

Table 34 Pearson's correlation coefficient and the two-tailed p-value between richness and diversity in each plot and the environmental variables for TBS using the SRTM DEM.

A number of interesting correlations are found between richness and diversity and the topographic variables. Elevation itself correlates with a high significance level (99%) for genera richness, and also non-significant but general trends of an increase in diversity with greater elevation for all other richness and diversity measures (p values in all cases < 0.15) (Figure 73).

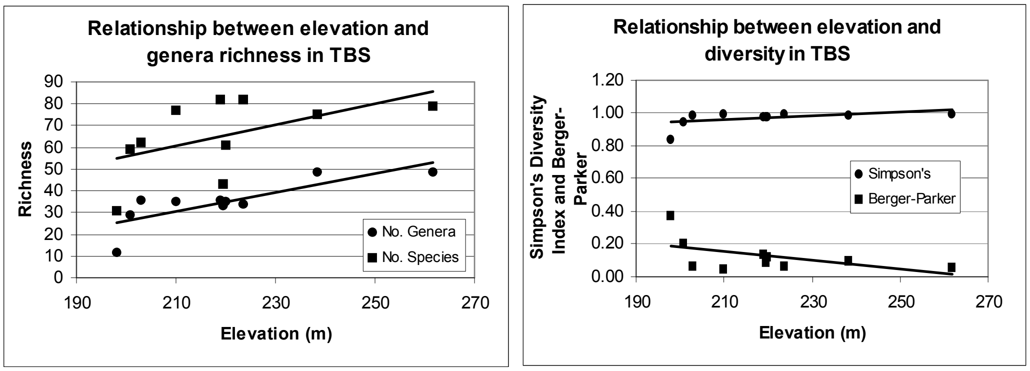


Figure 73 Elevational patterns in richness and diversity in TBS.

In many cases, the pattern of diversity and richness variation with elevation is non-linear, with the two lowest elevation plots (plot 5 and plot 4) having significantly lower diversity (Simpson's of 0.84 and 0.95 respectively) and high levels of dominance (Berger-Parker of 0.38 and 0.21 respectively). Plots above the 210 m elevation mark (the remaining plots except plot 1) on the whole have greater diversity (Simpson's diversity average of 0.99), though it is highly variable and not correlated with elevation (Simpson's diversity correlation $R^2 = 0.02$). The elevational gradient in TBS is so small (60 vertical metres) that climatic differences will be insignificant in this case. It is more likely that this pattern occurs as a result of flooding frequency or forest and soil age. Plots below 210m are frequently flooded, interrupting the successional process and favouring a few species well adapted to regular flooding. The high levels of dominance found in plots 4 and 5 provide further evidence that this is the case, with prevalence of *Sorocea sp.* in both plots (21 and 33 individuals respectively). This species was only found in one other plot (plot 6, 220m), with just 2 individuals.

If flooding is an important factor in defining the diversity, it is also important for examining the relationship between diversity and richness and the distance from the River Tiputini (Figure 74), which is another important factor when examining flooding frequency. Plots with low diversity are also close to the river, with the exception of plot 1 with mid-levels of diversity and which is just 46m from the river. However, this plot is some 10m above the normal river level, and so floods less frequently. Eliminating the plots closest to the river (plots 1, 4, and 5), there is no relationship between distance from river and diversity (Simpson's Index correlation $R^2 = 0.15$). These patterns in richness and diversity with respect to elevation and distance from river indicate that low diversity (specifically high dominance) is expected in regions frequently flooded. However, there is no clear pattern (linear or non-linear) between diversity and richness with elevation and distance from river for plots that are not frequently flooded. This indicates that other factors are likely responsible for shaping the variation in diversity observed in the plot data.

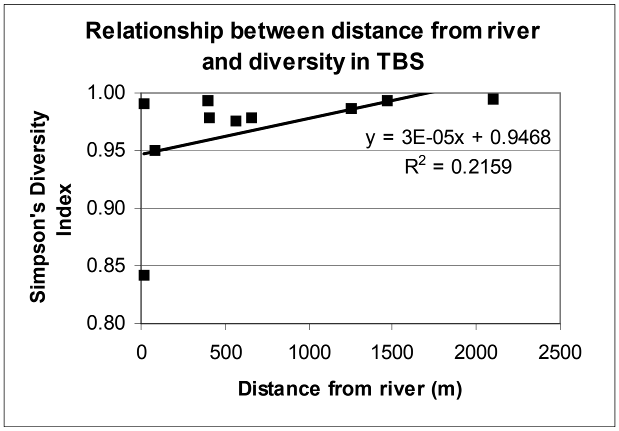


Figure 74 Relationship between diversity and distance from the River Tiputini in TBS

In general terms, the SRTM DEM provides the greatest number of correlations, despite having a much larger cell size which is unlikely to capture meso-scale variability.

In terms of variables, TopModel correlates best with diversity and richness (less wetness, greater diversity), though in all cases this relationship is highly dependent on the high wetness and low diversity found in plot 5. Exclusion of plot 5 from the correlation renders the correlation insignificant for all richness and diversity measures in both DEMs. After TopModel, the slope position variable correlates positively with genera diversity (i.e. higher up the slope higher the richness), though this is likely due to co-linearity with elevation (Pearson = 0.81, p = 0.004, n = 10), and likewise probably an effect of flooding frequency in low slope positions. Indeed, with the exclusion of plot 5 once more (identified as having low diversity due to frequent flooding), the correlation falls apart for the TOPO DEM, but is maintained for the SRTM DEM (Pearson and corresponding p-value unchanged) (Figure 75). Though the relationship appears solid, there is actually very little variation in genera richness in mid-slopes (slope position 20 – 70) where all plots have 34 – 37 genera present. The only other correlating variable is mean curvature using the SRTM DEM, which correlates positively with genera diversity (i.e. convex slopes have higher richness). Once again, mean curvature correlates highly significantly with elevation (Pearson = 0.79, p = 0.006, n = 10), and so this is not a new relationship but one brought about by the same pattern identified between elevation and slope position.

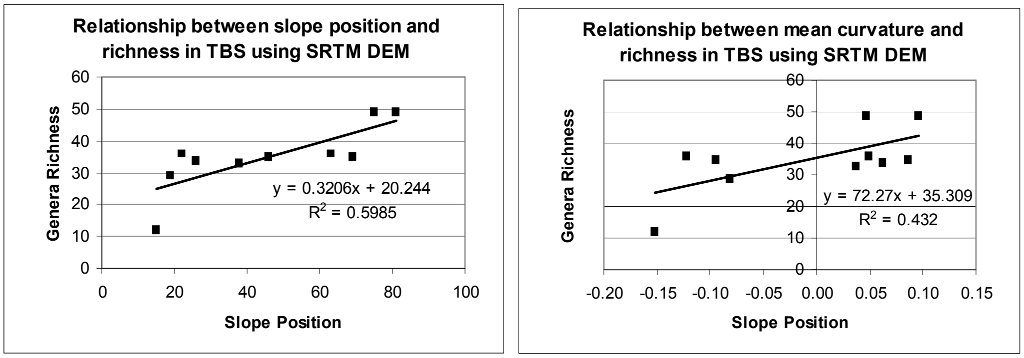


Figure 75 Relationship between slope position and mean curvature and genera richness in TBS using the SRTM DEM

All the correlations identified between genera richness and elevation, mean curvature and slope position appear to originate from the same pattern, but it is unclear where the causal relationship lies. In any case, these correlations only exist for genera richness, where in the mid-elevations, mid slope positions and mid-curvature levels no clear pattern is evident (only in the extremes for plots 4 and 5 and plots 8 and 9).

4.3.2.1.3 Multi-variate analysis of quantitative environmental variables

Multiple stepwise regression is once again applied to the data in order to identify multiple environmental interactions, and quantify the variability in diversity that is explainable through the topographic and environmental variables used in this study. For the TOPO DEM, topmodel and eastness combine to predict 78% of the variability in Simpson's diversity ($D = -0.025\ \mathrm{TopMod}_{\mathrm{TOPO}} - 0.033\ \mathrm{Eastness}_{\mathrm{TOPO}} + 1.26$, $R^2 = 0.78$, $n = 10$), but this relationship is highly dependent on the high wetness found in plot 5, and indeed the relationship collapses if plot 5 is excluded from the regression ($R^2 = 0.001$, $n = 9$). When plot 5 is excluded from the regression, no significant multiple regressions are found. It is a similar story when the variables from the SRTM DEM are analysed, with TopModel, slope and eastness explaining some 85% of the variability (D = 1.20 -1.679TopModel$_{SRTM}$ –0.023Slope$_{SRTM}$ – 0.022Eastness$_{SRTM}$, $R^2 = 0.85$, n =10), but this relationship once again collapses with the exclusion of plot 5 ($R^2 = 0.17$, n = 9), and when the analysis is preformed once more excluding plot 5, no significant multiple stepwise regressions are found.

When species richness is examined using multiple stepwise regression, no patterns are found using the TOPO DEM, but the SRTM DEM does predict species richness, accounting for 82% of the variability using eastness (55%) and elevation (a further 27%) (Species Richness = -48.35 - 19.32Eastness$_{SRTM}$ + 0.47Elevation$_{SRTM}$, R^2 = 0.82, n = 10). This relationship is not particularly dependent on any single plot richness, and is shown in Figure 76.

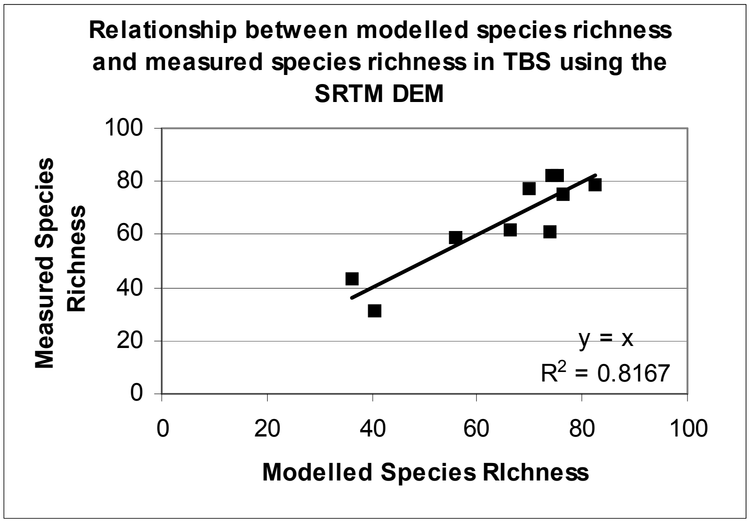


Figure 76 Modelled species richness (based on multiple stepwise regression) plotted against measured diversity in TBS using the SRTM DEM.

Under this model, highest species richness is found in west facing higher elevation slopes. Higher elevation slopes may be important in generating diversity due to lower frequency of flooding. Plots 4 and 5 (the two regularly flooded plots) showed high levels of dominance and resultant low diversity, and this is attributed to flooding earlier in this chapter. Furthermore some evidence exists that the distance from the river (co-linear with elevation) is important in defining composition, and it is hypothesized that this may in reality represent an edaphic gradient (section 4.3.1.2). These two factors may be at play in generating the trend of higher diversity in high elevation slopes.

The significance of eastness in generating diversity in TBS is attributable to a number of factors. Firstly, the wind direction is predominantly easterly in TBS, leading to believe that wind may be an important factor to consider, although the mechanism for such a relationship is unclear. Exposure to wind generates a higher probability of tree falls, though slope is also important in generating higher levels of tree falls and no relationship is found at all between diversity and slope. Wind is also important in terms of evaporation, and slopes exposed to the wind are likely to experience harsher evaporation regimes than more sheltered slopes, and this has important implications for water retention strategies, especially for high canopy trees. Finally, eastness is indicative of the time of day of the most direct sunlight, with east facing slopes receiving the strongest sun in the morning hours, and west facing slopes (in this case where greater diversity is found) receiving the strongest sun in the afternoon hours. Meterological station data from TBS indicates that solar radiation is in fact higher in the afternoons due to less atmospheric attenuation, although the difference is fairly minimal. It is unlikely that the solar radiation significance of eastness is controlling this relationship, as the low slopes render aspect relatively insignificant in varying solar radiation across the region. It is impossible to know which of these plausible explanations is the direct cause of the higher diversity on west facing slopes, if any, and this should be the subject of further investigation.

In conclusion, no clear correlation between environment and diversity is found using Simpson's Index (the most robust diversity measure) nor *single* variable correlations with species richness outside of the observed low richness and low diversity in the two regularly flooded plots (plots 4 and 5). However, multiple stepwise regression does provide a strong explanation of variability in species richness based on eastness and elevation using the SRTM DEM, with west facing high elevation sites having the highest richness. Ideally this model should be validated using a split sample but this was impossible with just 10 plots.

4.3.2.1.4 Analysis of categorical environmental variables

Having examined in detail the quantitative variables and identified few correlations, it is unlikely that the landscape classifications provide many significant correlations, as they are derivatives of the characteristics already examined. Nevertheless, statistical analyses are made (Pearson correlation coefficients) to examine if the diversity and richness is indeed distinct in different landscape classes based on the fuzzy membership to the feature and network feature classifications. The landscape class of each plot, and the respective fuzzy feature membership to the feature classification are first presented (Table 35 and Table 36).

Plot	Topoclass	Feature	Network Feature	Pit Membership	Channel Membership	Pass Membership	Ridge Membership	Peak Membership	Planar Membership
1	Valley Bottom	Ridge	Ridge	0.00	0.00	0.00	0.14	0.00	0.86
2	Toe Slope	Planar	Planar	0.00	0.00	0.00	0.00	0.00	1.00
3	Toe Slope	Planar	Channel	0.00	0.57	0.00	0.00	0.00	0.57
4	Slope	Ridge	Ridge	0.00	0.00	0.00	0.14	0.00	0.86
5	Toe Slope	Planar	Channel	0.00	0.00	0.00	0.00	0.00	1.00
6	Slope	Planar	Planar	0.00	0.00	0.00	0.00	0.00	1.00
7	Toe Slope	Channel	Channel	0.00	0.71	0.00	0.00	0.00	0.57
8	Ridge	Ridge	Ridge	0.00	0.00	0.00	1.00	0.00	0.00
9	Slope	Planar	Planar	0.00	0.00	0.00	0.00	0.00	1.00
10	Slope	Planar	Channel	0.00	0.00	0.00	0.14	0.14	0.71

Table 35 Landscape unit classifications for the plots in TBS using the TOPO DEM.

Plot	Topoclass	Feature	Network Feature	Pit Membership	Channel Membership	Pass Membership	Ridge Membership	Peak Membership	Planar Membership
1	Toe Slope	Planar	Pit	0.00	0.86	0.00	0.00	0.00	0.14
2	Slope	Channel	Pass	0.00	0.14	0.00	0.00	0.00	0.86
3	Toe Slope	Planar	Channel	0.29	0.14	0.14	0.14	0.00	0.29
4	Valley Bottom	Planar	Peak	0.00	0.71	0.00	0.00	0.00	0.29
5	Valley Bottom	Channel	Channel	0.00	0.86	0.00	0.00	0.00	0.14
6	Slope	Ridge	Peak	0.00	0.00	0.00	0.14	0.00	0.86
7	Toe Slope	Planar	Ridge	0.00	0.00	0.00	0.14	0.00	0.86
8	Slope	Ridge	Ridge	0.00	0.00	0.00	1.00	0.00	0.00
9	Toe Slope	Planar	Ridge	0.00	0.00	0.00	0.14	0.00	0.86
10	Toe Slope	Ridge	Ridge	0.00	0.00	0.00	0.57	0.00	0.43

Table 36 Landscape unit classifications for the plots in TBS using the SRTM DEM.

When multi-scale fuzzy feature classifications (explained in Chapter 3) are used (Table 37 and Table 38), there is no relationship between diversity and membership to any landscape class.

Pearson's Correlation Coefficient	Pit Membership	Channel Membership	Pass Membership	Ridge Membership	Peak Membership	Planar Membership
Family Richness	N/A	-0.22	N/A	0.42	0.18	-0.33
Genera Richness	N/A	-0.05	N/A	0.47	-0.03	-0.43
Species Richness	N/A	-0.21	N/A	0.31	0.34	-0.26
Endemic Species	N/A	-0.14	N/A	0.46	0.39	-0.44
Simpson's	N/A	0.19	N/A	0.22	0.20	-0.36
Shannon's	N/A	0.00	N/A	0.30	0.30	-0.36
Margalef	N/A	-0.16	N/A	0.31	0.36	-0.29
Menhinick	N/A	-0.08	N/A	0.30	0.38	-0.33
Berger-Parker	N/A	-0.28	N/A	-0.27	-0.23	0.47

Table 37 Correlation coefficients between feature membership and richness and diversity for TBS using the TOPO DEM.

Pearson's Correlation Coefficient	Pit Membership	Channel Membership	Pass Membership	Ridge Membership	Peak Membership	Planar Membership
Family Richness	0.00	-0.45	0.00	0.45	N/A	0.07
Genera Richness	0.01	-0.64	0.01	0.51	N/A	0.21
Species Richness	0.24	-0.54	0.24	0.45	N/A	0.07
Endemic Species	0.11	-0.39	0.11	0.55	N/A	-0.13
Simpson's	0.19	-0.62	0.19	0.36	N/A	0.26
Shannon's	0.25	-0.61	0.25	0.46	N/A	0.13
Margalef	0.26	-0.56	0.26	0.47	N/A	0.07
Menhinick	0.28	-0.58	0.28	0.48	N/A	0.07
Berger-Parker	-0.26	0.61	-0.26	-0.44	N/A	-0.15

Table 38 Correlation coefficients between feature membership and richness and diversity for TBS using the SRTM DEM.

4.4 Conclusions

In terms of species composition and diversity, TBS was found to have greater richness at the species level (average of 57 species per plot against 42 in Tambito), but similar richness in families. In TBS the study found 53 families compared with 52 in Tambito. Some 28 of these families were common to both sites. Notable differences in composition were in the low abundance of *Melastomataceae* and *Rubiaceae* in TBS in comparison to high abundances in Tambito. TBS was found to have much higher abundances in *Moraceae* and *Mimosaceae*. *Fabaceae* was the most abundant family found in TBS, whilst just four individuals were recorded in Tambito.

The terrain characteristics found to correlate with the species composition in the two sites were few, but clearly reflect the effect of very different processes in each site. In Tambito, only elevation was found to control composition, but this in itself explains only 36% of the variability according to the Jaccard coefficient. Furthermore, elevation fails to accurately reflect compositional similarity between sites of similar elevations, though in all cases sites elevationally distant exhibited clear compositional differences, so only significant differences in elevation (and the factors that it controls) affect species composition. Clearly other processes that are not captured with the terrain characteristics presented here are important in controlling composition at the micro-scale in Tambito.

In TBS, composition was found to be controlled in part by distance to the main river channel (just 16% of variability), and a hypothesis is presented that isolates this correlation to being caused by forest age, with distance to river acting as a surrogate of time since a region was occupied by river channel. It is hypothesized that this represents a gradient of soil development and forest succession (to a lesser extent), though no soil data is available to validate this supposition. Similarly to the case with elevation in Tambito, sites equally distant from the river tended to have high compositional differences (indicating that other factors are also important), but sites with large differences in their distance from river do have significantly different composition in all cases. Distance to river was not the only factor exhibiting significant correlation with composition in TBS, toposcale and northness for the SRTM DEM both show significant correlations independently of distance to river (that is, they are not co-linear with distance to river), though the validity of these correlations is questioned and no biological interpretation can be offered at this time.

In conclusion, at neither site is composition convincingly correlated with the terrain characteristics, and the majority of variability remains to be unexplained. This may be due to the DEMs poor representation of the small-scale topography, and this error in the terrain characteristics calculated from them. In Tambito the DEM is likely a good reflection of the real topography, but the 25m resolution may fail to capture terrain variability at a relevant scale for composition, though this is unlikely. In TBS neither of the DEMs sufficiently capture the topographic variability observed in the field, and they are likely both inaccurate to some degree and, more importantly, are not at the best scale for identifying compositional differences. Also of importance to note is the plot size used in this study. 25m x 25m plots may be highly sensitive to successional dynamics compared with larger plots, and though some terrain characteristics may indicate the frequency of processes that interrupt succession (slope indicating likely frequency of tree fall, for example), they are stochastic processes (in both space and time (Salvador-Van Eysenrode et al., 2000)) that cannot be properly identified in relation to terrain characteristics with so few plots. In order to get to grips with this interplay of deterministic and stochastic processes, more plots would be required, lowering the dependence of the result on each single data point.

In terms of patterns in diversity, clear correlations between terrain characteristics and diversity are found in Tambito, but in TBS patterns appeared to be less clearly defined. A clear peak in diversity is found for Tambito in mid-elevations, though this only applied to diversity measures, and not richness measures. Two potential explanations of this are presented, including a mid-domain effect and an area-based hypothesis. Whatever the cause, 70% of variation in diversity is explained by elevation through a polynomial regression, with a diversity peak at 1800m. This macro-scale observation is complemented by a strong micro-scale relationship between curvature and richness and diversity, with convex slopes having higher species diversity. This may be due to a greater diversity in light environments through lateral penetration of the canopy, but may also be due to greater exposure to cloud inputs (water and nutrients), and indirectly to soil quality with greater leaching leading to lower soil nutrient levels. The latter explanation has been observed by other authors, showing monotonic decrease in diversity with soil quality (Hall and Swaine, 1976; Huston, 1982; Oliveira and Mori, 1999). Without further investigation it is impossible to ascertain exactly which of these is the dominant process in explaining diversity, but a considerable amount of variability can be explained through terrain characteristics.

In TBS fewer and weaker patterns are found, though analysis is complicated by the strong co-linearity between many characteristics, and the poor quality of the DEM. Low richness and diversity is found in the two sites most regularly flooded (both low in elevation and close to the river channel), but no other patterns in diversity variation are found. The low diversity in the regularly flooded sites is principally due to high dominance of a single species (*Sorocea sp*.) found in these two plots, but which is rare in other plots. Though multi-variate analyses using multiple stepwise linear-regressions manage to account for 82% of variability in species richness, no biological interpretation can be provided, and further data collection and analysis is required to confirm the validity of this. The lack of clear result in TBS may be due to deficiencies in the quality of the terrain information, brought about by coarse resolution DEMs, which fail to capture the all important micro-scale topographic variability central to this thesis. Section 3.7 in Chapter 3 shows that the DEMs reflect little of the on-the-plot conditions, and so there is little wonder that patterns have not been found. Alternatively, there simply may not be clear terrain controls on richness and diversity in a tropical lowland rain forest such as TBS (thus supporting non-equilibrium theories of species diversity maintenance), though further investigation with better quality DEMs is required.

Despite using 12 different terrain characteristics in this analysis, just two variables provide robust explanations of composition and diversity; elevation and mean curvature. Further investigation should focus on these relationships in order to broaden the understanding of the specific biological and ecological processes that these variables are capturing.

Chapter 5

5 Micro-scale spatial variation in forest structure

5.1 Introduction

In this chapter the spatial variation in forest structure is briefly explored, once again using the environmental and topographic variables to identify correlations and discuss the possible mechanisms behind such relationships. It is well documented that forest height tends to diminish, the density of individuals increases and DBH reduces with increasing elevation (Huston, 1994; Pendry and Proctor, 1996; Pendry and Proctor, 1997; Kappelle, 2004). The reasons behind tree stunting, for example, with greater elevation are the subject of many studies, and many different hypotheses have been suggested to explain this phenomenon. Overall, stuntedness is thought to be an indicator of low primary productivity. This in turn may be the result of one or many factors which include high humidity (Odum, 1970), nutrient limitation (Vitousek, 1984; Vitousek and Sanford, 1986), low temperature (Kitayama and Aiba, 2002), soil acidity (Hafkenscheid, 2000), leaf wetness (Letts, 2003) and cloud cover (Grubb, 1977; Letts, 2003)

There is still significant debate as to the factor, or indeed the combination of factors behind such a relationship. This chapter examines micro-scale variation in structure, examining both elevational gradients (specifically for Tambito) and the role of topography (at both sites) in generating structural variation. It is hoped that in Tambito examination of the fine-scale variation may shed some light on the mechanisms behind tree stunting along elevational gradients, whilst in lowland rain forests the effects of micro-topography and flooding frequency on structure are examined in the hope that this will also shed some light on the plant-significant environmental gradients that exist in this environment.

In addition to using the environmental and topographic variables in the analysis, diversity itself is also incorporated and the role of diversity on forest structure (and vice-versa) is examined. The relationship between diversity and structure is likely to be complex and bi-directional. Diversity of tree forms is one factor behind the complex structures of trees in a forest, with different species having different branching patterns, sizes, and shapes. Meanwhile, the structure of the forest also filters energy inputs (light, water, temperature) changing the physical conditions from the upper canopy to the forest floor, which in turn favours certain species adapted to a specific conditions and creates a diverse sub-canopy light environment. Chapter 4 identified some topographic factors that, through control on energy inputs, explain some of the variability in diversity and composition. Therefore this complex two-way relationship between diversity and structure may be significant, and is included in the analysis.

This chapter is structured similarly to Chapter 4, with the two study sites being treated separately at first, and site comparisons made at the end of the chapter. Two aspects of structure are examined at each study site, each of which is analysed in a similar way to that of composition and diversity in Chapter 4. Analogous with the composition analysis, the similarity in the frequency distribution of tree forms at a plot (height, DBH, DBH/Height) is plotted against environmental difference between plots, and Mantel tests used to test for correlation. Analogous to the diversity analysis, the average values of structural parameters are compared with the environmental and topographic variables at each plot. For easier interpretation, the sections are presented starting with between-plot variability in average structural values, and moving onto a more detailed examination of the distribution of structural parameters in each plot. In both cases, correlations are made on a variable-by-variable basis at first, and then multi-variate analyses are applied to search for how combinations of factors may explain the forest structure.

5.2 Reserva Tambito

In Tambito the plots cover a large elevational gradient of nearly 1000m, and based on other studies in similar environments, should show clear patterns of structural change along this gradient. Furthermore the rugged topography and almost constant wetness of soil and trunks make treefall a common occurrence, with a high density of fallen trunks visible throughout the twin catchments. This temporally stochastic process drives much of the variability in forest structure (Kappelle, 2004), but the spatial distribution of treefall occurrence may be tightly controlled by physical factors such as slope and soil stability. But it is important to reiterate that the plot scale measurements represent only a snapshot of the highly dynamic system that results.

5.2.1 Average structure

5.2.1.1 Forest Structure in general

In general, Tambito has high stem densities (average 1773 stems Ha^{-1} for the 10 plots), with relatively low diameters at breast height (DBH) (average 11.3cm, maximum 79.6cm) and few tall trees (average tree height 7.84m, maximum 30m). The frequency distributions for the three major structural characteristics (height, DBH and DBH/Height) are shown in Figure 77. Some 98.4% of individuals were less than 20m tall, with 62.6% of trees measuring 4-8m tall (itself possibly an artifact of only measuring tree with DBH>5cm). The greatest frequency for DBH occurred between 7-9cm, with 96.2% of individuals having a DBH less than 30cm. It is interesting that there are more stems at 7-9cm than at 5-7cm, possibly indicating that there are a number of species which reach maturity at 7-9cm DBH and cease to continue to grow. The DBH/Height ratio is a measure of the stem girth per unit height, and is shown to be important when comparing plots and sites later in the chapter. However, it is important to note that the majority (57.0%) have ratio values between 1-1.6, with just 9.1% of individuals having ratio values below 1 (indicating relatively low DBH compared with height) and a longer tail towards higher ratio values with the remaining 33.9% of individuals having ratio values greater than 1.6 (reaching a maximum of 7.6). High ratio values represent individuals with a relatively high DBH compared to height. This may indicate an investment in stem strength (to combat tree fall) over height (to search for light). This kind of investment may be particularly necessary in situations where steep slopes and exposure to wind and fog potentially destabilize a tree leading to the potential for fall.

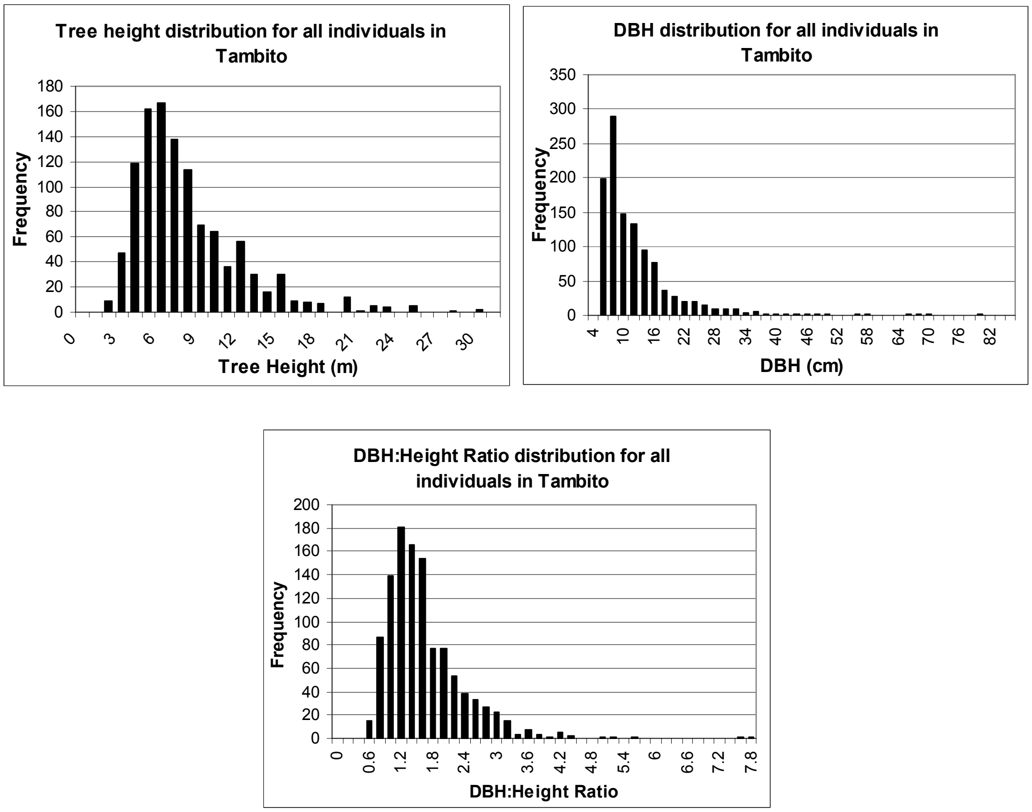


Figure 77 Frequency histograms for the three major structural characteristics for all individuals in Tambito

In terms of variability, the greatest variability between individuals occurred in DBH (coefficient of variability 69.6%), followed by tree height (53.9%) and finally for the DBH/Height variable (48.7%). At this stage no more discussion is provided on the general patterns of structure. These figures are discussed further in Section 5.4 at the end of the chapter in direct comparison with TBS.

5.2.1.2 Between-Plot Structural Variability

5.2.1.2.1 General discussion

Having identified significant range and variability in structural forms in Tambito, this section addresses the between-plot variability of the average structural parameters, using the environmental and topographic variables to explain this variation. The structural conditions at each plot are shown in Table 39.

Plot	Elevation (m)	Stem Density (stems/ha)	DBH (cm)	DBaseH (cm)	DBH/DBaseH	DBH/Height	Basal Area (m^2)	Height (m)	Height of 1st Branch (m)
1	1651	1552	13.36	15.55	0.83	1.54	3.21	8.90	6.12
2	1684	1712	11.85	13.92	0.85	1.24	2.44	10.19	7.47
3	1449	1888	10.87	12.24	0.89	1.35	1.70	9.02	6.86
4	1966	2192	10.89	12.69	0.87	1.76	2.62	6.39	4.22
5	1299	1792	9.92	11.55	0.87	1.58	1.49	6.67	4.10
6	1749	1392	11.57	13.73	0.83	1.81	1.70	6.97	4.20
7	2253	2816	9.61	11.27	0.87	1.42	2.15	7.06	4.63
8	1856	1696	10.71	13.60	0.82	1.46	2.15	7.62	3.98
9	1950	1200	13.92	16.91	0.82	1.48	2.72	8.99	5.84
10	1600	1488	12.70	15.22	0.83	1.65	2.33	7.79	4.84

Table 39 Structural characteristics of the plots in Tambito

Plots 7 and 4 have the highest stem densities (2816 and 2192 stems Ha^{-1} respectively) and also happen to be the two highest elevation plots. However, the lowest stem density is found in plot 9 (less than half the density with 1200 stems Ha^{-1}), which is the third highest elevation plot (though this site has already been identified in Chapter 4 as an outlier in diversity patterns). Plot 9 also has the highest DBH (average 13.9cm), with Plot 7 having the lowest (average 9.6cm). Plot 2 has the greatest average tree height (10.2m), with Plot 4 having the lowest (6.4m). The highest trees were found in Plot 1 (*Elaeagia sp.* - 30m, and *Protium sp.* – 28m) and Plot 2 (Clusiaceae *spp.* – 30m). Plot 2 had the lowest value for DBH/Height (1.24) and plot 6 has the highest (1.81).

5.2.1.2.2 Single-variate analysis of quantitative environmental variables

Prior to examining in detail the correlations between structural parameters and all environmental and topographic variables, the elevational gradient in structure is examined first (Figure 78).

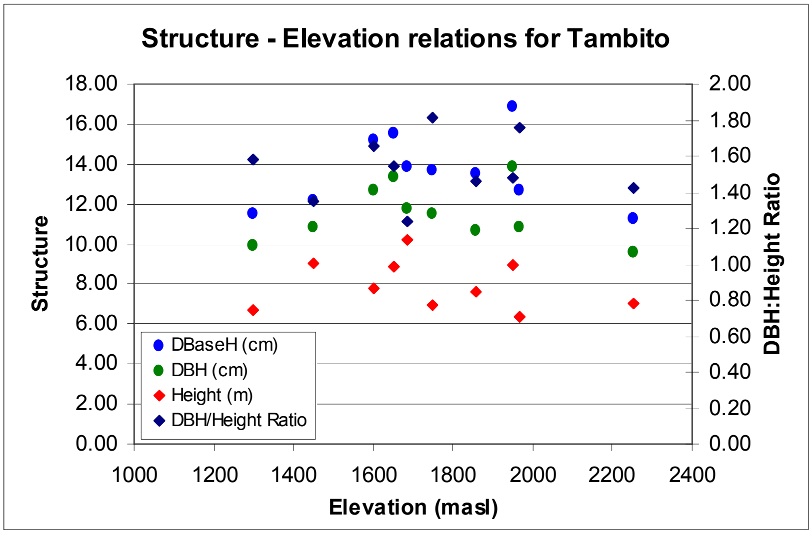


Figure 78 Elevational gradient in structural parameters for Tambito

Despite numerous accounts in the literature of a clear change in structure across the elevational gradient, this is clearly not the case in the data collected in Tambito. No relationship is evident in any of the major structural parameters shown in Figure 78, nor in any of the other variables measured. Though Plot 7 (the highest elevation plot, 2253m) has relatively low stature (7.1m) and the lowest DBH (9.6cm), Plot 5 at the other end of the elevational gradient (1299m) has an even lower average stature (6.7m) and comparably low DBH (9.9cm). If anything, there is evidence of the mid-elevations having the highest stature and greatest average DBH.

This goes against the findings of many studies in similar environments, but analysis of the environmental and topographic variables may explain some of this variability that is clearly not explained by elevation alone. Pearson correlation coefficients and their respective p-values are calculated between all structural parameters and the 9 quantitative environmental and topographic variables (Table 40).

Pearson's Correlation Coefficient	Elevation	Eastness	Northness	Curvature	Slope	Slope Position	Solar Radiation	Topmodel	Toposcale
Stem Density	0.46	-0.21	0.30	0.00	-0.35	0.25	0.38	-0.26	0.05
DBH	-0.05	-0.32	-0.08	0.19	0.03	0.02	-0.23	0.06	0.20
DBaseH	0.04	-0.26	-0.02	0.36	-0.08	0.17	-0.15	0.12	0.37
DBH/DBaseH	-0.16	-0.12	-0.10	-0.62	0.24	-0.39	-0.01	-0.29	-0.60
DBH/Height	0.02	0.44	-0.35	-0.10	-0.24	-0.03	0.28	0.82	-0.08
Basal Area	0.38	-0.62	0.47	0.46	-0.43	0.44	0.14	-0.15	0.47
Height	-0.19	-0.52	0.07	0.05	0.41	-0.17	-0.56	-0.56	0.03
Height of 1st Branch	-0.22	-0.59	0.01	-0.18	0.47	-0.31	-0.56	-0.60	-0.18

p-value	Elevation	Eastness	Northness	Curvature	Slope	Slope Position	Solar Radiation	Topmodel	Toposcale
Stem Density	0.18	0.56	0.41	0.99	0.33	0.48	0.28	0.46	0.89
DBH	0.90	0.37	0.82	0.61	0.93	0.96	0.53	0.86	0.58
DBaseH	0.92	0.46	0.95	0.31	0.83	0.65	0.69	0.73	0.30
DBH/DBaseH	0.67	0.75	0.77	0.05	0.50	0.26	0.99	0.42	0.07
DBH/Height	0.95	0.21	0.32	0.79	0.51	0.93	0.44	0.00	0.83
Basal Area	0.27	0.06	0.17	0.18	0.22	0.21	0.69	0.68	0.17
Height	0.61	0.12	0.85	0.89	0.24	0.65	0.09	0.09	0.94
Height of 1st Branch	0.54	0.07	0.98	0.62	0.17	0.38	0.09	0.07	0.61

Table 40 Pearson correlation coefficients and the respective p-values between structural characteristics of the forest and the environmental and topographic variables in Tambito.

As can be seen, only one significant correlation exists. This is found between the DBH/Height variable and topmodel (Figure 79), with a very high level of significance (Pearson = 0.83, p = 0.004). The nature of this relationship is such that the greater the surface soil moisture (as defined by TopModel) the higher the DBH relative to height (in other words the greater the investment in trunk girth per unit height).

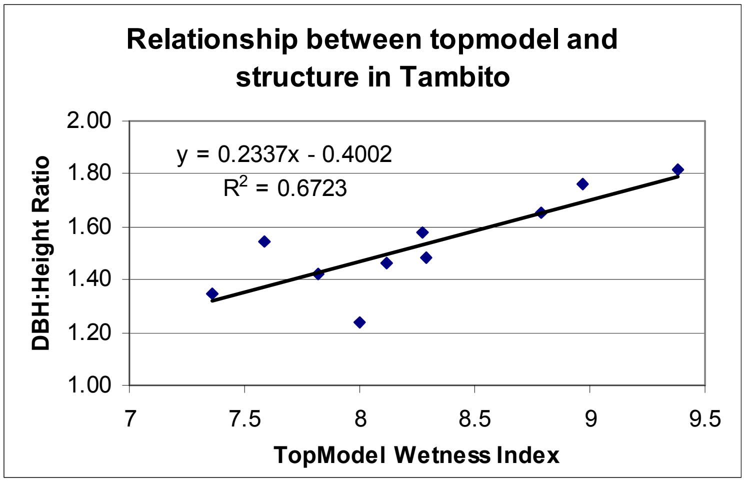


Figure 79 Significant correlation between DBH/Height and topmodel for Tambito

Topmodel (an indicator of soil moisture convergence) could be seen as a resource permitting trees to uptake water and augment trunk diameter, but this explanation fails to account for the relative large trunk diameter compared to height that the relationship is showing and in any case, water is unlikely to be limiting in these environments. Alternatively, surface soil moisture could be seen as an indicator of soil stability, with wetter soils having less stability. Given lower levels of stability, it is preferable for trees not to risk mortality from tree fall through excessive top heavy branch and leaf growth in the search of light, but instead to invest in solid lower trunk and root growth. However, soil moisture is just one mechanism that lowers stability for trees, with slope also being important, along with wind speed (more specifically gust velocity), wind direction and associated topographic exposure. Neither slope nor exposure or aspect related variables such as mean curvature, toposcale, northness or eastness show any relationship, somewhat weakening the argument that stability is an important variable in determining the DBH/height value. Furthermore, topmodel is calculated based on both upslope area and slope, and tends to be highest on low slopes with large contributing upslope area and so is not a good indicator of stability.

Treefall is more probable on steeper slopes (Gale, 2000), and also more likely on unstable soils, so to test if there is a relation between DBH/Height and stability an index is produced based on upslope area multiplied by slope, with the least stability found on steep slopes with a large contributing area (i.e. greater soil moisture). No significant relation is found, linear (DBH/Height = 7 e^{-7} Stability Index + 1.45, Pearson = 0.41, p = 0.24) nor non-linear. The lack of correlations with any other topographic variables makes the interpretation of this relationship between topmodel and DBH/Height difficult, and no explanation can be provided.

The lack of correlations between topography and tree structure is of interest in itself, with the basic structural variables (DBH and tree height) not only failing to show any elevational pattern, but also showing no relationship with the other 9 quantitative terrain derivatives. This is surprising, and leads to the conclusion that structure is principally controlled by stochastic processes, and little relationship exists between environment and structure in Tambito, at least at the micro-scale as measured in the plots. If stochastic processes are prominent at this scale in defining tree structure, the distinct structures observed in the plots in Tambito may be reflecting different age profiles since a disturbance drastically altered the structure.

The results presented here are in contrast to many prior studies showing clear elevational gradients, but may simply be an artifact of the small plot sizes used here capturing successional stage after specific recent tree falls rather than the average regional structure. Before this is discussed in depth, multi-variate analyses are applied to look for combinations of factors that may explain structure.

5.2.1.2.3 Multi-variate analysis of quantitative environmental variables

Multiple linear regressions are applied for the 5 major structural variables (stem density, DBH, height, DBH/height and basal area), using all 9 quantitative environmental and topographic variables. No significant multiple linear regressions were found for DBH, the DBH/Height value (on top of the already discussed single-variate relationship with topmodel) nor basal area.

For stem density, combinations of two variables jointly explain 53% of variability (Figure 80). These are elevation (explaining 21%) and toposcale (explaining a further 31%) (Stem Density = -1816 + 2.12Elevation - 4.72Toposcale, $R^2 = 0.53$, $p = 0.02$). Based on this equation the highest stem density is found in high elevations with exposed convex slopes, though there is a significant amount of variation (47%) not explained by these factors. Indeed, examination of the scatterplot of modelled against measured stem density shows that the model poorly explains low stem densities (Figure 80). However, this result agrees with patterns reported by Webb et al. (1999), where exposed ridges in American Samoa were found to have low stature and low DBH but high stem densities compared to slopes and valleys, with the authors attributing this pattern to wind-cropping and higher levels of disturbance.

For tree height a combination of two variables jointly explain 58% of the variability (Figure 80). These are topmodel (explaining 32%) and solar radiation (explaining the remaining 26%) (Height = 24.17 - 1.02Topmod – 0.0009Solar, $R^2 = 0.58$, $p = 0.01$). This relationship is interesting in that it once again highlights surface soil moisture (topmodel) as potentially important. Based on this relationship, the highest trees are found in areas with dry surface soils and low solar radiation receipt. These are areas where there is lower danger of tree fall due to soil instability, but where lower solar radiation resources makes the investment of energy into reaching higher into the canopy important. This way the trees in the community tend to grow higher as they compete for greater light resource at the upper canopy. Equally this relationship could be argued as questionable and possibly spurious, based on the argument that forest stature may be expected to be lower in areas with lower resources (less soil moisture and less light receipt). Once again, there is no way of showing (without the collection of substantially more field data) whether this is a truly causal relationship due to the process of stability and competition for light, or whether this is a spurious result with no causal relation.

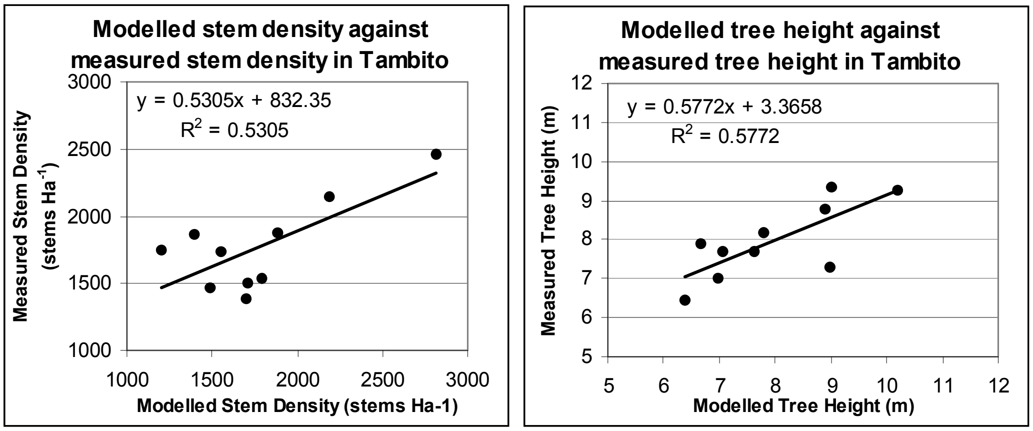


Figure 80 Modelled stem density against measured stem density in Tambito, based on the multiple stepwise linear regression model using elevation and toposcale (right) and modelled tree height against measured tree height in Tambito, based on the multiple stepwise linear regression model using topmodel and solar radiation receipt (left).

5.2.1.2.4 Average structure – diversity relationships

The final analysis using the average of structural variables for the plots looks at the relationship between diversity and structure. All structural variables are correlated with all diversity and richness measures, calculating the Pearson correlation coefficient and the respective p-value (Table 41).

Pearson's Correlation Coefficient	Stem Density	DBH	DBaseH	DBH/DBaseH	DBH/Height	Basal Area	Height	Height of 1st Branch
Family Richness	-0.04	0.01	0.10	-0.23	-0.27	0.12	0.22	0.07
Genera Richness	0.40	-0.61	-0.47	-0.11	0.08	-0.26	-0.46	-0.57
Species Richness	0.26	-0.22	-0.12	-0.27	0.11	0.15	-0.25	-0.37
Endemic Species	0.59	-0.46	-0.36	0.04	-0.08	0.05	-0.42	-0.48
Simpson's	-0.48	0.54	0.65	-0.84	0.23	0.46	0.15	-0.09
Shannon's	-0.25	0.27	0.39	-0.69	0.18	0.34	0.03	-0.19
Margalef	-0.04	0.01	0.13	-0.50	0.17	0.20	-0.14	-0.33
Menhinick	-0.41	0.31	0.42	-0.72	0.24	0.24	0.01	-0.23
Berger-Parker	0.56	-0.57	-0.68	0.86	-0.25	-0.35	-0.16	0.09

p-value	Stem Density	DBH	DBaseH	DBH/DBaseH	DBH/Height	Basal Area	Height	Height of 1st Branch
Family Richness	0.91	0.98	0.78	0.52	0.44	0.97	0.55	0.85
Genera Richness	0.25	0.06	0.17	0.77	0.83	0.22	0.18	0.09
Species Richness	0.46	0.53	0.74	0.45	0.77	0.95	0.49	0.29
Endemic Species	0.07	0.18	0.31	0.91	0.84	0.80	0.22	0.17
Simpson's	0.16	0.11	0.04	0.00	0.52	0.38	0.67	0.80
Shannon's	0.48	0.46	0.27	0.03	0.62	0.60	0.93	0.59
Margalef	0.92	0.98	0.73	0.14	0.63	0.86	0.70	0.35
Menhinick	0.23	0.39	0.22	0.02	0.51	0.75	0.98	0.52
Berger-Parker	0.09	0.08	0.03	0.00	0.49	0.51	0.66	0.80

Table 41 Correlation coefficients and respective p-values for all correlations between diversity and richness measures and structural variables in Tambito.

Some correlations are found between diversity indices and the diameter at the base of trees (DbaseH), and also the DBH/DbaseH variable. With DbaseH, Simpson's and Berger-Parker correlate to the 95% significance level, where highest diversity is found in plots with a high average DbaseH. In the case of DBH/DbaseH, Simpson's, Shannon's, Menhinick and Berger Parker all correlate such that highest diversity (*ergo* low dominance) are found in low index values, where the DBH is significantly smaller than the DbaseH. It is possible that the relationships with DBH/DbaseH are a result of some co-linearity with curvature, which has already been presented in Chapter 4 as a key driver of diversity in Tambito. Curvature narrowly fails to correlate significantly to the 95% confidence level with DBH/DbaseH (Table 40), but this relationship may be behind the significant correlation presented here. In the case of Simpson and Berger-Parker correlating with the average DbaseH, this appears to have no co-linearity with any of the environmental variables (Table 40). Though not significant at the 95% significance level, there is also a weak positive correlation between DBH and Simpson's (Pearson = 0.54, p = 0.11, n = 10) and negative correlation with Berger-Parker (Pearson = -0.57, p = 0.08, n = 10). It seems that in general, plots with greater tree girths tend to have lower dominance and higher diversity, contrary to a pattern reported by Givnish (1999). However, the mechanism behind such a relationship is not clear, but analysis of the frequency distribution of tree girths might shed further light. This is analysed in section 5.2.2.1.3.

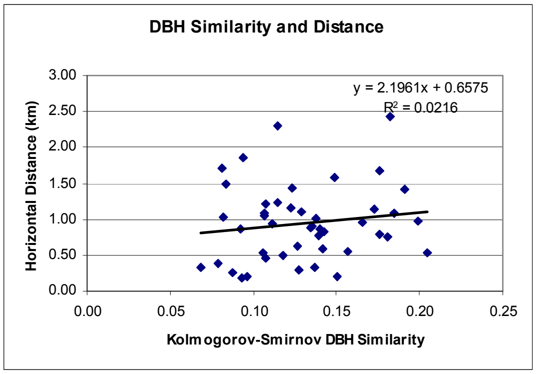
5.2.2 Structural distribution

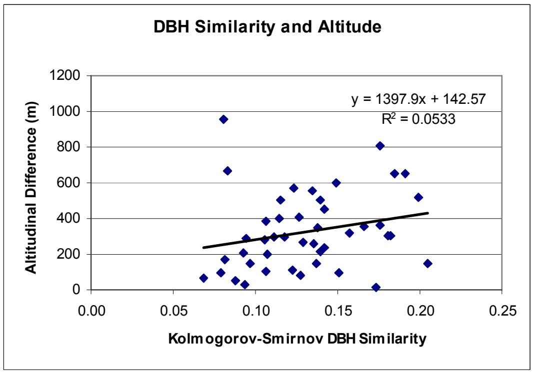
5.2.2.1.1 General discussion

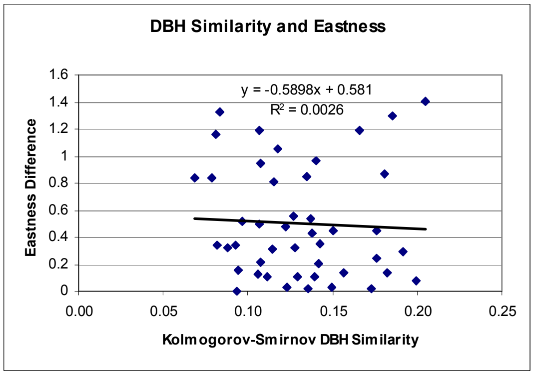
Having examined the environmental and topographic relationships with average structural parameters for each plot, the frequency distribution of structural parameters within each plot are examined here. Two plots may have the same average tree height, for example, but the distribution of tree heights for all the individuals may indeed be very different. This section examines the stratification of structure through analysis of frequency histograms for the three principal structural variables (DBH, height and DBH/height), and through correlating the similarity in the distribution of structural forms between plot pairs with the environmental and topographic similarity between the plot pairs themselves.

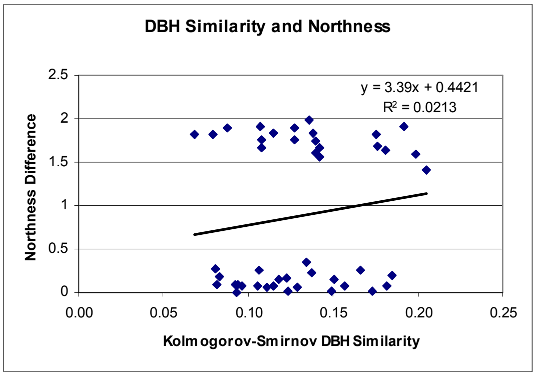
5.2.2.1.2 Single-variate analysis of quantitative environmental variables

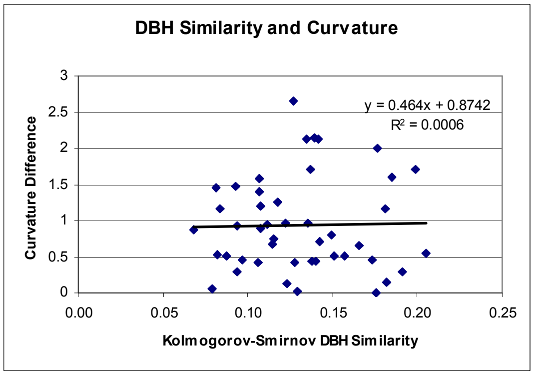
The Kolmogorov-Smirnov (K-S) test is used on the structural data for DBH, tree height and DBH/height for each plot pair to examine the difference in their distributions. The K-S test uses the mean and standard deviation of the distribution to indicate similarity between samples. The higher the K-S statistic, the more different the distributions, so the matrix between plot pairs is in fact a dissimilarity matrix of the structural variable (the method is discussed in greater detail in Section 3.6.4). Mantel tests are then used on the dissimilarity matrix of structural distribution and the dissimilarity matrix of environmental difference, in the same way as in Chapter 4. In each case, the scatterplots are shown (Figure 81, Figure 82 and Figure 83), along with a summary table indicating whether significant correlation was found (Table 42, Table 43 and Table 44).

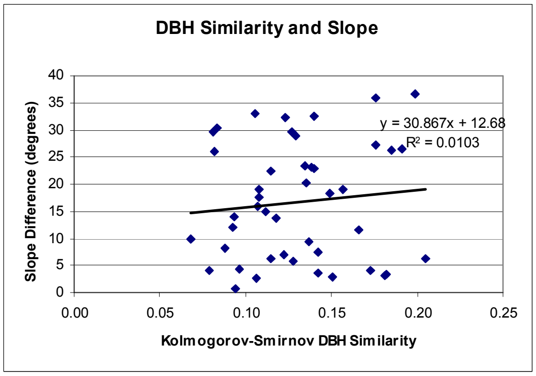

DBH Similarity and Distance
y = 2.1961x + 0.6575
R² = 0.0216
Horizontal Distance (km)
3.00
2.50
2.00
1.50
1.00
0.50
0.00
0.00
0.05
0.10
0.15
0.20
0.25
Kolmogorov-Smirnov DBH Similarity

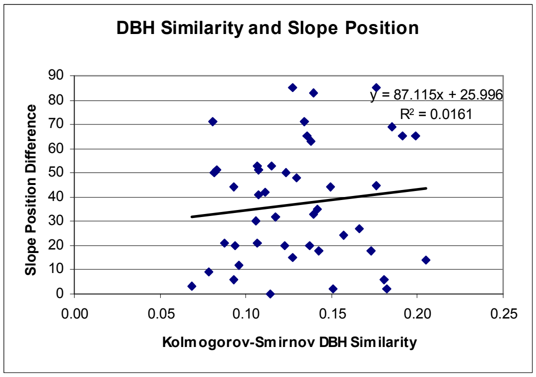

DBH Similarity and Altitude
y = 1397.9x + 142.57
R² = 0.0533
Altitudinal Difference (m)
1200
1000
800
600
400
200
0
0.00
0.05
0.10
0.15
0.20
0.25
Kolmogorov-Smirnov DBH Similarity

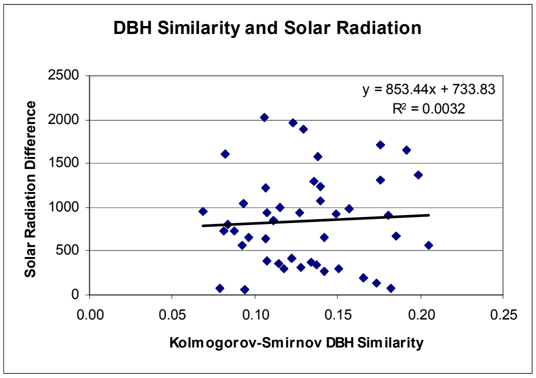

DBH Similarity and Eastness
y = -0.5898x + 0.581
R² = 0.0026
Eastness Difference
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0.00
0.05
0.10
0.15
0.20
0.25
Kolmogorov-Smirnov DBH Similarity


DBH Similarity and Northness
y = 3.39x + 0.4421
R² = 0.0213
Northness Difference
2.5
2
1.5
1
0.5
0
0.00
0.05
0.10
0.15
0.20
0.25
Kolmogorov-Smirnov DBH Similarity


DBH Similarity and Curvature
y = 0.464x + 0.8742
R² = 0.0006
Curvature Difference
3
2.5
2
1.5
1
0.5
0
0.00
0.05
0.10
0.15
0.20
0.25
Kolmogorov-Smirnov DBH Similarity


DBH Similarity and Slope
y = 30.867x + 12.68
R² = 0.0103
Slope Difference (degrees)
40
35
30
25
20
15
10
5
0
0.00
0.05
0.10
0.15
0.20
0.25
Kolmogorov-Smirnov DBH Similarity


DBH Similarity and Slope Position
y = 87.115x + 25.996
R² = 0.0161
Slope Position Difference
90
80
70
60
50
40
30
20
10
0
0.00
0.05
0.10
0.15
0.20
0.25
Kolmogorov-Smirnov DBH Similarity


DBH Similarity and Solar Radiation
y = 853.44x + 733.83
R² = 0.0032
Solar Radiation Difference
2500
2000
1500
1000
500
0
0.00
0.05
0.10
0.15
0.20
0.25
Kolmogorov-Smirnov DBH Similarity

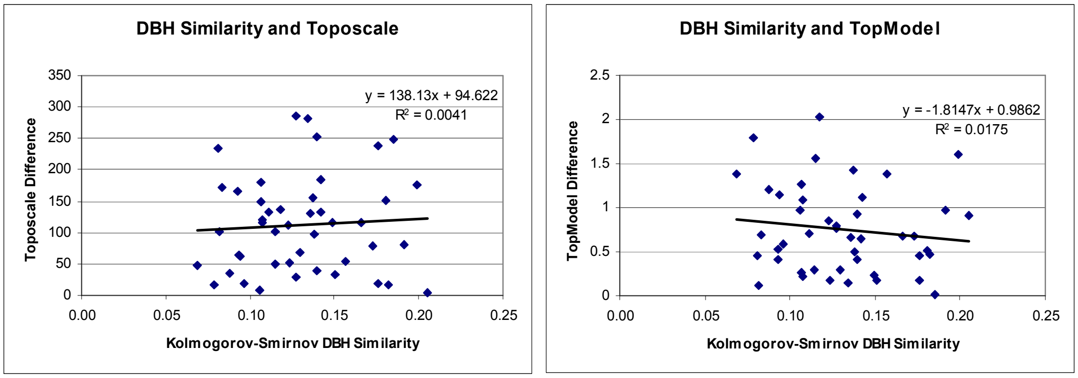
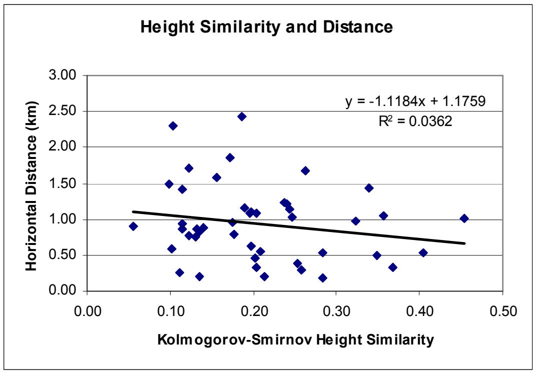
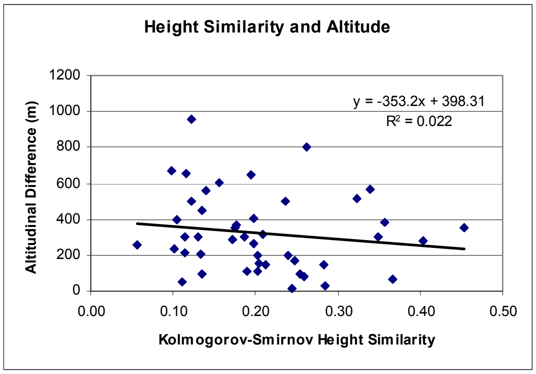


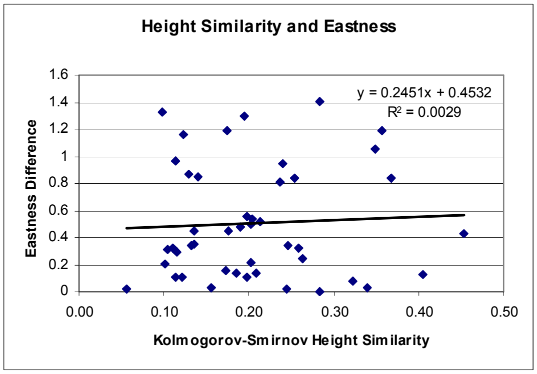
Figure 81 Scatterplots of similarity in distribution of DBH between plot-pairs (calculated using the K-S test of the distributions) against environmental difference between plot-pairs in Tambito.

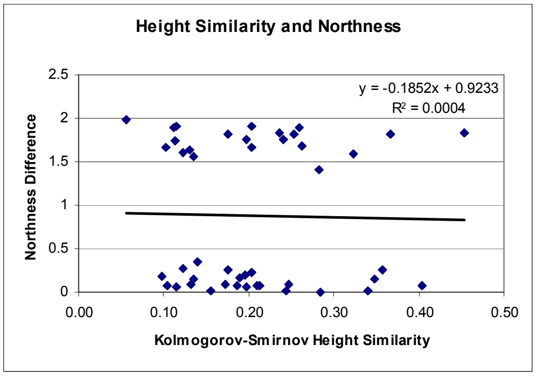
Variable	Mantel Test	One-tailed p-value	Correlation (alpha = 0.05)
Distance	0.15	0.250	Not-significant
Altitude	0.23	0.104	Not-significant
Eastness	-0.05	0.421	Not-significant
Northness	0.15	0.202	Not-significant
Curvature	0.03	0.448	Not-significant
Slope	0.10	0.185	Not-significant
Slope Position	0.13	0.171	Not-significant
Solar Radiation	0.06	0.344	Not-significant
Toposcale	0.06	0.354	Not-significant
TopModel	-0.13	0.240	Not-significant

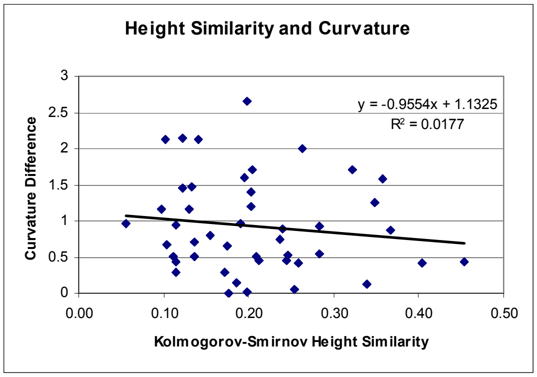
Table 42 Summary results of structural DBH similarity analysis with distance and environmental variables, using Mantel tests and a one-tailed Pearson. Note that structural dissimilarity was compared with environmental dissimilarity (difference). The northness variable produces very different results due to the heavily skewed distribution of plots in strongly northward and strongly southward facing slopes.

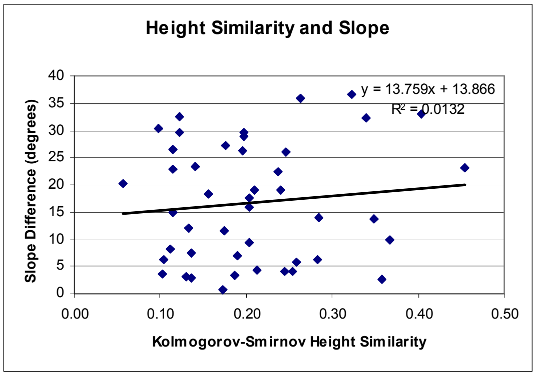

Height Similarity and Distance

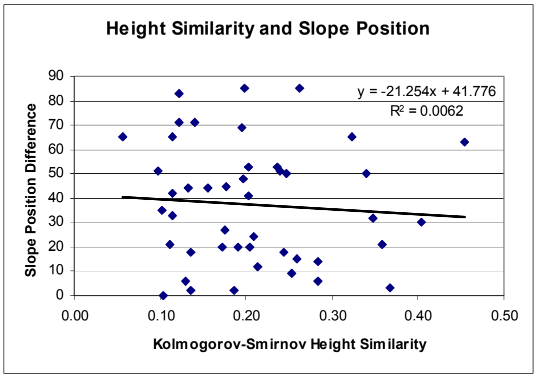

Height Similarity and Altitude

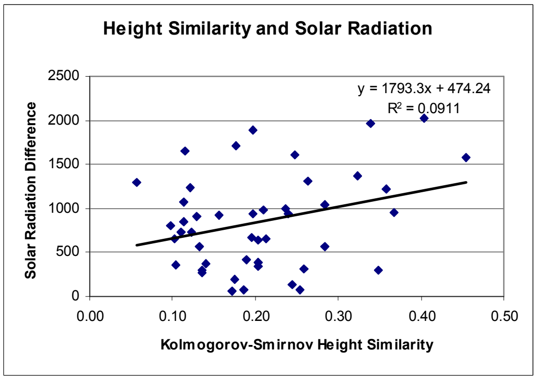

Height Similarity and Eastness


Height Similarity and Northness


Height Similarity and Curvature


Height Similarity and Slope


Height Similarity and Slope Position


Height Similarity and Solar Radiation

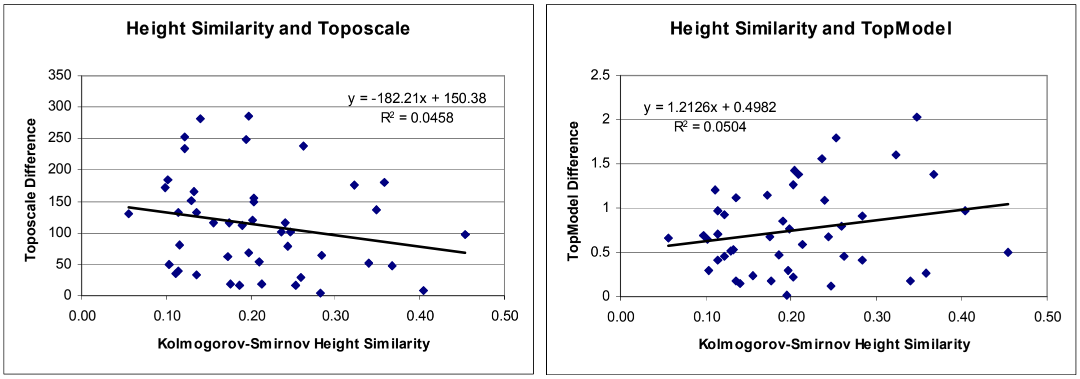
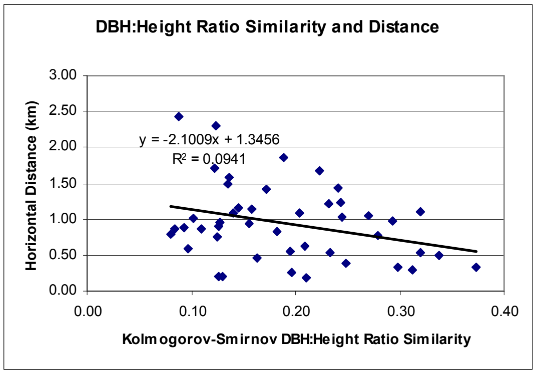
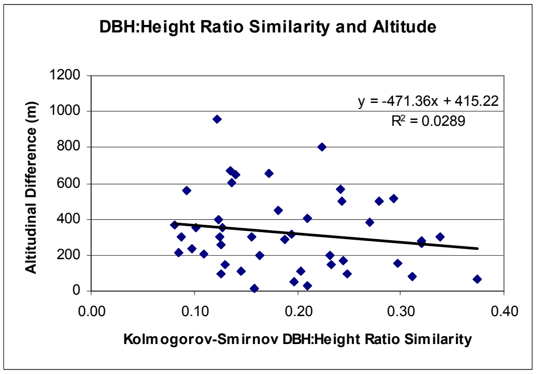


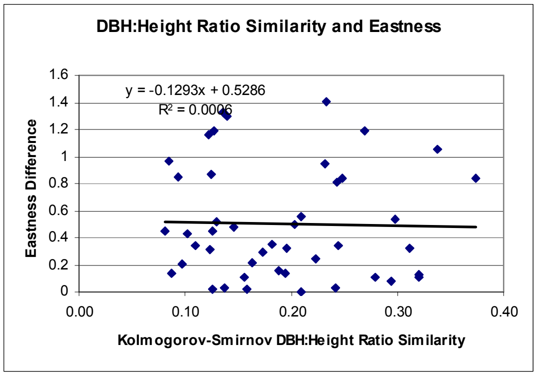
Figure 82 Scatterplots of similarity in distribution of tree height between plot-pairs (calculated using the K-S test of the distributions) against environmental difference between plot-pairs in Tambito.

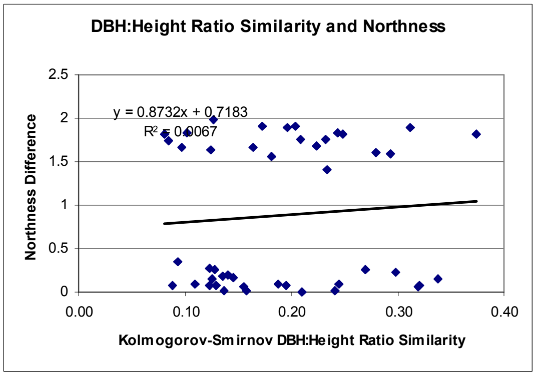
Variable	Mantel Test	One-tailed p-value	Correlation (alpha = 0.05)
Distance	-0.22	0.162	Not-significant
Altitude	-0.17	0.200	Not-significant
Eastness	0.07	0.285	Not-significant
Northness	-0.12	0.228	Not-significant
Curvature	-0.08	0.382	Not-significant
Slope	0.07	0.253	Not-significant
Slope Position	-0.18	0.089	Not-significant
Solar Radiation	0.21	0.103	Not-significant
Toposcale	-0.22	0.100	Not-significant
TopModel	0.29	0.071	Not-significant

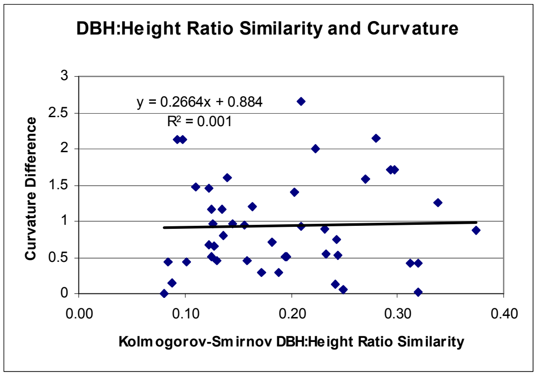
Table 43 Summary results of tree height similarity analysis with distance and environmental variables, using Mantel tests and a one-tailed Pearson. Note that structural dissimilarity was compared with environmental dissimilarity (difference). The northness variable produces very different results due to the heavily skewed distribution of plots in strongly northward and strongly southward facing slopes.

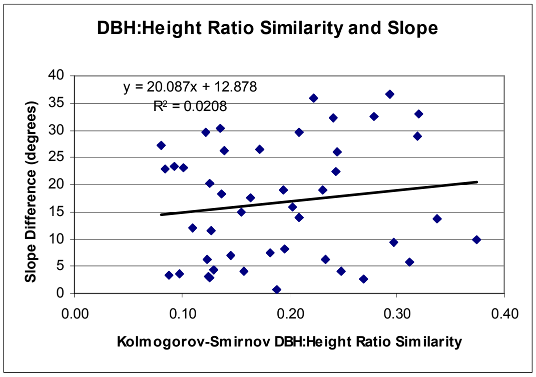

DBH:Height Ratio Similarity and Distance

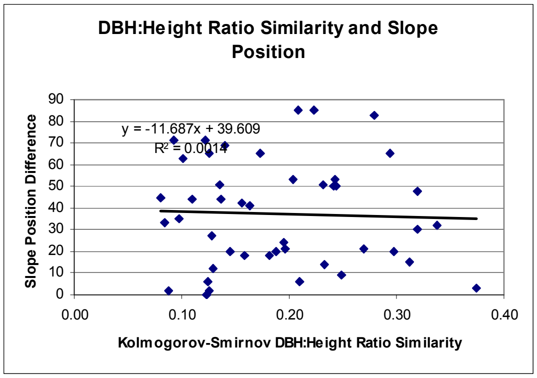

DBH:Height Ratio Similarity and Altitude

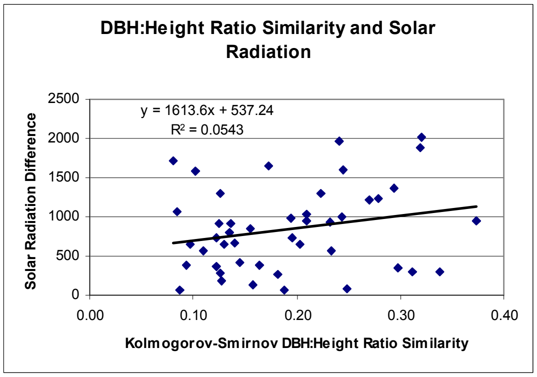

DBH:Height Ratio Similarity and Eastness


DBH:Height Ratio Similarity and Northness


DBH:Height Ratio Similarity and Curvature


DBH:Height Ratio Similarity and Slope


DBH:Height Ratio Similarity and Slope Position


DBH:Height Ratio Similarity and Solar Radiation

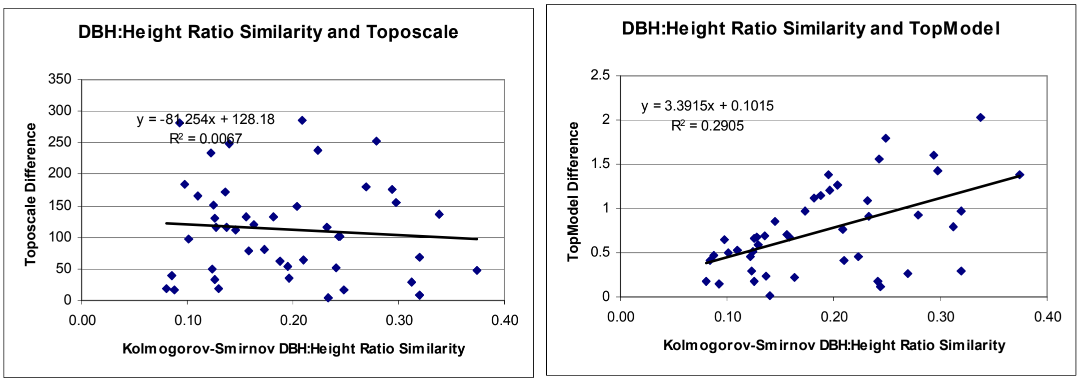


Figure 83 Scatterplots of similarity in distribution of the DBH/Height variable between plot-pairs (calculated using the K-S test of the distributions) against environmental difference between plot-pairs in Tambito.

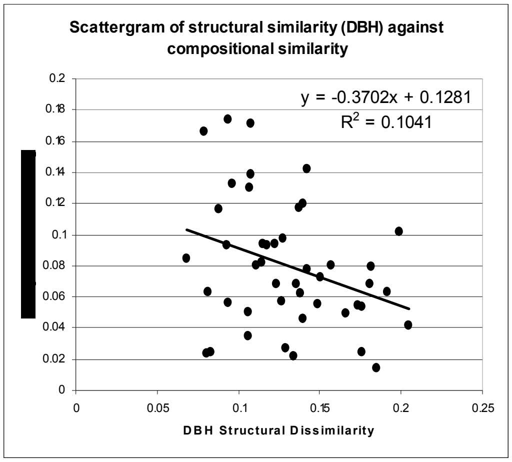
Variable	Mantel Test	One-tailed p-value	Correlation (alpha = 0.05)
Distance	-0.31	0.046	Significant
Altitude	0.22	0.224	Not-significant
Eastness	-0.03	0.502	Not-significant
Northness	0.11	0.162	Not-significant
Curvature	0.01	0.435	Not-significant
Slope	0.16	0.140	Not-significant
Slope Position	-0.01	0.536	Not-significant
Solar Radiation	0.27	0.060	Not-significant
Toposcale	-0.09	0.347	Not-significant
TopModel	0.53	0.005	Significant

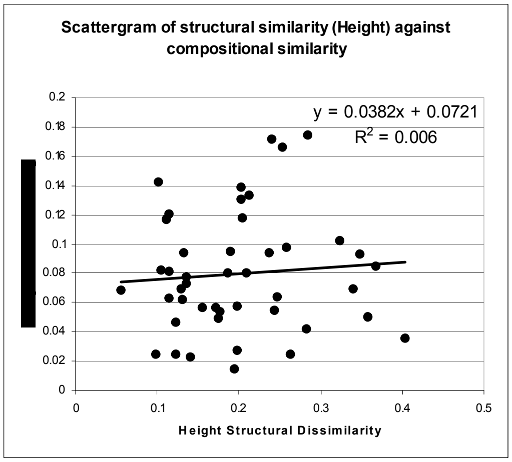
Table 44 Summary results of structural DBH/Height variable similarity analysis with distance and environmental variables, using Mantel tests and a one-tailed Pearson. Note that structural dissimilarity was compared with environmental dissimilarity (difference). The northness variable produces very different results due to the heavily skewed distribution of plots in strongly northward and strongly southward facing slopes.

No significant relationships were found between similarity in the distribution of DBH or tree height and difference in any of the 9 environmental and topographic variables between plot-pairs. This further confirms the findings in section 5.2.1.2.2, indicating that no relationship exists between environment and average DBH or height nor in the distribution of these structural forms. However, the significant correlation between structural dissimilarity and environmental difference in TopModel for the DBH/Height variable provides even greater evidence that the correlation already found in section 5.2.1.2.2 (Figure 79) is worthy of further discussion. This indicates that not only does the average value for DBH/Height correlate with topmodel wetness, but also the distribution of DBH/Height for individuals within each plot does. There are no plot-pairs that are similar in DBH/Height distribution with very different topmodel wetness indices, though there is greater variation in topmodel wetness index difference between plot-pairs with highly dissimilar DBH/Height distributions. This scale dependence in the relationship significantly lowers the level of correlation, though it is still significant to the 99% confidence level.

5.2.2.1.3 Structural distribution – species composition relationships

Finally for Tambito, the relationship between structural dissimilarity and compositional similarity is examined for the three major structural variables (DBH, Height and DBH/Height), also through K-S analyses and Mantel tests (Figure 84).





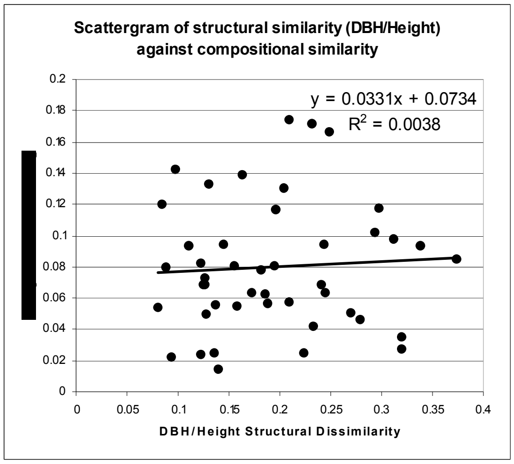


Figure 84 Scatterplots for plot-pairs of compositional similarity against structural dissimilarity for the major structural variables in Tambito.

There is a significant relationship between the similarity in DBH distribution and composition at the 95% significance level (Mantel = -0.32, p = 0.05), whereby compositionally similar plots are also similar in the distribution of DBH values, though as can be seen in the scatterplot just 10% of the variability is explained by this relationship. It is expected that individual species have specific structural forms, and that compositionally similar plots would therefore have similar distributions in structural forms, though clearly a great deal of variability is not explained in these relationships. This is likely due to the successional stage in each plot, whereby compositionally similar plots are likely to have significant variation in structural characteristics depending on the successional stage, but also due to environmental interactions causing further variability in the structural form of each species.

5.3 Tiputini Biodiversity Station

Surprisingly few patterns have been found between topographic characteristics and structure in Tambito, and for TBS (LRF) it would be expected that structural variability be much less pronounced. Furthermore, quality issues with the DEMs for TBS add a further problem in attributing confidence to the results of these analyses.

5.3.1 Average structure

5.3.1.1 Forest Structure in general

TBS has lower stem densities (average 1515 stems Ha^{-1} for the 10 plots), with average DBH of 12.8cm (maximum 92.3cm) and taller trees (average 10.4m, maximum 38m). The frequency distributions for the three major structural characteristics (height, DBH and DBH/Height) are shown in Figure 85. 92.8% of individuals are less than 20m tall, with 49.5% of individuals 4-8m tall. The greatest frequency of DBH occurs between 7-9cm (24.7% of all individuals, similar to Tambito in that there are more stems in this class than the 5-7cm class), and 93.2% of individuals have a DBH less than 30cm. 16.8% of individuals have a DBH/Height value below 1 (a greater percentage than in Tambito), and 67.4% of individuals with DBH/Height between 1-1.6. The highest DBH/Height value is 9.4, though this is a clear outlier with just 6 individuals with DBH/Height greater than 5. This distribution of DBH/Height values for TBS is significantly skewed towards lower values than found in Tambito (despite a higher maximum in TBS), indicating greater investment of resources in height relative to trunk diameter.

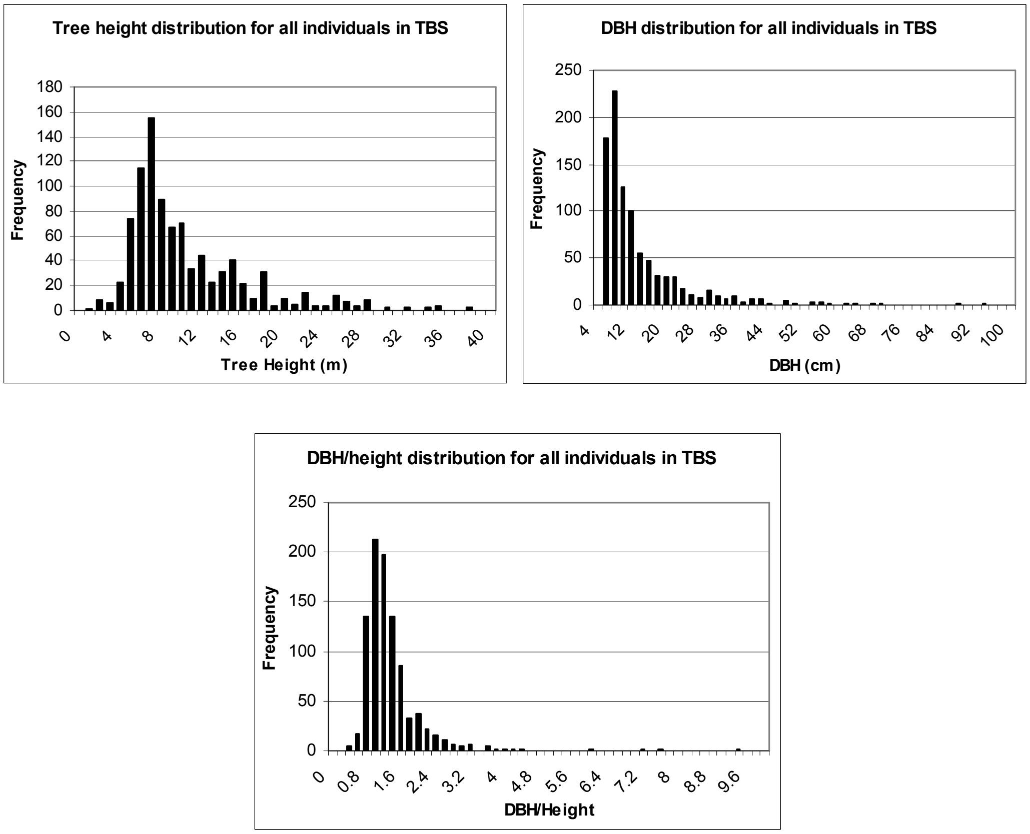


Figure 85 Frequency histograms for the three major structural characteristics for all individuals in TBS

In terms of variability, the greatest variability between individuals occurred in DBH (coefficient of variability 82.1%), followed by DBH/Height (57.2%) and finally tree height (56.8%). Further discussion of these patterns in direct comparison with Tambito is presented in Section 5.4.

5.3.1.2 Between-Plot Structural Variability

5.3.1.2.1 General discussion

This section addresses the between-plot variability of the average structural parameters, using the topographic characteristics to explain this variation. The structural conditions at each plot are shown in Table 45.

Plot	Elevation (m)	Stem Density (stems/ha)	DBH (cm)	DBaseH (cm)	DBH/DBaseH	DBH/Height	Basal Area (m^2)	Height (m)	Height of 1st Branch (m)
1	199	1280	15.66	17.09	0.90	1.38	3.26	10.86	7.48
2	219	2112	11.39	13.14	0.91	1.54	2.25	7.59	5.26
3	210	1520	11.31	13.30	0.87	1.28	1.82	9.59	6.70
4	201	1616	10.46	12.12	0.86	1.22	1.74	8.28	5.48
5	211	1408	13.28	14.89	0.87	1.35	3.10	9.27	5.88
6	220	1440	14.57	16.06	0.90	1.49	2.57	10.03	7.30
7	219	1056	11.93	13.67	0.86	1.29	1.35	9.53	6.27
8	262	1648	12.36	14.66	0.83	0.95	2.62	12.95	8.98
9	238	1520	13.21	15.62	0.84	1.00	3.12	12.51	8.19
10	224	1552	14.44	16.51	0.86	1.05	3.22	13.22	8.68

Table 45 Structural characteristics of the plots in TBS

Plot 2 has a significantly higher stem density (2112 stems Ha^{-1}) than the rest of the plots (average 1449 stems Ha^{-1}), with Plots 1 and 7 have the lowest stem density. Plots 8, 9 and 10 have the greatest stature with over 12m average tree height in all three plots, but these plots do not have the highest average tree girths, with Plot 1 having the highest average DBH (15.7cm) and highest basal area ($3.26m^2$). As well as the high stem density, Plot 2 is also distinct from the other plots in terms of average tree height with an average of just 7.6m. There is significant variability in the average DBH/Height between plots, with Plot 2 having an average value of 1.54, whilst Plot 8 has an average DBH/Height value of just 0.95. The tallest trees were found in Plot 9 (38m, *Micropholis sp.* (Sapotaceae)), Plot 8 (37.3m, *Jacaranda copaia* Aublet.) and Plot 10 (34m, *Ardisia sp.* (Myrsinaceae)).

5.3.1.2.2 Single-variate analysis of quantitative environmental variables

As in Section 5.2.1.2.2 for Tambito, variation in average structural characteristics are compared with the topographic characteristics through Pearson correlation coefficients, in the case of TBS applied for the TOPO DEM (Table 46) and the SRTM DEM (Table 47).

Pearson's Correlation Coefficient	Elevation	Eastness	Northness	Curvature	Slope	Slope Position	Solar Radiation	Topmodel	Toposcale
Stem Density	0.21	-0.24	0.03	0.31	-0.37	0.02	0.16	-0.15	0.22
DBH	-0.01	-0.63	-0.48	-0.15	-0.18	0.26	-0.44	0.40	-0.15
DBaseH	0.15	-0.58	-0.39	-0.04	-0.16	0.38	-0.34	0.35	-0.03
DBH/DBaseH	-0.53	-0.72	-0.28	-0.58	-0.28	-0.34	-0.46	0.26	-0.61
DBH/Height	-0.64	-0.54	-0.20	-0.64	-0.21	-0.51	-0.40	0.34	-0.66
Basal Area	0.13	-0.60	-0.47	0.08	-0.38	0.17	-0.34	0.51	0.01
Height	0.66	0.05	-0.03	0.51	0.11	0.72	0.14	-0.12	0.55
Height of 1st Branch	0.71	0.01	0.02	0.55	0.12	0.78	0.13	-0.20	0.58

p-value	Elevation	Eastness	Northness	Curvature	Slope	Slope Position	Solar Radiation	Topmodel	Toposcale
Stem Density	0.57	0.51	0.94	0.38	0.29	0.95	0.66	0.69	0.54
DBH	0.99	0.05	0.16	0.68	0.61	0.47	0.20	0.25	0.69
DBaseH	0.67	0.08	0.26	0.92	0.65	0.27	0.33	0.32	0.94
DBH/DBaseH	0.12	0.02	0.43	0.08	0.44	0.34	0.18	0.47	0.06
DBH/Height	0.05	0.10	0.58	0.05	0.57	0.13	0.26	0.34	0.04
Basal Area	0.73	0.07	0.17	0.83	0.28	0.64	0.33	0.13	0.97
Height	0.04	0.89	0.93	0.13	0.77	0.02	0.71	0.73	0.10
Height of 1st Branch	0.02	0.99	0.96	0.10	0.74	0.01	0.72	0.58	0.08

Table 46 Pearson correlation coefficients and the respective p-values between average structural characteristics for each plot and the topographic characteristics derived from the TOPO DEM in TBS

Pearson's Correlation Coefficient	Elevation	Eastness	Northness	Curvature	Slope	Slope Position	Solar Radiation	Topmodel	Toposcale
Stem Density	0.21	-0.56	-0.09	0.25	0.31	0.37	-0.47	-0.25	0.06
DBH	-0.01	-0.25	0.20	0.03	-0.10	-0.09	0.12	0.12	0.13
DBaseH	0.15	-0.27	0.27	0.13	-0.12	0.02	0.18	0.07	0.19
DBH/DBaseH	-0.53	-0.32	0.05	-0.14	0.22	-0.14	-0.35	0.06	-0.13
DBH/Height	-0.64	-0.09	-0.10	-0.28	0.26	-0.20	-0.38	0.18	-0.22
Basal Area	0.13	-0.39	0.07	-0.04	-0.08	-0.01	0.06	0.23	-0.02
Height	0.66	-0.14	0.27	0.41	-0.27	0.29	0.38	-0.16	0.36
Height of 1st Branch	0.71	-0.25	0.24	0.47	-0.25	0.40	0.30	-0.21	0.42

p-value	Elevation	Eastness	Northness	Curvature	Slope	Slope Position	Solar Radiation	Topmodel	Toposcale
Stem Density	0.57	0.09	0.81	0.49	0.39	0.30	0.17	0.49	0.86
DBH	0.99	0.48	0.59	0.93	0.78	0.81	0.74	0.74	0.73
DBaseH	0.67	0.45	0.45	0.72	0.74	0.95	0.62	0.85	0.60
DBH/DBaseH	0.12	0.36	0.90	0.69	0.55	0.71	0.33	0.86	0.73
DBH/Height	0.05	0.80	0.78	0.43	0.48	0.58	0.27	0.61	0.55
Basal Area	0.73	0.27	0.85	0.92	0.82	0.97	0.87	0.53	0.95
Height	0.04	0.70	0.45	0.24	0.45	0.42	0.27	0.67	0.31
Height of 1st Branch	0.02	0.49	0.51	0.17	0.48	0.26	0.40	0.57	0.23

Table 47 Pearson correlation coefficients and the respective p-values between average structural characteristics for each plot and the topographic characteristics derived from the TOPO DEM in TBS.

The greatest number of correlations occur with elevation, with DBH/Height, tree height and height of first branch all correlating significantly. It is important to note that elevation in the plots is measured by GPS and not derived from the DEMs, so issues with DEM quality are not relevant in these correlations with elevation. The correlations are such that greater tree height and height of first branch are found at higher elevations, with the DBH/Height lower in higher elevations (i.e. greater height relative to DBH) (Figure 86).

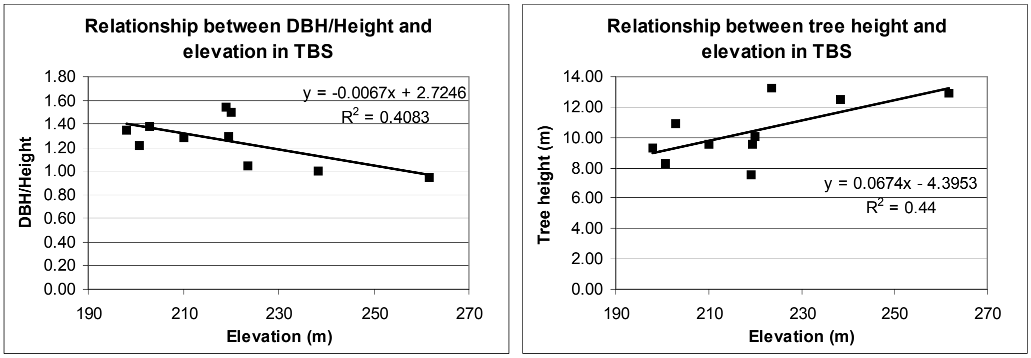


Figure 86 Significant correlations for plot average DBH/Height and tree height with elevation in TBS

Both the correlations shown in Figure 86 appear to consist of high tree height and low DBH/Height in the three high-elevation plots (8, 9 and 10), and respectively low tree height and high DBH/Height values for the remaining seven lower elevation plots. The significant correlations are due to this general pattern, and indeed no significant correlation is found between elevation and tree height or DBH/Height when only the seven lower elevation plots are included (for example for tree height, Pearson = -0.11, p = 0.81). As discussed in depth in Chapter 4, there is a great deal of co-linearity between elevation, distance from river and slope position (also correlates significantly for the TOPO DEM with tree height and height of first branch), and it appears that all these correlations are in fact related. The correlation between tree height and distance from river is also highly significant (Figure 87), though once again there is a clear difference between the seven low elevation plots and the three high elevation plots.

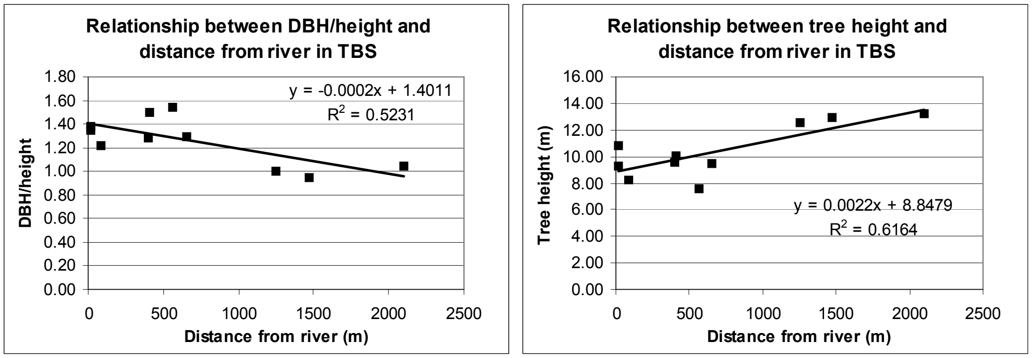


Figure 87 Relationship between plot average DBH/Height and tree height and distance from river in TBS

These relationships with tree height and DBH/height, whereby the three higher elevation plots have higher average tree heights and a respective lower DBH/height value could be for a number of reasons, many of which are similar to those discussed in Chapter 4, Section 4.3.2.1.2. These include flooding frequency (higher frequency at lower elevations), forest age (possibly greater forest age with greater distance from river) and an edaphic gradient with greater distance from the river (associated with forest age). The fact that there is greater average tree height in Plots 8, 9 and 10, and that the tallest trees recorded in the plots are also found in these plots is an indication that either there is less disturbance in these plots, permitting the survival of large individuals, or that the forest is older (in the sense of river migration), that has permitted that some trees reach very large sizes. However, the abrupt change in tree height evident in the scatterplots above 220m elevation also indicates that flooding may be a factor which limits tree height, with all plots that are at least occasionally flooded containing lower forest stature. This is further supported by the low stature found in the two regularly flooded plots (4 and 5). Indeed this may be evidence of the distinct structural forms found between *varzea* forest (Plots 1-7) and *terra firma* forest (Plots 8-10).

In addition to the elevational pattern (and the correlation with slope position/distance from river which is closely related), there is a significant correlation between mean curvature and toposcale and DBH/Height when the TOPO DEM is used, and eastness and DBH/DbaseH also for the TOPO DEM, though neither of these correlations hold for the SRTM DEM. However, the relationship between curvature and toposcale and DBH/Height is heavily dependent on the high curvature/exposure (i.e. convex slope) and the low DBH/Height found in Plot 8 (Figure 88), and so these cannot be considered a robust relationship.

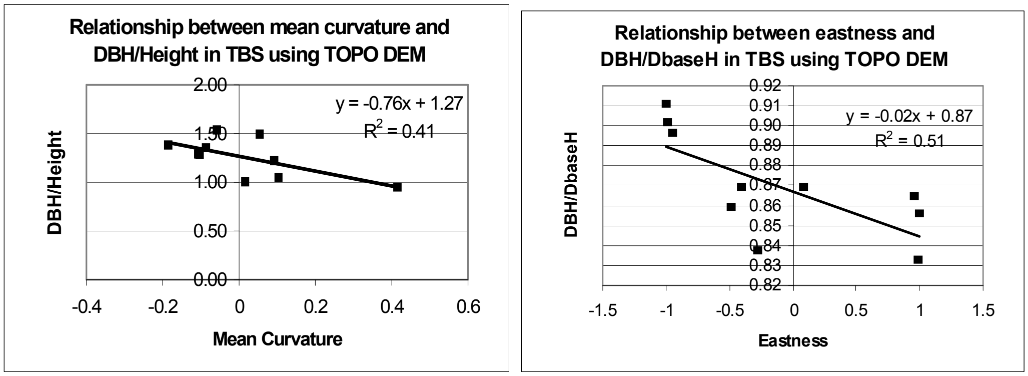


Figure 88 Significant relationships between mean curvature and DBH/Height (left) and eastness and DBH/DbaseH (right) in TBS using the TOPO DEM.

The relationship between eastness and DBH/DbaseH is however more robust based on eastness measured by the TOPO DEM (Figure 88), though the relationship does not hold for eastness derived from the high-resolution plot DEMs (DBH/DbaseH = -0.02 Eastness + 0.87, Pearson = -0.33, p = 0.36). The significance of eastness in TBS is related to exposure to wind from the south-east and east, meaning that strongly east facing slopes (i.e. high eastness) are more exposed to winds. It may be that eastness as measured at the ground level is not significant in indicating exposure to wind at the canopy level, whilst the TOPO DEM captures canopy level exposure better. Under these circumstances it may be that trees exposed to wind at the canopy level invest greater in basal area (including buttresses) in order to have greater stability, a pattern supported by the low DBH/DbaseH found in strongly east facing slopes.

5.3.1.2.3 Multi-variate analysis of quantitative environmental variables

Multiple stepwise linear regressions are applied to explain the variation in the major structural characteristics (DBH, tree height, DBH/Height). No significant multi-variate correlations are found to explain the variability in any of these structural variables for either of the DEMs on top of the already discussed single-variate relationships.

5.3.1.2.4 Average structure – diversity relationships

Finally, average structural characteristics are compared with diversity measures for each plot, in order to search for structural-diversity relations (Table 48).

Pearson's Correlation Coefficient	Stem Density	DBH	DBaseH	DBH/DBaseH	DBH/Height	Basal Area	Height	Height of 1st Branch
Family Richness	0.27	0.09	0.19	-0.19	-0.42	0.08	0.49	0.59
Genera Richness	0.20	0.03	0.16	-0.33	-0.49	0.05	0.55	0.63
Species Richness	0.63	-0.06	0.06	-0.08	-0.33	0.14	0.38	0.46
Endemic Species	0.40	0.10	0.21	-0.15	-0.43	0.23	0.53	0.57
Simpson's	0.09	0.07	0.14	-0.02	-0.24	-0.15	0.38	0.49
Shannon's	0.33	0.06	0.16	-0.07	-0.32	0.03	0.46	0.55
Margalef	0.54	0.00	0.11	-0.10	-0.36	0.14	0.44	0.52
Menhinick	0.39	0.08	0.20	-0.14	-0.40	0.14	0.52	0.60
Berger-Parker	0.05	-0.16	-0.24	0.09	0.31	0.08	-0.49	-0.59

p-value	Stem Density	DBH	DBaseH	DBH/DBaseH	DBH/Height	Basal Area	Height	Height of 1st Branch
Family Richness	0.46	0.79	0.60	0.60	0.23	0.82	0.15	0.07
Genera Richness	0.58	0.94	0.65	0.36	0.15	0.89	0.10	0.05
Species Richness	0.05	0.88	0.87	0.82	0.35	0.71	0.27	0.18
Endemic Species	0.25	0.79	0.56	0.67	0.21	0.53	0.12	0.08
Simpson's	0.81	0.85	0.70	0.95	0.50	0.69	0.28	0.16
Shannon's	0.35	0.87	0.65	0.85	0.36	0.93	0.19	0.10
Margalef	0.11	0.99	0.75	0.77	0.31	0.70	0.20	0.12
Menhinick	0.27	0.84	0.59	0.71	0.25	0.70	0.12	0.07
Berger-Parker	0.90	0.67	0.50	0.81	0.39	0.82	0.15	0.07

Table 48 Correlation coefficients and respective p-values for all correlations between diversity and richness measures and structural variables in TBS.

As can be seen, no significant relationships exist, with structure completely independent of diversity for all variables, unlike the situation in Tambito, though there are few theoretical reasons as to why such a relationship should occur. It is far more likely that correlations exist between structural distribution and composition, as is examined later in Section 5.3.2.1.3.

5.3.2 Distribution in structure

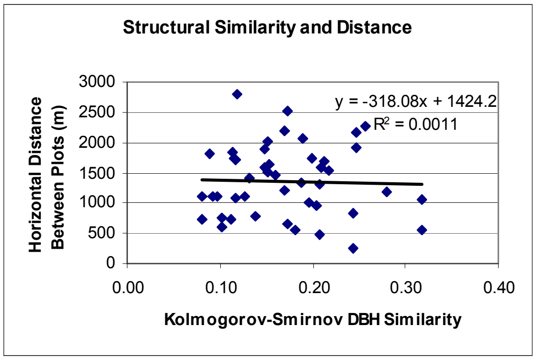
5.3.2.1.1 General discussion

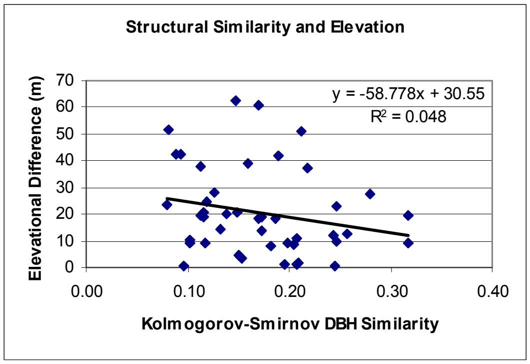
Having examined the patterns of variability in average structural characteristics for each plot, this section examines the distribution in structural forms for each major structural variable (DBH, Height, and DBH/Height), comparing it with topographic characteristics. The same method adopted for Tambito is used here for TBS.

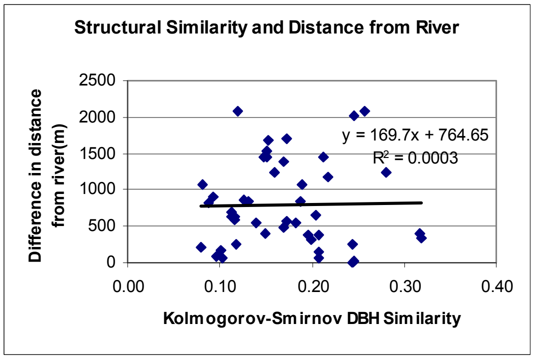
5.3.2.1.2 Single-variate analysis of quantitative environmental variables

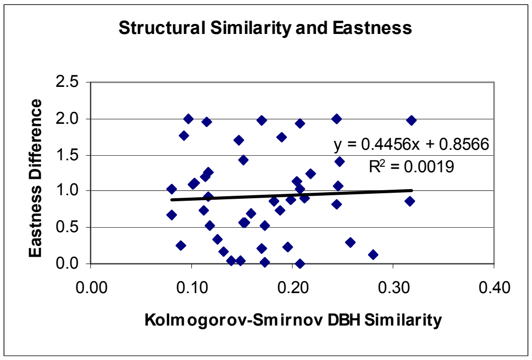
The single-variate analysis of structural distribution in the plots involves the application of Mantel tests between similarity matrices for each structural parameter (calculated using Kolmogorov-Smirnov tests between plot pairs for each structural variable, as explained in Section 3.6.4) along with the difference in topographic conditions for plot-pairs. This is performed for the TOPO DEM (Figure 89, Figure 90 and Figure 91), with associated tables summarizing the results (Table 49, Table 50 and

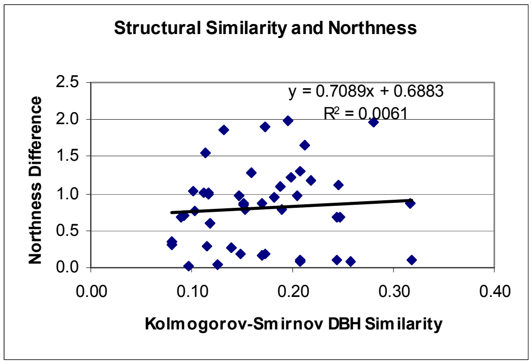
Table 51), and for the SRTM DEM (Figure 92, Figure 93 and Figure 94), also with summary tables of the results (Table 52, Table 53 and Table 54).

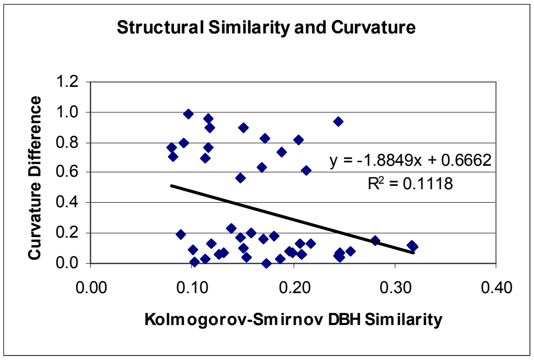

Structural Similarity and Distance

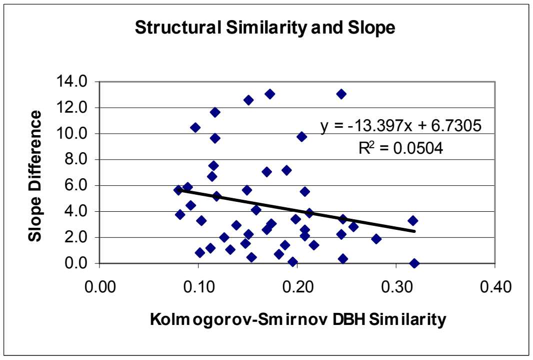

Structural Similarity and Elevation

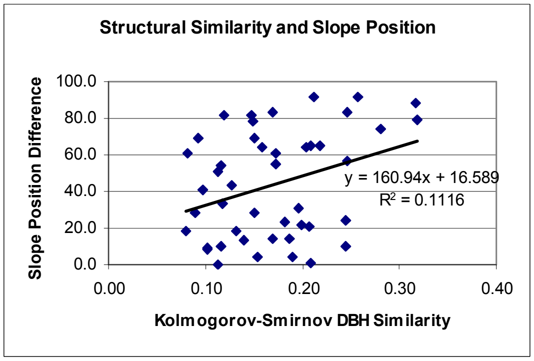

Structural Similarity and Distance from River


Structural Similarity and Eastness


Structural Similarity and Northness


Structural Similarity and Curvature


Structural Similarity and Slope


Structural Similarity and Slope Position

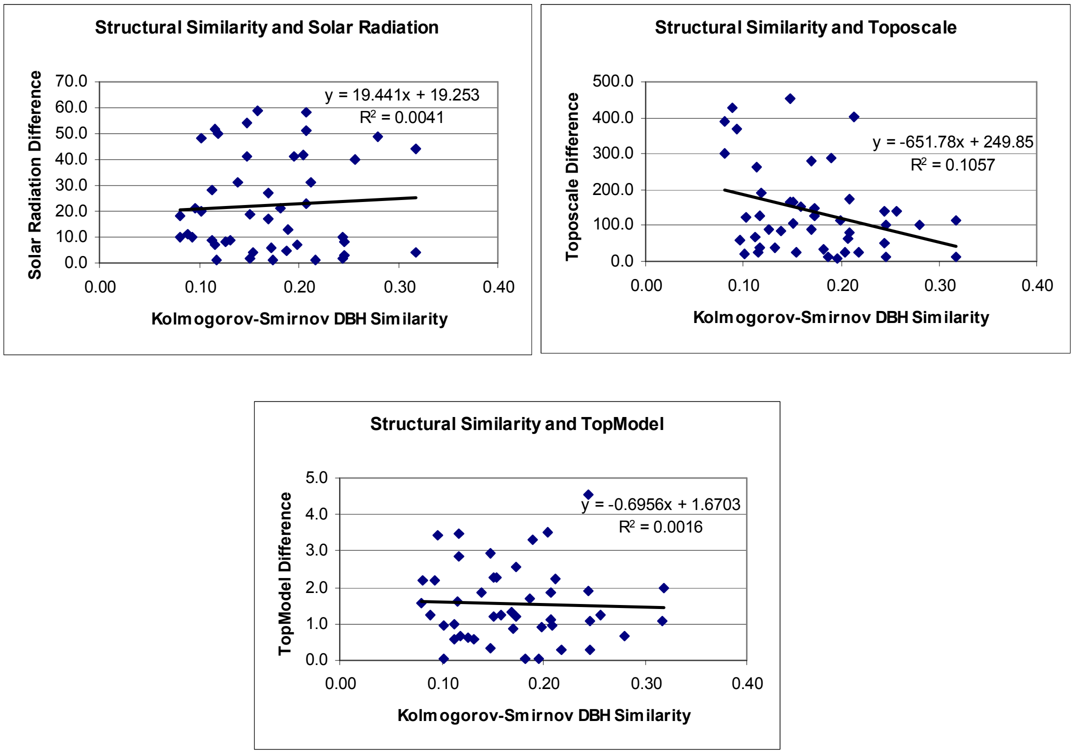
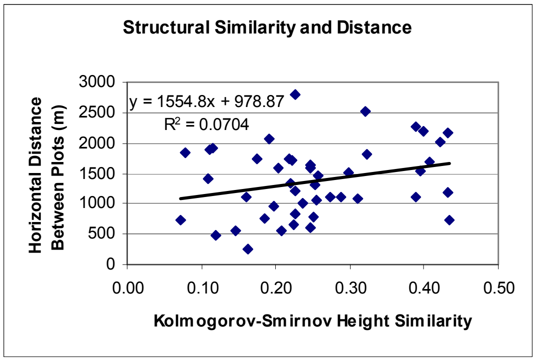


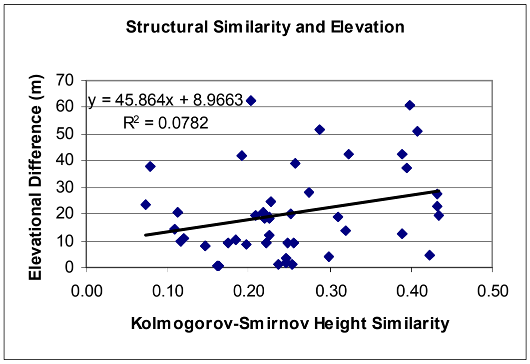
Figure 89 Scatterplots of similarity in distribution of DBH between plot-pairs (calculated using the Kolmogorov-Smirnov test of the distributions) against environmental difference between plot-pairs in TBS for derivatives of the Topo DEM.

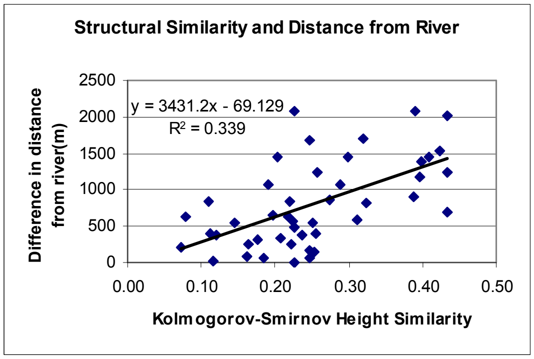
Variable	Mantel Test	One-tailed p-value	Correlation (alpha = 0.05)
Distance	-0.03	0.490	Not-significant
Distance from River	0.02	0.383	Not-significant
Altitude	-0.22	0.185	Not-significant
Eastness	0.04	0.338	Not-significant
Northness	0.08	0.347	Not-significant
Curvature	-0.33	0.030	Significant
Slope	-0.22	0.156	Not-significant
Slope Position	0.33	0.012	Significant
Solar Radiation	0.06	0.357	Not-significant
Toposcale	-0.33	0.040	Significant
TopModel	-0.04	0.454	Not-significant

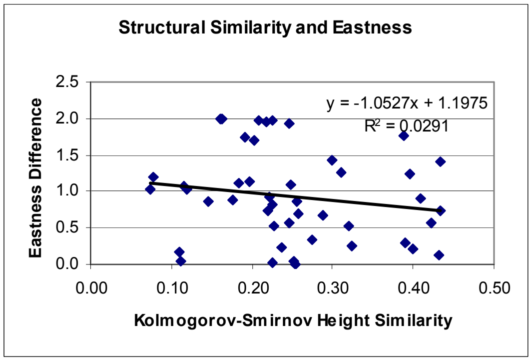
Table 49 Summary results of structural DBH similarity analysis with distance and environmental variables derived from the Topo DEM, using Mantel tests and a one-tailed

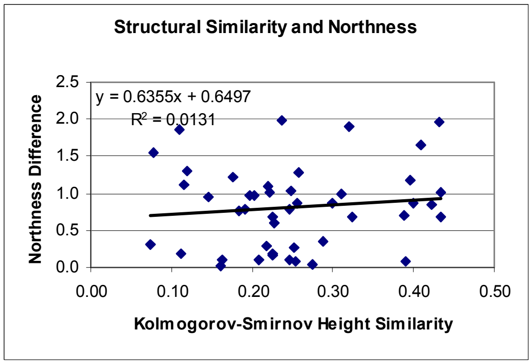
Pearson. Note that structural dissimilarity was compared with environmental dissimilarity (difference).

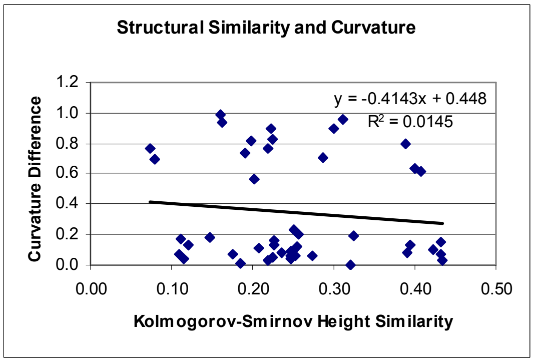


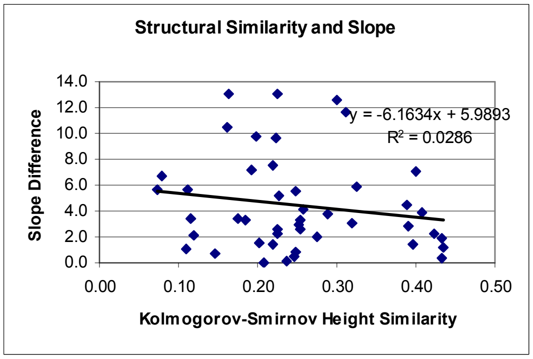


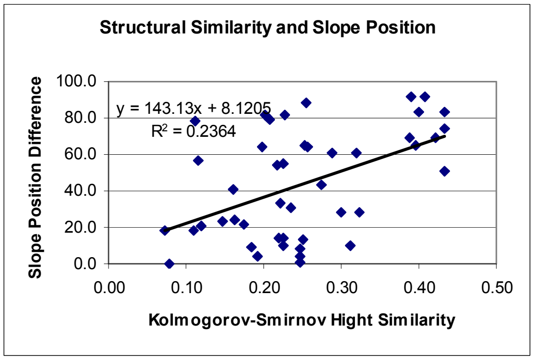












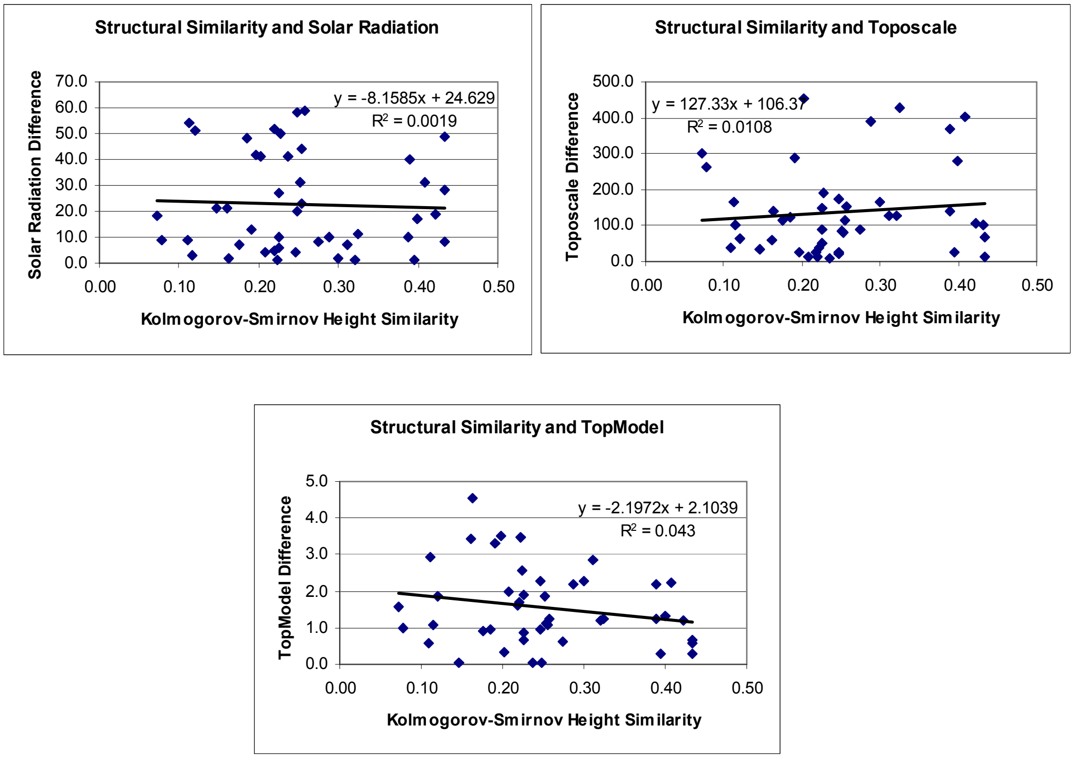
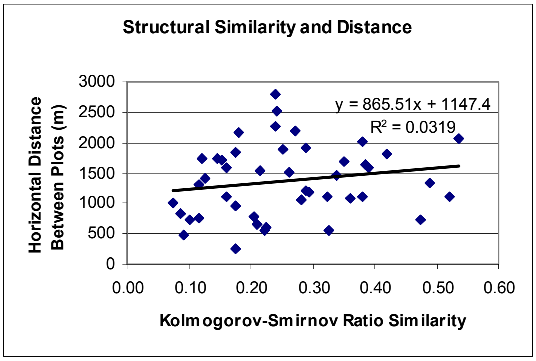


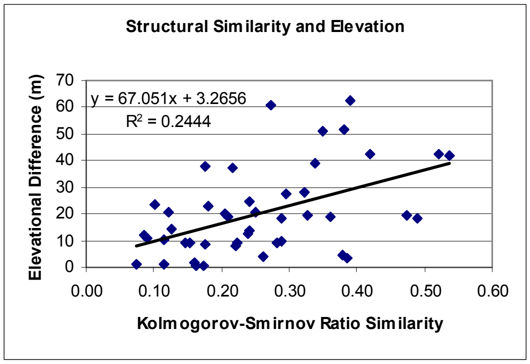
Figure 90 Scatterplots of similarity in distribution of height between plot-pairs (calculated using the Kolmogorov-Smirnov test of the distributions) against environmental difference between plot-pairs in TBS for derivatives of the Topo DEM.

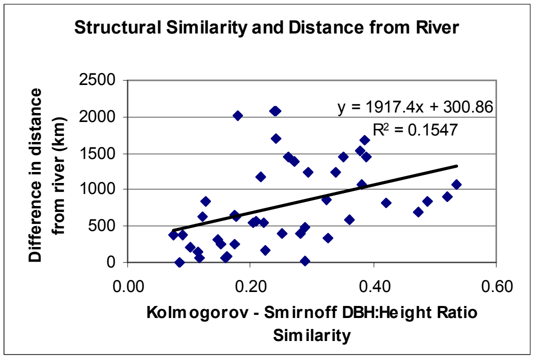
Variable	Mantel Test	One-tailed p-value	Correlation (alpha = 0.05)
Distance	0.27	0.063	Not-Significant
Distance from River	0.58	0.002	Significant
Altitude	0.28	0.034	Significant
Eastness	-0.17	0.085	Not-Significant
Northness	0.11	0.203	Not-Significant
Curvature	-0.12	0.224	Not-Significant
Slope	-0.17	0.192	Not-Significant
Slope Position	0.49	0.012	Significant
Solar Radiation	-0.04	0.423	Not-Significant
Toposcale	0.10	0.281	Not-Significant
TopModel	-0.21	0.077	Not-Significant

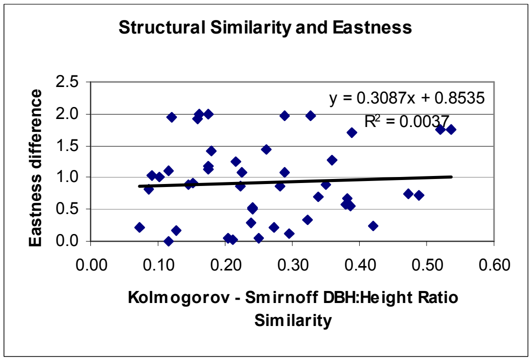
Table 50 Summary results of structural height similarity analysis with distance and environmental variables derived from the Topo DEM, using Mantel tests and a one-tailed

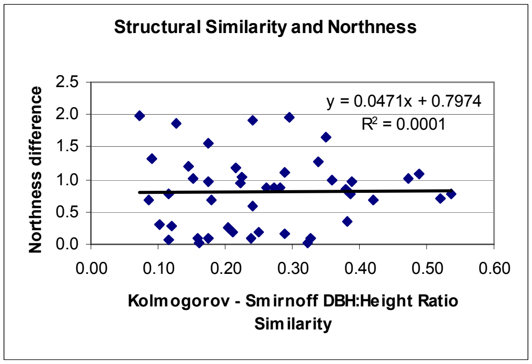
Pearson. Note that structural dissimilarity was compared with environmental dissimilarity (difference).

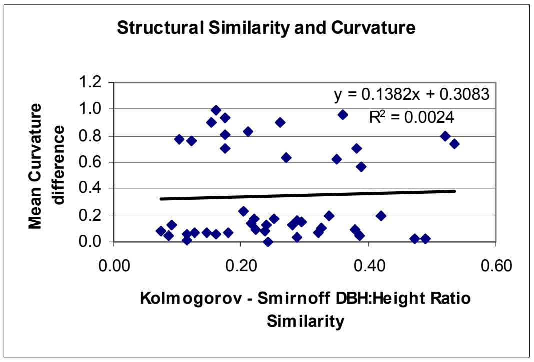


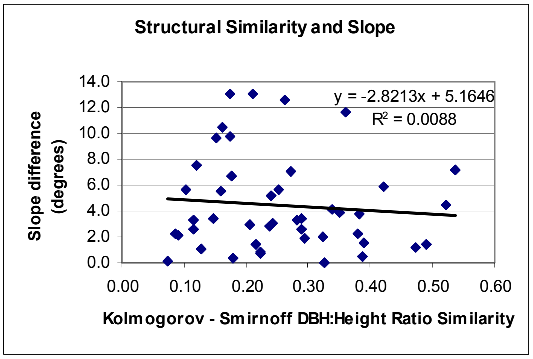


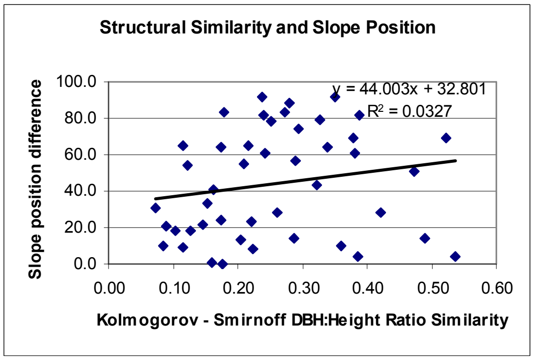












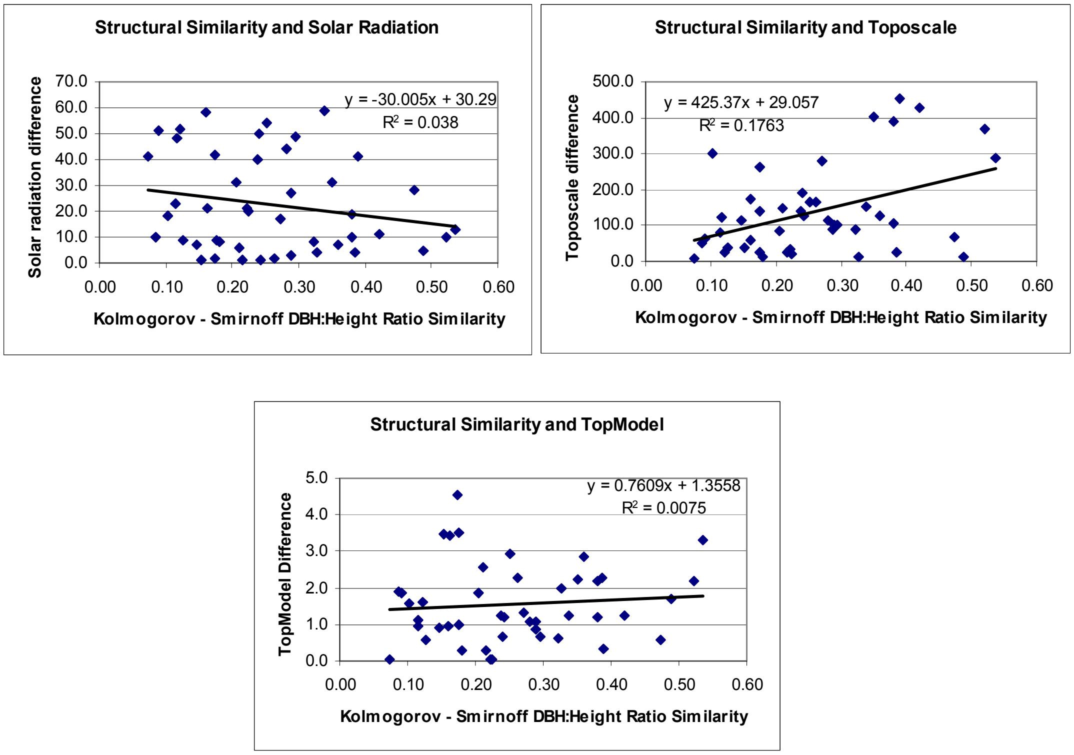
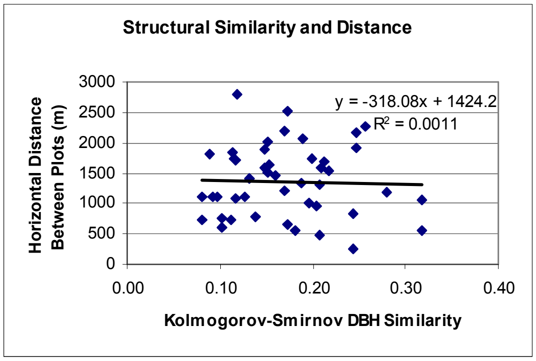


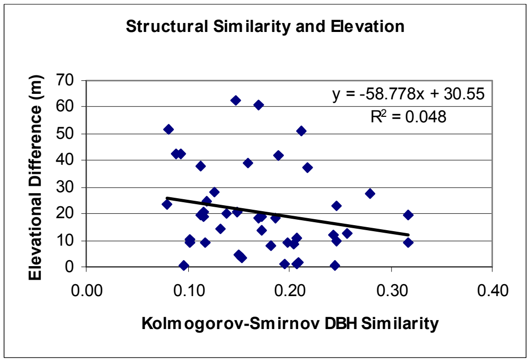
Figure 91 Scatterplots of similarity in distribution of the DBH/Height between plot-pairs (calculated using the Kolmogorov-Smirnov test of the distributions) against environmental difference between plot-pairs in TBS for derivatives of the Topo DEM.

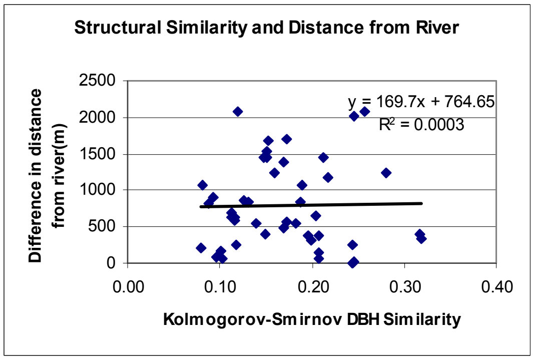
Variable	Mantel Test	One-tailed p-value	Correlation (alpha = 0.05)
Distance	0.18	0.161	Not-Significant
Distance from River	0.39	0.029	Significant
Altitude	0.49	0.010	Significant
Eastness	0.06	0.280	Not-Significant
Northness	0.01	0.426	Not-Significant
Curvature	0.05	0.373	Not-Significant
Slope	-0.09	0.439	Not-Significant
Slope Position	0.18	0.102	Not-Significant
Solar Radiation	-0.19	0.134	Not-Significant
Toposcale	0.42	0.014	Significant
TopModel	0.09	0.300	Not-Significant

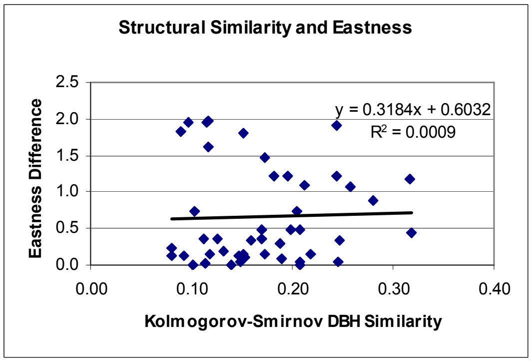
Table 51 Summary results of structural DBH/Height similarity analysis with distance and environmental variables derived from the Topo DEM, using Mantel tests and a one-tailed

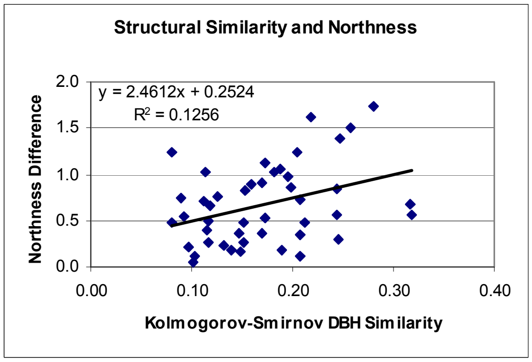
Pearson. Note that structural dissimilarity was compared with environmental dissimilarity (difference).

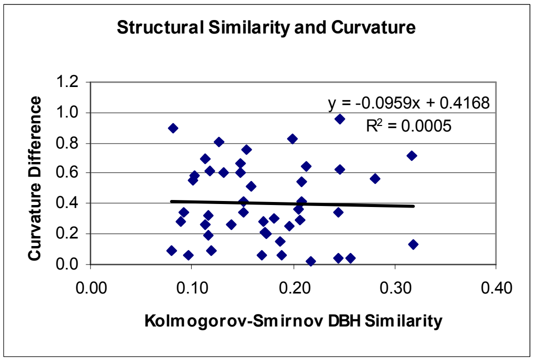












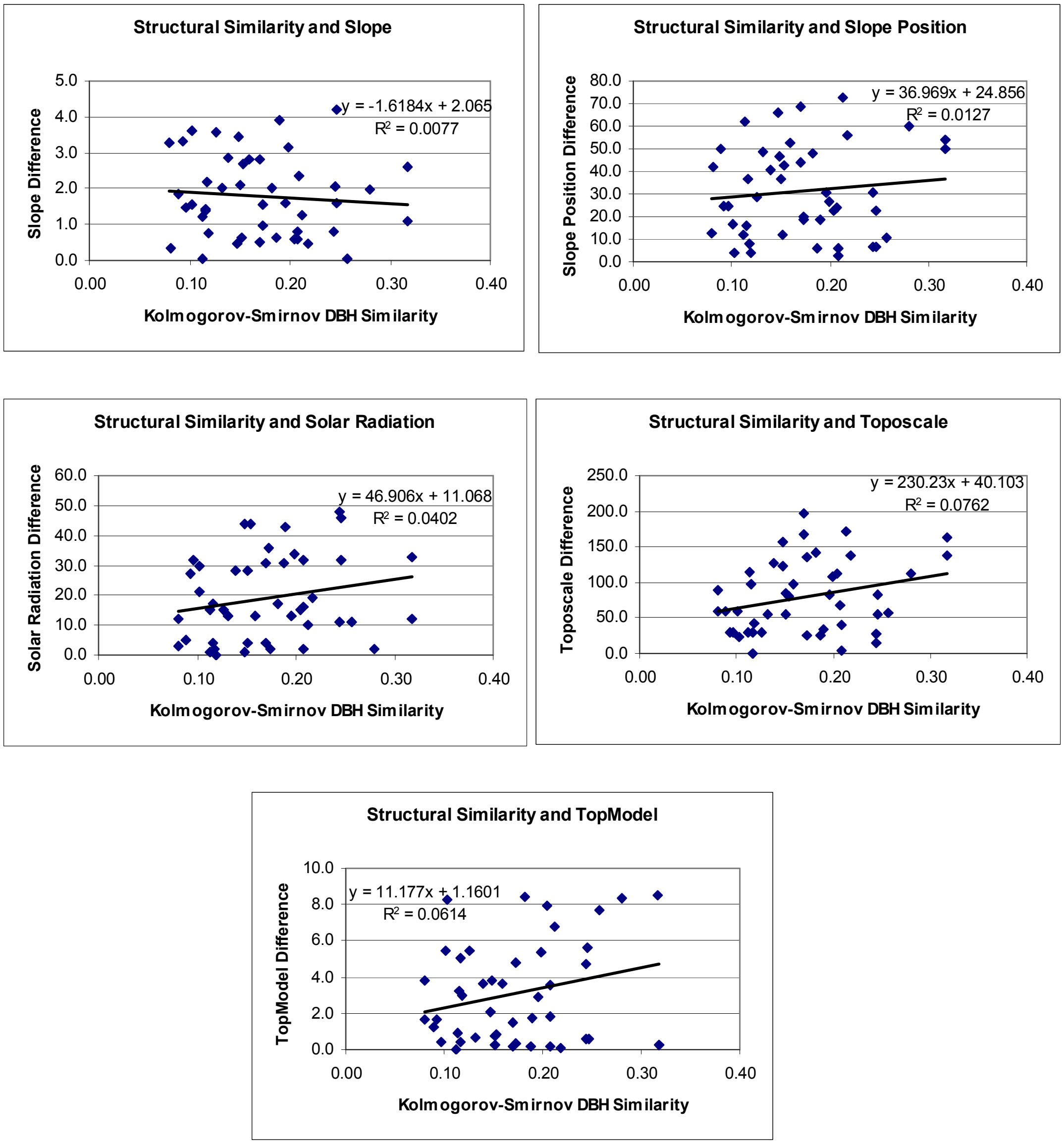
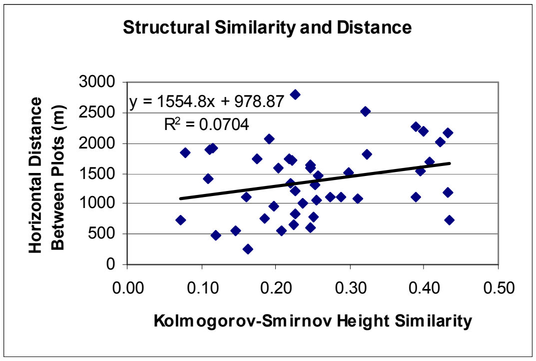
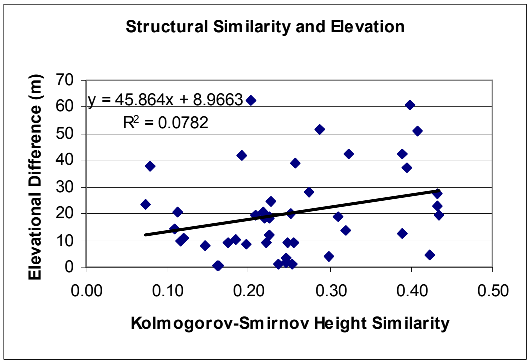


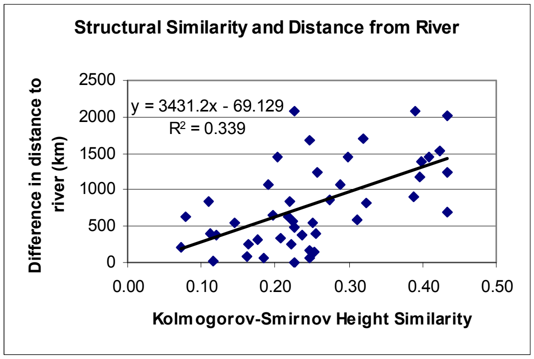
Figure 92 Scatterplots of similarity in distribution of DBH between plot-pairs (calculated using the Kolmogorov-Smirnov test of the distributions) against environmental difference between plot-pairs in TBS for derivatives of the SRTM DEM.

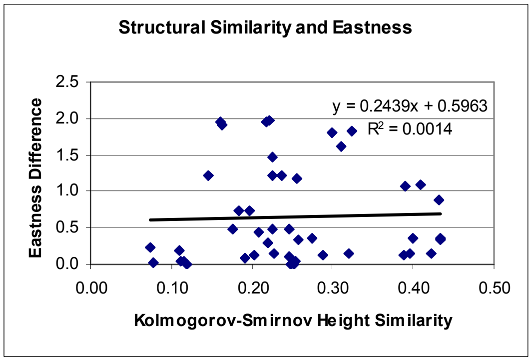
Variable	Mantel Test	One-tailed p-value	Correlation (alpha = 0.05)
Distance	-0.03	0.455	Not-Significant
Distance from River	0.02	0.400	Not-Significant
Altitude	-0.22	0.175	Not-Significant
Eastness	0.03	0.397	Not-Significant
Northness	0.35	0.038	Significant
Curvature	-0.02	0.481	Not-Significant
Slope	-0.09	0.307	Not-Significant
Slope Position	0.11	0.212	Not-Significant
Solar Radiation	0.20	0.184	Not-Significant
Toposcale	0.28	0.068	Not-Significant
TopModel	0.25	0.158	Not-Significant

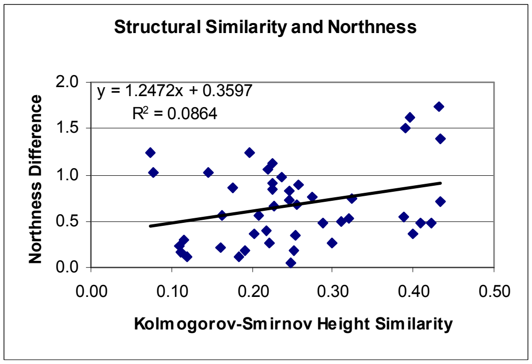
Table 52 Summary results of structural DBH similarity analysis with distance and environmental variables derived from the SRTM DEM, using Mantel tests and a one-tailed Pearson. Note that structural dissimilarity was compared with environmental dissimilarity (difference).

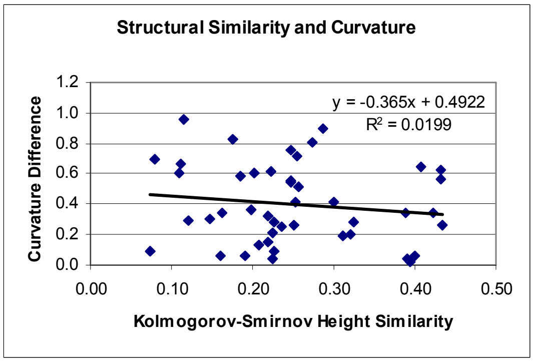

Structural Similarity and Distance
Horizontal Distance Between Plots (m)
3000
2500
2000
1500
1000
500
0
y = 1554.8x + 978.87
R² = 0.0704
0.00
0.10
0.20
0.30
0.40
0.50
Kolmogorov-Smirnov Height Similarity

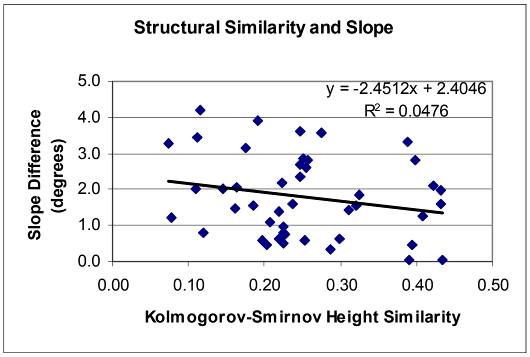

Structural Similarity and Elevation
Elevational Difference (m)
70
60
50
40
30
20
10
0
y = 45.864x + 8.9663
R² = 0.0782
0.00
0.10
0.20
0.30
0.40
0.50
Kolmogorov-Smirnov Height Similarity

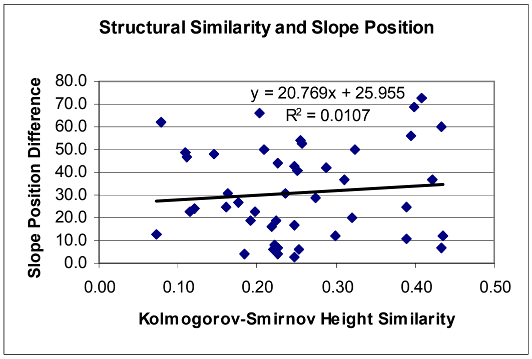

Structural Similarity and Distance from River
Difference in distance to river (km)
2500
2000
1500
1000
500
0
y = 3431.2x - 69.129
R² = 0.339
0.00
0.10
0.20
0.30
0.40
0.50
Kolmogorov-Smirnov Height Similarity


Structural Similarity and Eastness
Eastness Difference
2.5
2.0
1.5
1.0
0.5
0.0
y = 0.2439x + 0.5963
R² = 0.0014
0.00
0.10
0.20
0.30
0.40
0.50
Kolmogorov-Smirnov Height Similarity


Structural Similarity and Northness
Northness Difference
2.0
1.5
1.0
0.5
0.0
y = 1.2472x + 0.3597
R² = 0.0864
0.00
0.10
0.20
0.30
0.40
0.50
Kolmogorov-Smirnov Height Similarity


Structural Similarity and Curvature
Curvature Difference
1.2
1.0
0.8
0.6
0.4
0.2
0.0
y = -0.365x + 0.4922
R² = 0.0199
0.00
0.10
0.20
0.30
0.40
0.50
Kolmogorov-Smirnov Height Similarity


Structural Similarity and Slope
Slope Difference (degrees)
5.0
4.0
3.0
2.0
1.0
0.0
y = -2.4512x + 2.4046
R² = 0.0476
0.00
0.10
0.20
0.30
0.40
0.50
Kolmogorov-Smirnov Height Similarity


Structural Similarity and Slope Position
Slope Position Difference
80.0
70.0
60.0
50.0
40.0
30.0
20.0
10.0
0.0
y = 20.769x + 25.955
R² = 0.0107
0.00
0.10
0.20
0.30
0.40
0.50
Kolmogorov-Smirnov Height Similarity

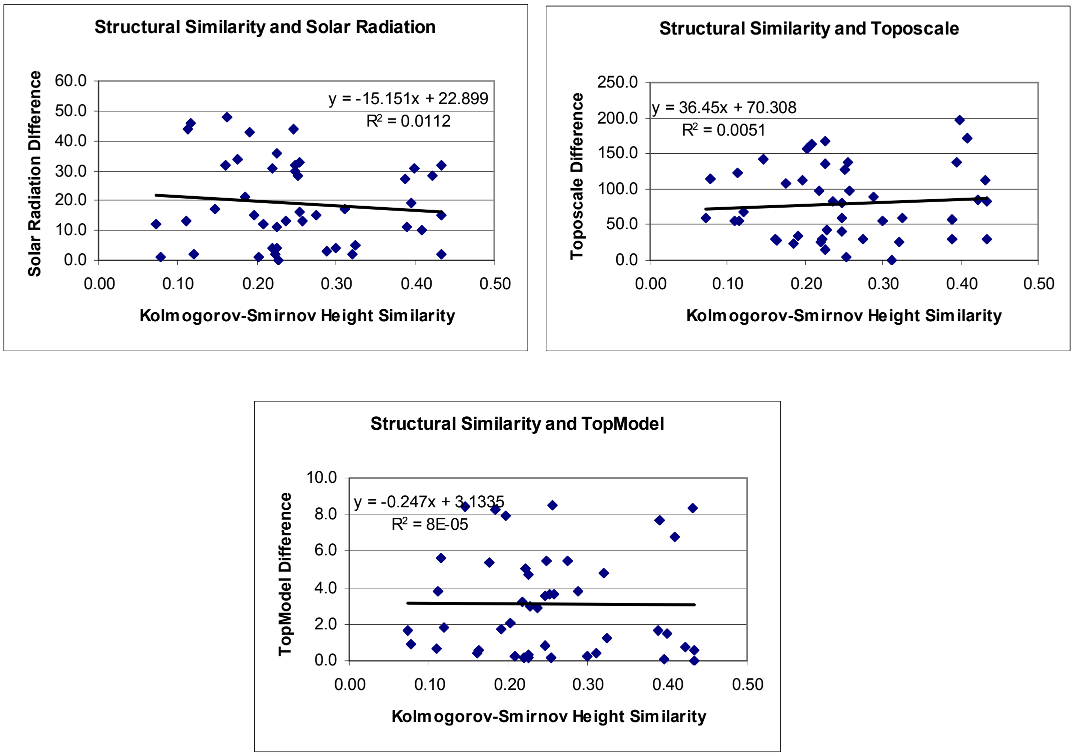
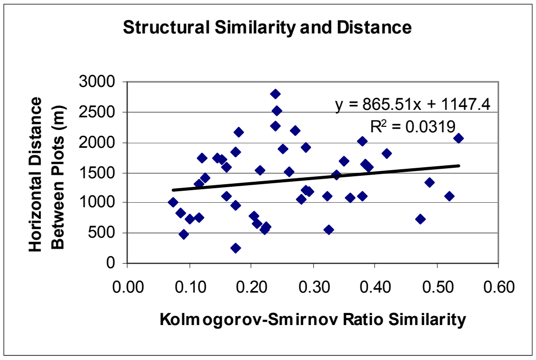


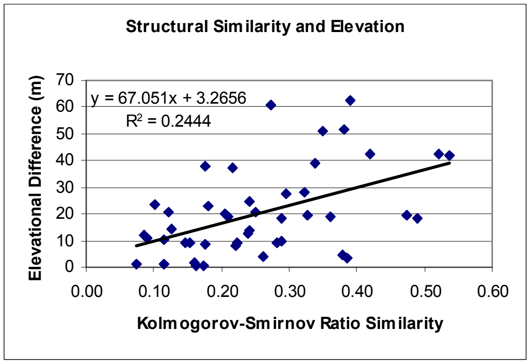
Figure 93 Scatterplots of similarity in distribution of height between plot-pairs (calculated using the Kolmogorov-Smirnov test of the distributions) against environmental difference between plot-pairs in TBS for derivatives of the SRTM DEM.

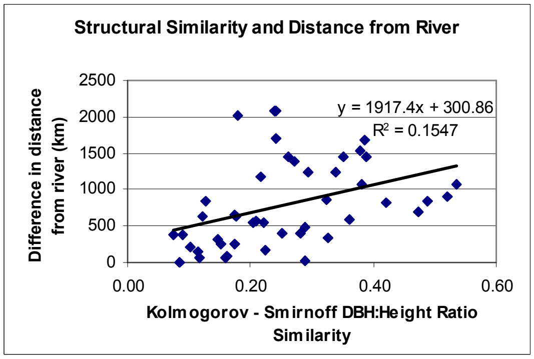
Variable	Mantel Test	One-tailed p-value	Correlation (alpha = 0.05)
Distance	0.27	0.053	Not-Significant
Distance from River	0.58	0.004	Significant
Altitude	0.28	0.037	Significant
Eastness	0.04	0.428	Not-Significant
Northness	0.29	0.040	Significant
Curvature	-0.14	0.156	Not-Significant
Slope	-0.22	0.025	Significant
Slope Position	0.10	0.178	Not-Significant
Solar Radiation	-0.11	0.258	Not-Significant
Toposcale	0.07	0.266	Not-Significant
TopModel	-0.01	0.498	Not-Significant

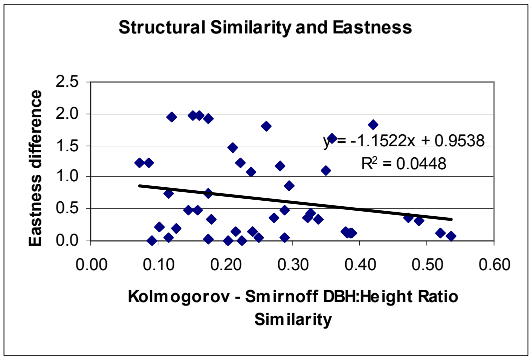
Table 53 Summary results of structural height similarity analysis with distance and environmental variables derived from the SRTM DEM, using Mantel tests and a one-tailed

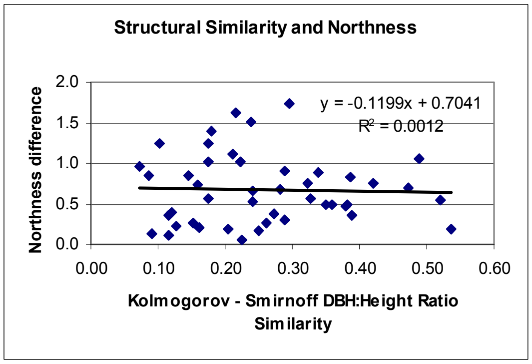
Pearson. Note that structural dissimilarity was compared with environmental dissimilarity (difference).

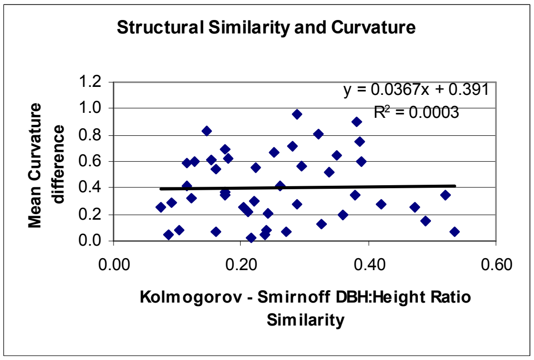


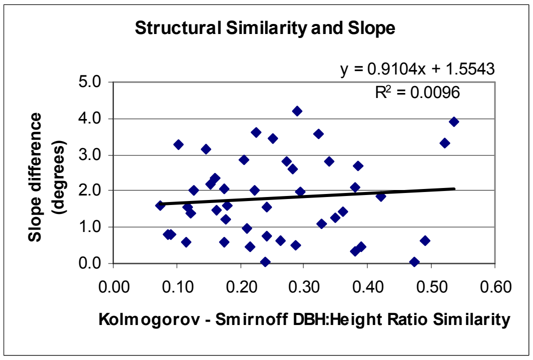


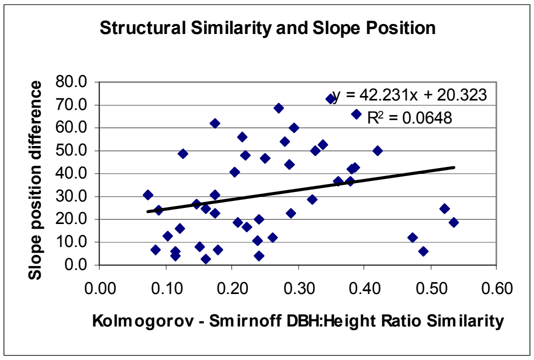












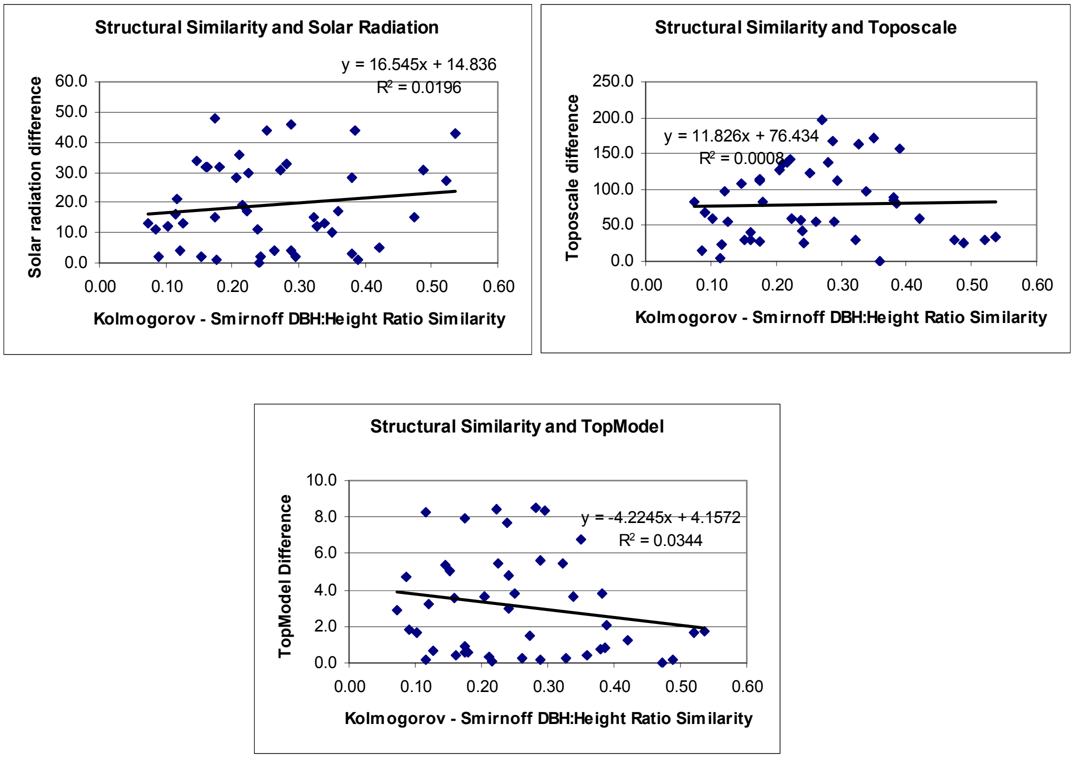


Figure 94 Scatterplots of similarity in distribution of DBH/Height between plot-pairs (calculated using the Kolmogorov-Smirnov test of the distributions) against environmental difference between plot-pairs in TBS for derivatives of the SRTM DEM.

Variable	Mantel Test	One-tailed p-value	Correlation (alpha = 0.05)
Distance	0.18	0.164	Not-Significant
Distance from River	0.39	0.031	Significant
Altitude	0.49	0.008	Significant
Eastness	-0.21	0.149	Not-Significant
Northness	-0.03	0.440	Not-Significant
Curvature	0.02	0.397	Not-Significant
Slope	0.10	0.231	Not-Significant
Slope Position	0.25	0.066	Not-Significant
Solar Radiation	0.14	0.191	Not-Significant
Toposcale	0.03	0.362	Not-Significant
TopModel	-0.19	0.173	Not-Significant

Table 54 Summary results of DBH/Height similarity analysis with distance and environmental variables derived from the SRTM DEM, using Mantel tests and a one-tailed

Pearson. Note that structural dissimilarity was compared with environmental dissimilarity (difference).

A number of correlations are found between structural frequency distribution similarity and topographic similarity between plot pairs. Independent of the DEMs, the structural frequency distributions of tree height and DBH/Height correlate significantly with both distance from river and elevation (both variables are strongly co-linear, and likely correlating as a result of the same causal process, Pearson = 0.40, p = 0.01), whereby greater structural dissimilarity occurs in plots elevationally highly different or highly different in their distances from river (both of which amount to the same pattern due to co-correlation).

In terms of topographic characteristics derived from each DEM, the TOPO DEM provides the greatest number of correlations with DBH and tree height similarity correlating positively with slope position similarity (co-linear with elevational similarity, Pearson = 0.35, p = 0.02), and DBH similarity inversely correlating with toposcale and mean curvature similarity (with these two variables co-linear, Pearson = 0.38, p = 0.01). The latter inverse correlation is likely spurious or due to inverse co-linearity as there is no reasonable explanation for significantly differently "curved" sites having similar structural distributions. DBH/Height similarity also positively correlates with toposcale similarity.

There are three significant correlations for the SRTM DEM, including positive correlation between similarity in DBH and northness, and between tree height similarity and northness similarity (with northness difference for the SRTM DEM being significantly co-linear with distance from river difference, Pearson = 0.29, p = 0.05). Finally an inverse correlation between tree height similarity and slope similarity is found (and slope difference is weakly inversely correlated with northness difference, Pearson = -0.27, p = 0.07). No significant correlations are found for the DBH/Height variable using the SRTM DEM.

After unraveling many of the co-linearities in the data, only one correlation is worth highlighting and merits further discussion. This is the correlations between tree height and DBH/Height similarity and difference in distance from river / elevation (which are strongly co-linear). This pattern provides stronger evidence of the variation in structural characteristics across the elevational gradient and with greater distance from the main river channel. However, as shown in Section 5.2.1.2.2, this correlation is not consistent when only low elevation plots are included in the analysis. When a Mantel test is performed for tree height similarity and difference in distance from river for Plots 1 – 7 only, the correlation is no longer significant (Mantel = 0.07, p = 0.30, n = 21), similarly for the DBH/Height variable (Mantel = 0.16, p = 0.20, n = 21).

Once again, the conclusion is that there are two distinct forests in TBS in terms of structural tree height and DBH/Height, with upland sites distant from the river (i.e. *terra firme* forest) having significantly greater tree height and lower DBH/Height values. The exact reason for this pattern cannot be identified with the data available.

5.3.2.1.3 Structural distribution – diversity relationships

For each of the three major structural variables (DBH, Height and DBH/Height), K-S analyses and Mantel tests are applied between structural similarity and compositional similarity in order to quantify the relationships between structure and species composition (Figure 95).

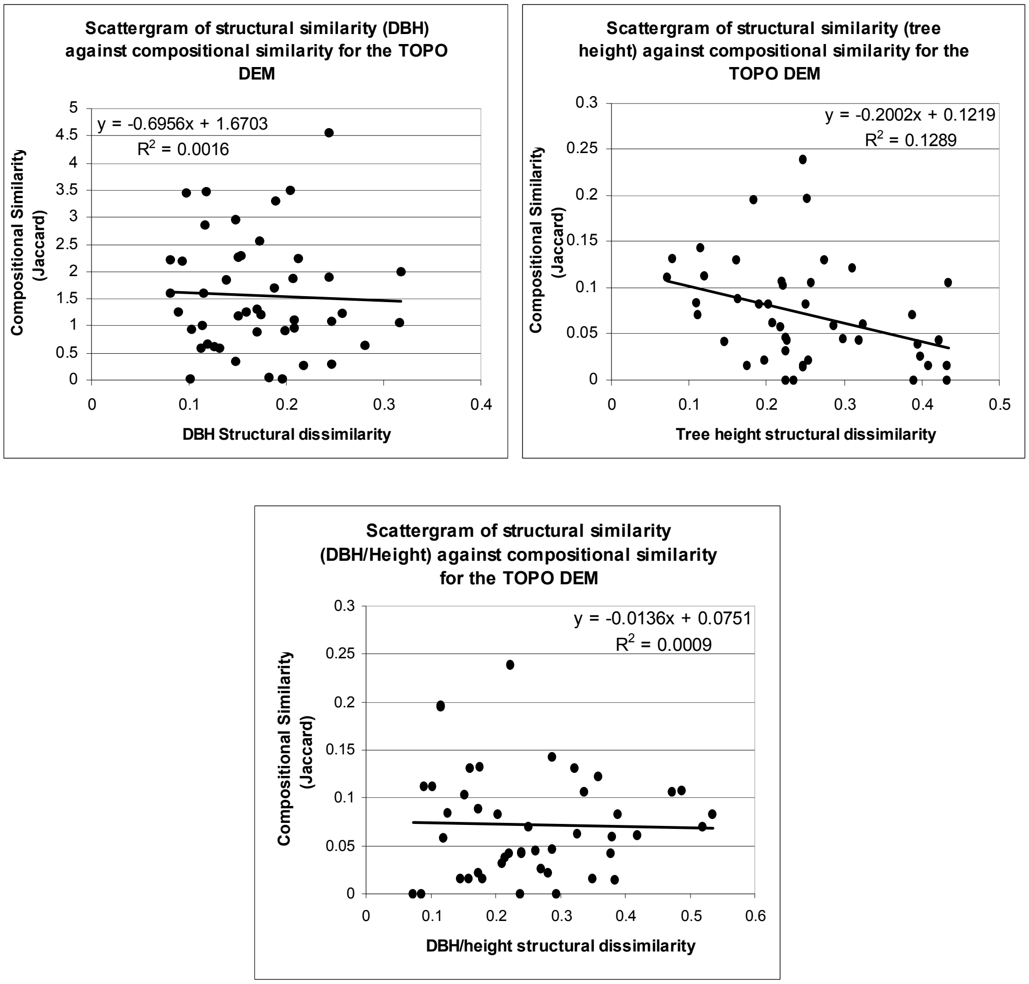


Figure 95 Scatterplots for plot-pairs of compositional similarity against structural dissimilarity for the major structural variables in TBS.

As can be seen, significant correlation is found between tree height similarity and species composition (Mantel = -0.359, p = 0.02, n = 45), whereby structurally similar plots also tend to be compositionally similar, though just 13% of variability is explained through this relationship. The lack of correlation in DBH and DBH/Height and the 87% of unexplained variability in the tree height similarity may be due to a combination of two factors. First, compositionally identical plots with individuals of different ages would be expected to have different structural characteristics. Secondly, it is also likely that the poor correlations are the result of varying environment, whereby tree structure for any species is strongly dependent on the environment where it is found. In this sense compositionally identical plots may have very different structural characteristics if found in different environments.

5.4 Conclusions

This chapter has described the structure in a tropical montane (cloud) forest (Tambito) and in a lowland Amazonian forest (TBS), with marked differences between the sites. Stem density in Tambito is higher (average 13.5% higher), with an associated lower average diameter at breast height (13.3% higher in TBS). Basal area is also significantly greater in TBS (49% greater in TBS than in Tambito), possibly as a result of greater density of individuals with buttress roots (reported by Richards, 1996). However, conversely the DBH/Height in TBS is higher, indicating that relative to height trees in Tambito invest greater in trunk growth, possibly as a response to lower stability due to high slopes and unstable soils, and high wetness increasing the chances of trunk rot. Average tree height is the most contrasting between the sites, with TBS having an average tree height which is 36.5% greater than in Tambito, with 7.2% of individuals being over 20m tall in TBS compared to just 1.6% in Tambito. This difference in tree height between sites is well documented in the literature (Whitmore, 1998), and can also be attributed to the lower stability of trees in montane sites due to the steep slopes and high wetness, which make the establishment of large individuals unlikely due to frequent tree fall.

When micro-scale variability is examined within each site, surprisingly few patterns emerge in the structural data. In Tambito no elevational patterns are evident, despite numerous reports in the literature of increasing stem densities and decreasing tree stature with increasing elevation (Huston, 1994; Pendry and Proctor, 1996; Pendry and Proctor, 1997; Kappelle, 2004). However, a strong significant correlation is found between DBH/Height (average and the distribution of values) and topmodel (an indicator of surface soil moisture, also an indicator of fluvial incision into the landscape), whereby individuals make greater investment in trunk diameter relative to their height on modelled more moist (incised) slopes. Whilst sites with potentially high soil moisture may have low levels of soil stability indicating a higher risk of tree fall, soil moisture is also highest on flatter slopes where water tends to accumulate, rather than on steeper slopes. This renders topmodel a poor indicator of risk of tree fall, and indeed when a model of tree fall risk is produced based on cumulative upslope area and local slope, no correlations are found. The significant correlation between DBH/Height and topmodel may be either spurious/non-causal, or indicate a physiological response of trees to invest in trunk diameter in sites with higher soil moisture. No reports of this are available in the literature to provide further discussion on the topic.

When multi-variate statistics are applied to explain the micro-scale variability in structure in Tambito, interesting patterns are found with stem density and tree height. Micro-scale variability in stem density is explained through a combination of elevation and curvature/exposure (measured with the toposcale variable), whereby stem density increase with elevation, and is higher on more exposed sites. This may be explained by the potential stunting of trees on exposed ridges due to wind-cropping and prolonged leaf wetness (supported by Letts, 2003) meaning that the site may support a greater number of smaller tree individuals. This is a finding supported in the literature by a similar study by Webb et al. (1999). Tree height is also found to be highest in sites with low topmodel values (i.e. dry soils) and in areas of low solar radiation, though the validity of this relationship is more questionable as few ecologically interpretations are available and solar radiation alone does not capture many important aspects of solar radiation receipt in Tambito (discussed in depth in Section 3.4.1.3.1). More plot points would be required to conclude that this be a causal relationship.

In TBS, a number of significant correlations are found between topographic characteristics and structure (in terms of both average and distribution), though strong co-linearity between variables means that it is likely that only one clear pattern emerges in the data. Significant difference is found in tree height between the three highest elevation plots and the lower-elevation plots, possibly different in terms of flooding regime with plots below 220m elevation being subjected to occasional flooding and having significantly lower average tree stature than the three higher elevation plots (high elevation plots have 28% greater average tree height). However, significant correlation is also found between distance from river and tree height, meaning that the observed difference in tree heights between Plot 8-10 and Plots 1-7 may also be as a result of a long-term gradient in edaphic and successional conditions brought about by river migration (a theory also presented and discussed in Section

4.3.2.1.2 with respect to an observed diversity gradient). It is important to note that a gradient in tree height is not observed with greater distance from river or elevation (i.e. the correlation does not stand for Plots 1-7 only), but that rather two unique classes are observed between *terra firme* and *varzea* forest. No other correlations are found to explain the remaining variability, though DEM quality issues in TBS also limit the degree to which it can be concluded that environment has no role in explaining variability in structure.

Finally, this chapter has briefly examined relationships between diversity and structure, and composition and structure. In Tambito a significant correlation is found between plot average DBaseH and DBH/DbaseH and diversity, with plots with higher average DbaseH and lower DBH/DbaseH ratio values having the higher diversity. The latter correlation is likely due to co-linearity with curvature and therefore spurious (found in Chapter 4, Section 4.2.2.1.2 to be significant in explaining diversity), and few ecological interpretations are available for the former correlation. Compositional similarity is also shown to explain some variability in DBH structural similarity between plots, though a remaining 90% of variability (the vast majority) is unexplained. No such pattern was found for tree height or the DBH/Height variable. In TBS even fewer relationships between structure and diversity were found, except for composition explaining 13% of variability in tree height. In both sites, a large degree of structural variability is not explained by composition, indicating that tree age and stochastic processes such as tree fall and the subsequent successional processes prevent many species from reaching full maturity. However, the DBH/Height variable is less sensitive to tree age (though DBH/Height is likely to increase slightly over time as the tree reaches the canopy, but nevertheless the value is far more stable with age than basic DBH or tree height), and the abject lack of correlations between compositional similarity and DBH/Height similarity between-plots also leads to believe that environment significantly affects the structural forms of individuals of the same species. More in depth studies could be made to quantify this ‘plasticity’ in structural form of species across environmental gradients.

In conclusion, a great deal of variability in structure is not accounted for using the topographic variables adopted in this study. This signifies that either the variables themselves are not capturing environmental conditions that are significant in driving structural variability, or a large degree of micro-scale variability in structure is actually controlled by processes such as tree fall, predominantly stochastic in both space and time. These stochastic processes result in different age distributions of individuals, and resultant differences in structural characteristics especially when examined at the 25 m plot-scale. Furthermore, forest structure itself is a significant factor in further partitioning landscape-controlled resources, resulting in a feedback mechanism which changes alongside the dynamic in tree age distribution. Instead of considering how landscape controls the partitioning of resources and thus the structure of the forest (as studied here), it may be more important to consider how a combination of landscape and chance disturbances control forest age distributions, which alongside landscape controlled resources affect forest structure through a feedback mechanism. Temporal studies of forest structural change across a landscape are required to understand these complex interactions.

Chapter 6

6 Effect of spatial heterogeneity of environmental variables on the diversity

6.1 Research Strategy

Previous chapters have examined the conditions found at each plot, and examined the relationship between topography and the structure and diversity of the forest. Some significant relationships have been found, and some variability can be explained through *within-plot* conditions. This chapter endeavours to explain more of the variability in composition and diversity through examining how the topographic conditions *surrounding* each plot may shape the within-plot diversity and composition that has been measured *within-plot*. The rationale for this analysis is that many *within-plot* processes are affected by local effects through inherently spatial (neighbourhood) ecological processes such as seed dispersal and competition, which permit the movement and interaction of species across a landscape, maintaining diversity and driving evolution. Ecological research has often cited "environmental heterogeneity" as an important driver of diversity (starting with Ricklefs, 1977), under the hypothesis that regions with abrupt environmental gradients contain a high number of different species because of their greater availability of different niches, which creates a rich local seed pool. Central to this theory is the notion that species distributions are associated with their environment, so that a diverse surrounding environment does indeed signify a diverse local pool of species. Recent studies have questioned the degree to which habitat associations occur in tropical lowland forests (discussed in Section 2.3.2) with 20% - 80% of species found to have habitat association depending on the study and the site (Webb and Peart, 2000; Harms et al., 2001; Phillips et al., 2003; St-Louis et al., 2004). In montane forests there are many studies that show strong associations between elevation (representing an environmental gradient in many climatic factors) and species composition (discussed in Section 2.3.1), though none of these focus on micro-scale environmental variability. The analysis presented in this thesis has shown strong evidence of habitat association in species composition in Tambito (association between composition and elevation), along with some degree of habitat association in TBS (association between composition and northness, toposcale and elevation, though the validity of this has been questioned). Given this evidence, it is reasonable to expect that spatial heterogeneity is an important factor in shaping the diversity in a montane forest, and to a lesser extent in a lowland forest.

As already introduced in Chapter 2, the concept of environmental heterogeneity in tropical forests may provide a degree of unification between non-equilibrium and equilibrium based theories of species diversity maintenance. If in tropical forests the random occurrence in both space and time of tree and branch fall means that recruitment in gaps is dominated by chance occupants (Brokaw and Busing, 2000), but that there is also some degree of niche-specialization in some tree species (for example Phillips et al., 2003, also discussed in depth in Section 2.3.2), spatially heterogeneous environments would potentially provide a diverse local seed pool for gap recruitment because habitat preferences would mean that the pool of potential immigrants were diverse, increasing the chances that a specialist to the conditions in the gap may arrive through short-distance seed dispersal. This argument is centered on the process of seed dispersal, though spatial heterogeneity is also of importance for biotic interactions, specifically herbivory and competition Spatially heterogeneous landscapes are considered to be favourable for diversity through the prevention of competitive exclusion (discussed in detail by Huston (1994)) assuming species to have some niche specialisation. The resultant increase in diversity of host species is also argued to intensify herbivory, further preventing competitive exclusion and thus promoting higher species diversity through what has been termed a positive feedback (DeAngelis et al., 1986).

The significance of spatial heterogeneity on tropical tree diversity in the context of this thesis is outlined in Figure 96, showing how the environmental conditions in neighbourhood regions may be relevant to the species composition and diversity within the plots. The central assumption of the model is that habitat association occurs at least to some extent in tropical forests. In this example, Plot A is located where the neighbouring regions are environmentally heterogeneous, therefore through a degree of habitat association there is also a diverse surrounding local seed pool. This increases the chances of immigration of many different species into the plot through seed dispersal. For these reasons, Plot A is expected to be more diverse than Plot B on the basis of heterogeneity alone. In the real system there will also be interactions of the effect of the heterogeneity on other important properties such as total resources (light would be less in plot A than plot B here).

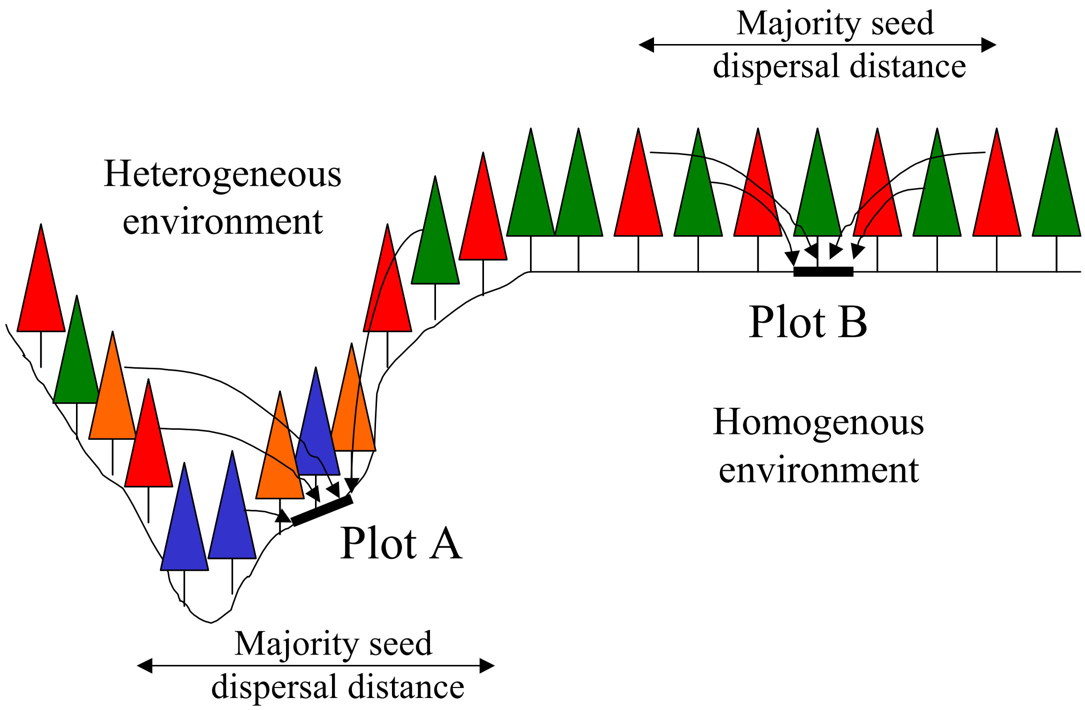


Figure 96 Model role of environmental heterogeneity on within-plot diversity in tropical forests through seed dispersal. Plot A, located in a heterogeneous environment is likely to receive seeds from more local habitats than Plot B.

There are numerous examples of studies which examine the role of spatial heterogeneity on ecological processes (Harner and Harper, 1976; Bell et al., 2000; Barberis et al., 2002; Lundholm and Larson, 2003; Pausas et al., 2003). Few of these actually quantify heterogeneity numerically (though there are notable exception, for example Burnett et al., 1998), and none examine the role of spatial heterogeneity in shaping diversity in tropical forests. This chapter aims to quantify the spatial heterogeneity for the terrain characteristics used in previous chapters, and examine how heterogeneity relates to the tree diversity measured in the plots in Tambito and in TBS. The approach here is to take each variable, quantify heterogeneity at multiple scales and compare for each scale the relationship between topographic heterogeneity and tree diversity. Multiple-scales are used because there is insufficient literature quantifying the probability of seed dispersal against distance for the "average" tropical species, and indeed, since much seed dispersal is through animal movements, the patterns of dispersal are likely to be complex. There are numerous examples that quantify the distance-function of seed dispersal for specific species (for example Peres and Baider, 1997; Wenny, 1999), but insufficient information is available to restrict this analysis to one single scale representing the average distance function for the community as a whole.

As described in Chapter 3, 16 scales are used on 12 terrain derivatives. This means that a total of 192 correlations are performed per site, and there are two sites with two different DEMs used for one of them (TOPO and SRTM DEMs in TBS). This results in a total of 576 correlations presented in this chapter, and for this reason not all scattergrams are presented. Instead, graphs of the correlation coefficients across all scales for each variable are presented, and summary tables provide a summary of the most significant results for each variable. Graphs are plotted for each variable across all scales, with a line (black) plotting the Pearson correlation, and a second line (blue) which plots the respective p-value. For ease of interpretation, a solid blue line is also shown representing the threshold at which point a correlation becomes significant (p-value < 0.05). This 95% confidence limit means that one in twenty correlations would be significant in a randomly generated set of numbers, so if we are to conclude any significance in the relationship between heterogeneity and diversity in this case the number of significant correlations per DEM should far exceed 9.6 (5% of the 192 correlations). As spatial heterogeneity for any one variable between different scales is likely co-linear, significant correlations should also occur across multiple scales for any concrete conclusion to be reached. A random control is used in the analysis to further examine this problem of non-causal random relationships being found.

As in the previous chapters each site is treated separately, and in this case the results are presented separately for each DEM in the case of TBS. The chapter concludes by discussing in detail the results from both sites, attempting to extract generalities in the findings and to link these to the biological processes that may be creating the patterns.

6.2 Reserva Tambito

The Tambito site is a tropical montane forest with dramatic environmental gradients. The environmental heterogeneity is apparent in any photograph of the landscape, with strong changes in elevation across short distances which closely control a number of associated environmental variables). In the field, this is noticeable simply by walking along the network of paths, with rapid changes in micro-climates depending on exposure, aspect, and slope amongst other factors. Slopes reach 60 degrees in the steepest parts of the catchments, meaning that in just 100m of horizontal distance the elevation may change by 173m, signifying a change in temperature of 1.0^{o}C. Slope is a key variable, where steep slopes are likely to imply rapid change in many other variables, including elevation, wetness (TopModel), and slope position. However, steep slopes also imply higher levels of disturbance through tree fall (Gale, 2000), and favour the establishment and dominance of species adapted to gaps with rapid growth under high light levels. In this respect high heterogeneity in some variables could also have a detrimental affect on diversity.

6.2.1.1 Spatial heterogeneity results

6.2.1.2 Cross-correlation matrix

Having run the heterogeneity model, the resultant grids of heterogeneity for each variable are cross-correlated to examine their degree of co-linearity (Figure 97). As all terrain derivatives originate from the same DEM, it is expected that heterogeneity in many of these derivatives will be somewhat cross-correlated.

	Elevation	**Eastness**	**Northness**	**Curvature**	**Slope**	**Slope Position**	**Solar**	**Toposcale**	**Topmodel**	**Topoclass**	**Feature**	**Feature (network)**
Elevation	-	-0.11	-0.21	0.57	0.04	0.28	0.55	0.52	-0.01	0.44	0.19	-0.36
Eastness		-	-0.40	0.07	0.13	-0.16	0.67	0.07	-0.01	0.21	-0.06	0.18
Northness			-	0.06	0.17	-0.10	-0.38	0.01	0.17	0.06	-0.07	0.29
Curvature				-	0.53	-0.09	0.52	0.51	0.23	0.68	0.33	0.30
Slope					-	-0.16	0.22	0.36	0.17	0.44	0.26	0.31
Slope Position						-	0.04	0.24	-0.37	-0.15	0.09	-0.45
Solar							-	0.34	-0.06	0.49	0.14	-0.05
Toposcale								-	0.18	0.65	0.23	0.03
Topmodel									-	0.19	0.06	0.29
Topoclass										-	0.06	0.26
Feature											-	-0.11
Feature (network)												-

Figure 97 Cross-correlation matrix between all spatial heterogeneity variables with the median distance set at 1 cell in Tambito (n = 69,678 in all cases).

Greatest cross correlation exists between topoclass and curvature (Pearson = 0.68), eastness and solar radiation (Pearson = 0.67), and toposcale and topoclass (for obvious reasons as topoclass is simply a reclassification of toposcale, Pearson = 0.65). The heterogeneity in the feature classification is only slightly negatively correlated with heterogeneity in the network feature classification (Pearson = -0.11). Also worth mentioning is that heterogeneity in northness inversely correlates with heterogeneity in eastness (Pearson = -0.40), not surprising as they are both directly derived from aspect. This results from the complex relationship between eastness and northness (when northness is plotted against eastness a perfect circle of radius 1 index unit is formed). The inverse correlation originates with this relationship, where moderate-low heterogeneity is actually impossible in both variables simultaneously. Heterogeneity in mean curvature is on average the most cross-correlated variable, and the heterogeneity of the feature classification and topmodel are the most independent.

On the whole, cross-correlations of heterogeneity in the terrain derivatives correlate slightly more than the cross-correlation of the derivatives themselves (average Pearson = 0.24 for heterogeneity cross-correlations compared with average Pearson = 0.23 for the cross-correlations of the derivatives themselves). This is important, and signifies that a specific site cannot be described as universally heterogeneous. Heterogeneity in one variable does not necessarily signify heterogeneity in other variables, and indeed in some cases may signify homogeneity.

6.2.1.3 Comparison with plot data

6.2.1.3.1 Control Experiment

Prior to performing detailed analyses of relationships between environmental and topographic heterogeneity and plot diversity, it is necessary to make a control experiment using pseudo-random 'environmental' data to understand to what extent correlations may arise through chance rather than causal relationship. Twelve random grids were produced using Arc/Info (RAND command), with values ranging from 0 -

1, and the heterogeneity model applied to these grids using all 16 scales. The Pearson correlation coefficients between the plot diversity data and the resultant random grid heterogeneity results for each scale are then calculated (Table 55), and an example multi-scale correlation graph is shown for one of the random grids (Figure 98), in the same way as the results of the terrain derivatives are to be presented.

Random Run	Maximum Pearson	Minimum Pearson	No. Scales with significant correlation
Random grid 1	0.29	0.10	0
Random grid 2	0.26	0.08	0
Random grid 3	0.25	-0.24	0
Random grid 4	0.25	0.12	0
Random grid 5	0.25	0.02	0
Random grid 6	0.30	0.24	0
Random grid 7	0.44	0.25	0
Random grid 8	0.25	0.07	0
Random grid 9	0.25	0.06	0
Random grid 10	0.29	0.00	0
Random grid 11	0.25	0.11	0
Random grid 12	0.54	0.25	0

Table 55 Results of the heterogeneity analysis for the 12 random grids in Tambito.

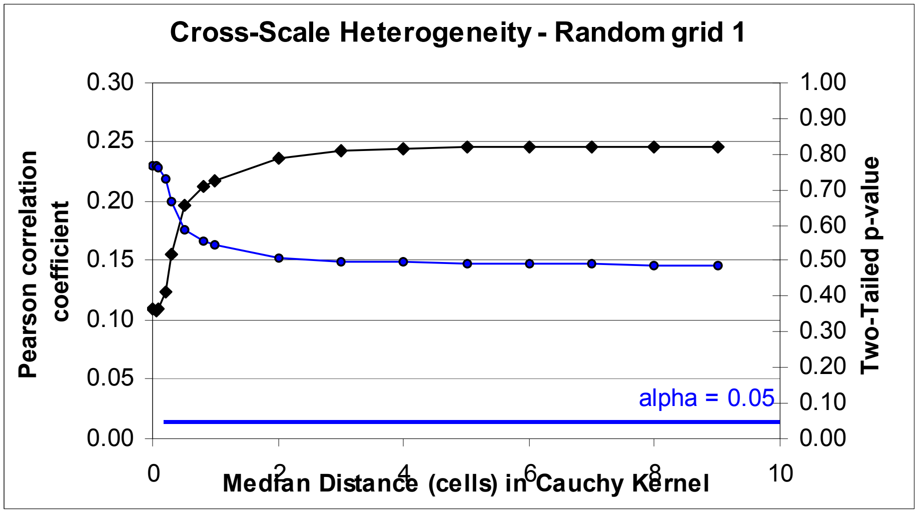


Figure 98 Control experiment of cross-scale heterogeneity for Random Grid 1, a grid with random values. Black line represents the Pearson correlation coefficient, whilst the blue line

represents the respective p-value. The solid blue line is placed at the 95% confidence level, meaning that a correlation is considered statistically significant when the plot of p-values goes under the thick blue line.

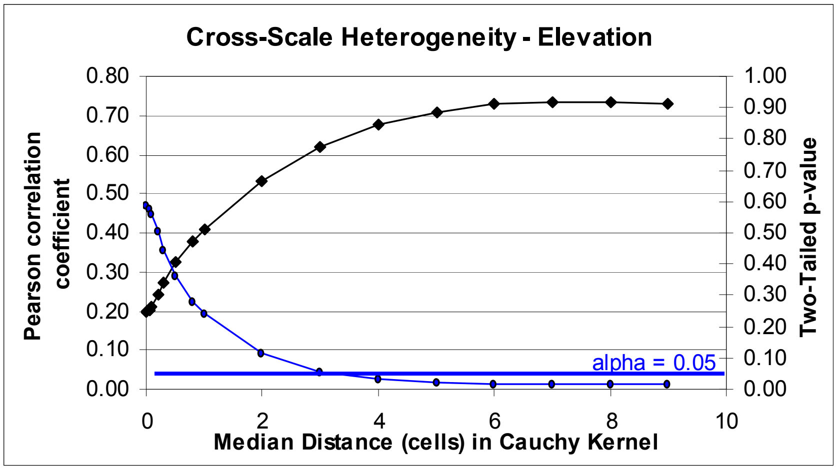
No significant correlations are found between heterogeneity in any of the random grids and the diversity found in the plots, though steady movement of the points in the analysis for each scale produce smooth cross-scale correlation curves (as evident in Figure 98). This gradual movement of points between scales arises from the effect of heterogeneity at one scale being somewhat correlated with heterogeneity at a similar scale. This produces smooth peaks in the correlation at specific scales, but it is questionable the depth to which these curves can be used to ascertain if there is a scale-dependent relationship; with only 10 points in the statistical analysis, there is likely heavy reliance of each correlation on the position of one single point.

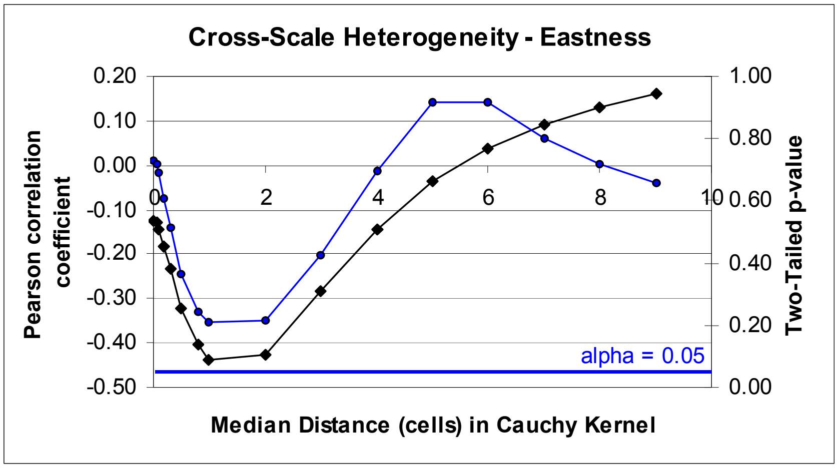
The co-correlation between heterogeneity at similar scales for each grid (average Pearson correlation coefficient between adjoining scales is 0.99, n = 180) signifies that the 192 correlations being calculated for the twelve variables are not independent of each other, and thus less than the 5% of correlations would be expected to correlate significantly as a result of chance. This is reflected in these results, with no spurious correlations being found.

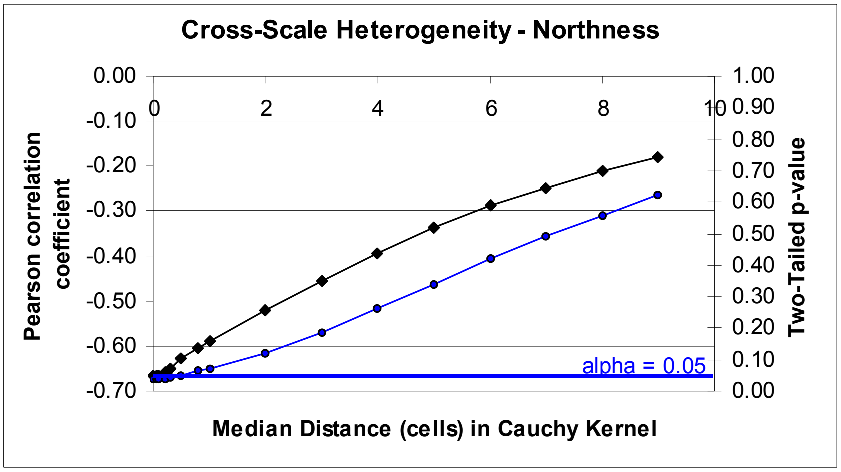
Whilst it would be preferable to repeat this analysis 100 times to gain a better insight into the average number of expected spurious correlations in this analysis, computational (amongst other) limitations make this impossible.

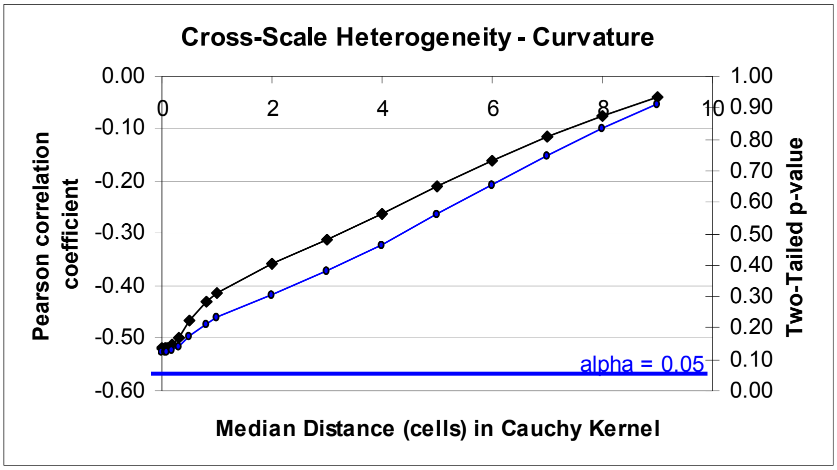
6.2.1.3.2 Single-variate comparison

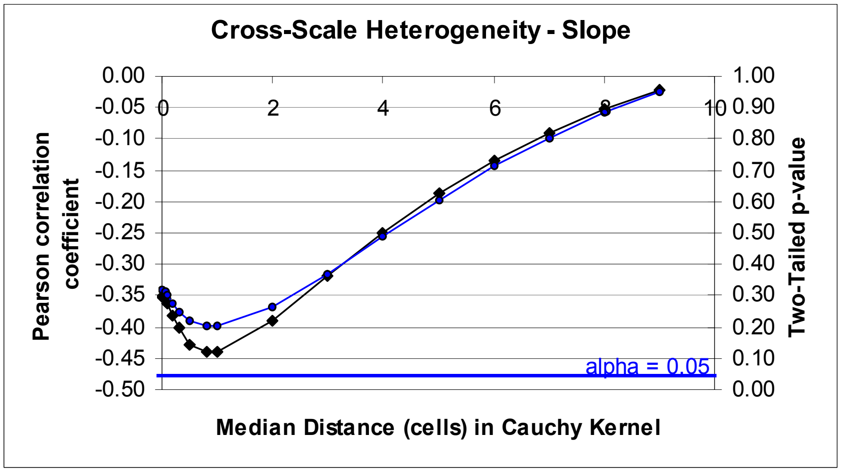
Firstly, the relationship between each environmental and topographic variable is examined separately, with multi-variate analyses being produced later in the chapter. For each plot in Tambito, the heterogeneity for each variable is extracted, and Simpson's diversity index is then correlated with heterogeneity at each individual scale. Graphs of correlation coefficient and p-value are plotted against the scale (Figure 99), and a summary table provided indicating whether significant correlations were found for each variable, and the scale (median distance) at which the most significant correlation was found (Table 56).

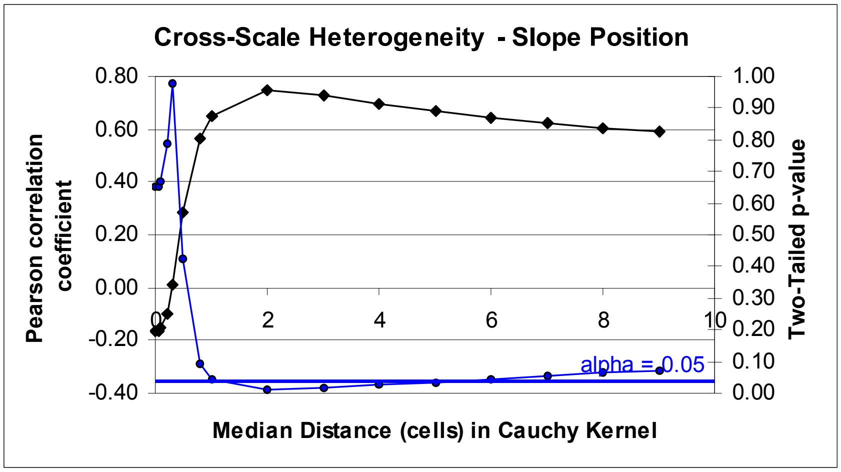

Cross-Scale Heterogeneity - Elevation
Pearson correlation coefficient
Two-Tailed p-value
Median Distance (cells) in Cauchy Kernel
alpha = 0.05
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
0
2
4
6
8
10

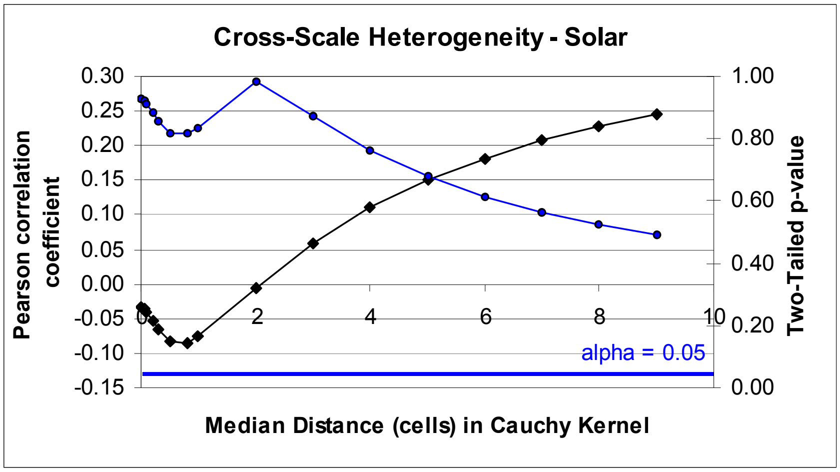

Cross-Scale Heterogeneity - Eastness
Pearson correlation coefficient
Two-Tailed p-value
Median Distance (cells) in Cauchy Kernel
alpha = 0.05
0.20
0.10
0.00
-0.10
-0.20
-0.30
-0.40
-0.50
1.00
0.80
0.60
0.40
0.20
0.00
0
2
4
6
8
10

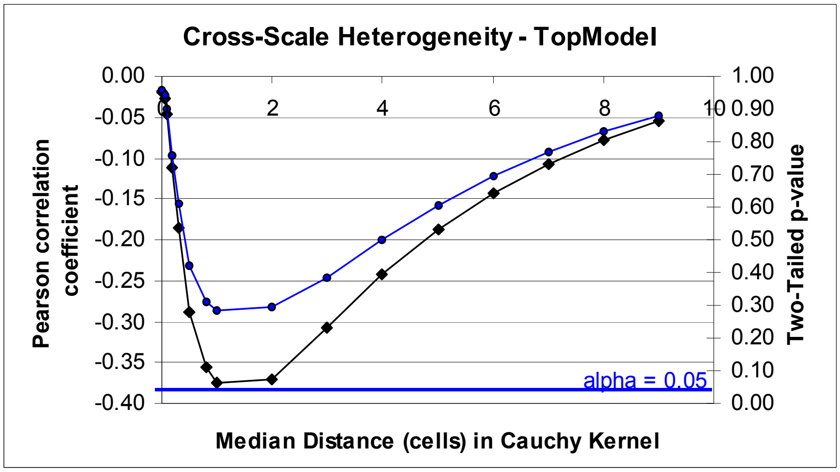

Cross-Scale Heterogeneity - Northness
Pearson correlation coefficient
Two-Tailed p-value
Median Distance (cells) in Cauchy Kernel
alpha = 0.05
0.00
-0.10
-0.20
-0.30
-0.40
-0.50
-0.60
-0.70
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
0
2
4
6
8
10

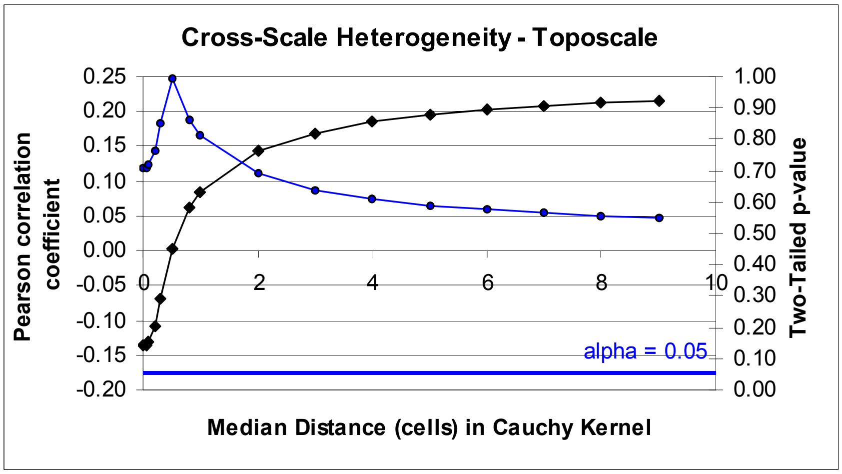

Cross-Scale Heterogeneity - Curvature
Pearson correlation coefficient
Two-Tailed p-value
Median Distance (cells) in Cauchy Kernel
alpha = 0.05
0.00
-0.10
-0.20
-0.30
-0.40
-0.50
-0.60
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
0
2
4
6
8
10

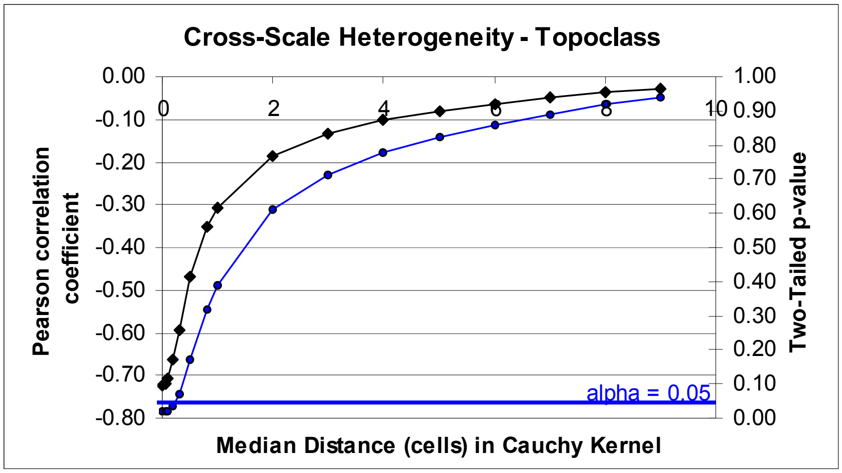

Cross-Scale Heterogeneity - Slope
Pearson correlation coefficient
Two-Tailed p-value
Median Distance (cells) in Cauchy Kernel
alpha = 0.05
0.00
-0.05
-0.10
-0.15
-0.20
-0.25
-0.30
-0.35
-0.40
-0.45
-0.50
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
0
2
4
6
8
10

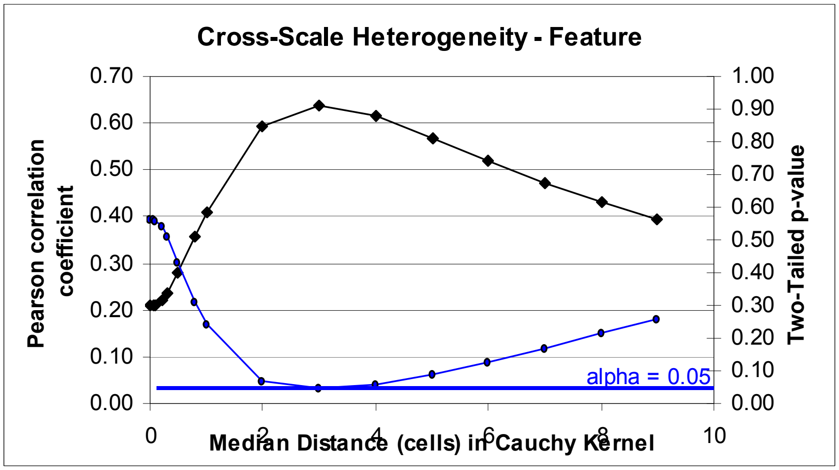

Cross-Scale Heterogeneity - Slope Position
Pearson correlation coefficient
Two-Tailed p-value
Median Distance (cells) in Cauchy Kernel
alpha = 0.05
0.80
0.60
0.40
0.20
0.00
-0.20
-0.40
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
0
2
4
6
8
10


Cross-Scale Heterogeneity - Solar
Pearson correlation coefficient
0.30
0.25
0.20
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
0
2
4
6
8
10
1.00
0.80
0.60
0.40
0.20
0.00
Two-Tailed p-value
alpha = 0.05
Median Distance (cells) in Cauchy Kernel


Cross-Scale Heterogeneity - TopModel
Pearson correlation coefficient
0.00
-0.05
-0.10
-0.15
-0.20
-0.25
-0.30
-0.35
-0.40
0
2
4
6
8
10
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
Two-Tailed p-value
alpha = 0.05
Median Distance (cells) in Cauchy Kernel


Cross-Scale Heterogeneity - Toposcale
Pearson correlation coefficient
0.25
0.20
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
-0.20
0
2
4
6
8
10
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
Two-Tailed p-value
alpha = 0.05
Median Distance (cells) in Cauchy Kernel





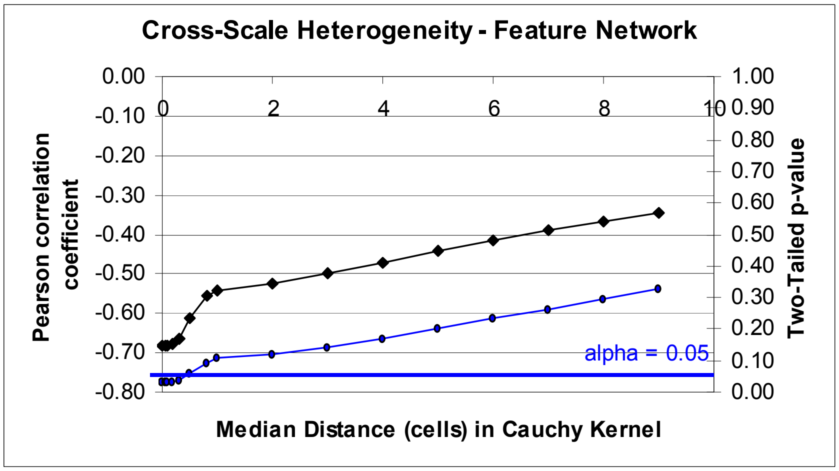


Figure 99 Cross-scale correlations between species diversity (Simpson's) and spatial heterogeneity for each environmental variable in Tambito. The black line represents the Pearson correlation coefficient, whilst the blue line indicates the respective p-value. For ease

of interpretation, the thick blue line shows the threshold for significant correlations at the alpha = 0.05 level.

Variable	Minimum Pearson Correlation Coeffcient	Maximum Pearson Correlation Coeffcient	Minimum p-value	Significance (alpha=0.05)	Scale of lowest p-value (median distance in cells)
Elevation	0.20	0.74	0.02	Significant	9
Eastness	-0.44	0.16	0.21	Not-significant	1
Northess	-0.67	-0.18	0.04	Significant (inverse)	0.01
Curvature	-0.52	-0.04	0.12	Not-significant	0.01
Slope	-0.44	-0.02	0.20	Not-significant	0.8
Slope Position	-0.16	0.75	0.01	Significant	2
Solar Radiation	-0.08	0.25	0.49	Not-significant	0.8
Topmodel	-0.38	-0.02	0.29	Not-significant	1
Toposcale	-0.14	0.22	0.55	Not-significant	9
Topoclass	-0.72	-0.03	0.02	Significant (inverse)	0.01
Feature	0.21	0.64	0.05	Significant	3
Network Feature	-0.68	-0.34	0.03	Significant (inverse)	0.01

Table 56 Summary table of results of multi-scale environmental heterogeneity modeling, examining maximum correlations between species richness and heterogeneity for the ten plots in Tambito.

Six variables correlate (at least at one scale) between heterogeneity and Simpson's diversity, three of which do so inversely (i.e. in these cases greater homogeneity = greater diversity). Some 27 significant correlations are found when counting all scales, the most of which are for heterogeneity in elevation (correlates at six of the 16 scales), slope position (correlates at six of the 16 scales), northness and network feature (inversely correlate at five of the 16 scales). No variable correlated with diversity independently of scale. These figures are above the expected number of correlations at the 95% confidence limit (if 5% of the 192 correlations performed are randomly expected, we would expect 9.6 correlations, furthermore in the random control no spurious correlations were found, see Section 6.2.1.3.1).

Given that we find more than the expected number of random correlations, it suggests that heterogeneity for some variables is indeed important in shaping diversity (or some covariate of it, e.g. heterogeneity in altitude signifying high slopes, or that the same processes which generate spatial heterogeneity also generate high species diversity). However, it is important that we consider co-linearity in the discussion of these correlations, as some of the correlations may indeed be spurious and correlate only due to co-linearity with other causal variables. Whilst Table 56 shows cross-correlations between variables for the whole of Tambito, it is important to re-analyse the cross-correlations only for the variables found to correlate, using just the ten points where the plots are located (Table 57).

	Elevation (median distance 9)	Northness (median distance 0.01)	Slope Position (median distance 2)	Topoclass (median distance 0.01)	Feature (median distance 3)	Network Feature (median distance 0.01)
Elevation (median distance 9)	-	-0.60	0.71	-0.40	0.67	-0.47
Northness (median distance 0.01)	-0.60	-	-0.39	0.44	-0.75	0.48
Slope Position (median distance 2)	0.71	-0.39	-	-0.84	0.51	-0.48
Topoclass (median distance 0.01)	-0.40	0.44	-0.84	-	-0.46	0.57
Feature (median distance 3)	0.67	-0.75	0.51	-0.46	-	-0.29
Network Feature (median distance 0.01)	-0.47	0.48	-0.48	0.57	-0.29	-

Table 57 Cross-correlation of heterogeneity values for the six correlating variables in Tambito, using only the heterogeneity values for the ten plots (n = 10). Cells are shaded dark grey when the correlation coefficient is above 0.80 and light grey when the correlation coefficient is between 0.60 – 0.80 in order to highlight the most significant correlations.

As suspected, strong and significant correlations are evident between the variables, with all presenting some degree of positive or negative co-linearity. Deciphering the direct cause and effect from this mix of non-independent variables is difficult, especially considering that some are positively correlated with heterogeneity and others negatively. For example, if we assume that heterogeneity in elevation is indeed the true direct driver of diversity, this renders the slope position correlation as in-direct, along with a large proportion of the inverse correlation with northness and feature classification. Only topoclass and the network feature classifications are left accounting for some of the remaining unexplained variability in diversity. This is just one scenario, and a number of different scenarios exist. In reality, heterogeneity in slope position actually correlates best (Pearson = 0.75, p = 0.01), leading one to believe that this is the direct driver and that many of the others are in fact spurious. However, the correlation with heterogeneity in slope position is only marginally better than elevational heterogeneity (Pearson = 0.74, p = 0.01), and indeed topoclass (Pearson = -0.72, p = 0.02). Heterogeneity in northness and the feature classification provide significant correlations at the 95% confidence level, but have the weakest correlations of the six variables (Pearson = -0.67 and 0.64 respectively).

Though it is impossible to statistically separate out the direct and indirect linkages behind the correlations without establishing more plots, some informal speculation in the context of ecological theory can provide some insight as to the likely causal factors. Having already established that composition is strongly influenced by elevation (and no other factors measured in this study), it is expected that spatial heterogeneity in elevation would likewise be important in generating diversity through overlapping distributions and seed sources. Furthermore the ecological literature has long attributed high spatial heterogeneity to generating high diversity, therefore we would expect elevationally heterogeneous regions to have the highest diversity. This is essentially found here (Figure 100), though plots 3 and 5 have lower than expected diversity.

Also significant in this argument is the scale dependence of this relationship, with a correlation only occurring with median distances above 3 cells (75 metres, which can represent a change of as much as 100m of altitude or 0.6°C temperature in Tambito). In other words, heterogeneity only becomes significant in shaping diversity when broader scale patterns are examined, rather than the small-scale heterogeneity represented in small-median distances.

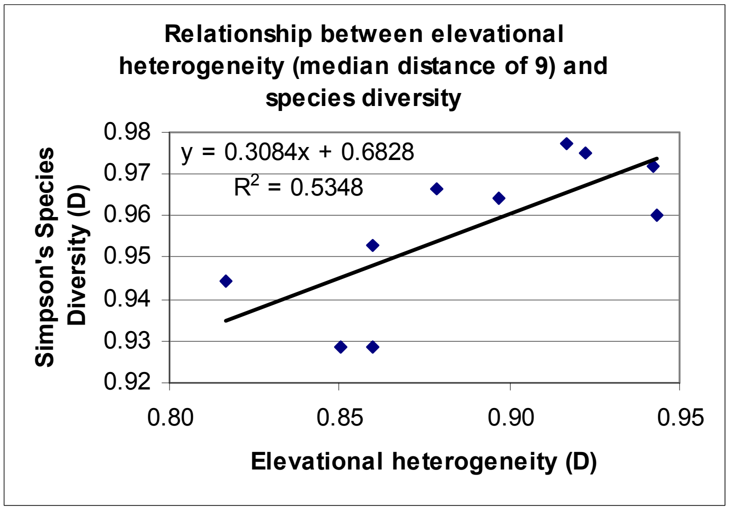


Figure 100 Elevational heterogeneity (median distance 9 cells) against species diversity for Tambito.

This correlation between elevational heterogeneity and diversity once again provides another possible explanation of the mid-elevation diversity peak found in Chapter 4, as elevational heterogeneity also peaks in mid-elevations, in this case at 2100m (Figure 101).

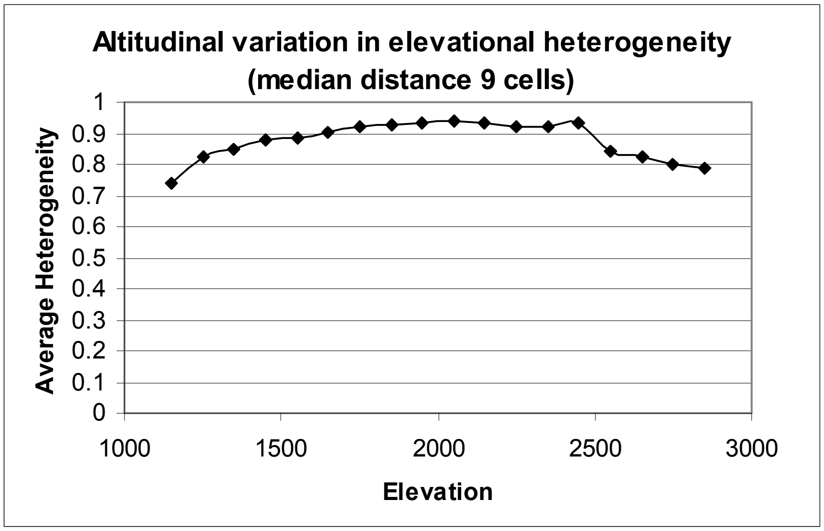


Figure 101 Elevational gradient of heterogeneity in elevation in Tambito.

It is important to also consider that elevation is not the only likely causal relationship, with 5 other variables providing significant relationships. Heterogeneity in slope position itself is likely to be very similar to that of elevation, and is unlikely to be the causal relationship (slope position alone has already shown little explanatory power in terms of composition and diversity in Tambito). Likewise, heterogeneity of the feature classification is unlikely to be providing the causal relationship due to its clear derivation from other factors and its abstraction of gradients into specific classes, though this is an interesting and potentially useful surrogate. The inverse correlation between diversity and heterogeneity in northness, topoclass and network feature classification is a little more interesting though, and one which deserves some further attention.

The correlation with heterogeneity in topoclass may simply be an artifact, as toposcale itself provides no significant correlation, and topoclass is merely a reclassification of toposcale. Furthermore, significant edge effects occur around topoclass boundaries (clearly more heterogeneity around the boundaries than in the centre of a particular class), and so the result is highly dependent on the subjectivity of the reclassified boundaries. The heterogeneity in the network feature classification also has the problem of strong boundary effects, though these boundaries are less generalized and less subjective in their definition. It is indeed surprising that the heterogeneity in the network feature classification inversely correlates with the network feature classification, but no plausible explanation for this can be provided.

However, the inverse correlation with heterogeneity of northness (though weak) must be taken seriously, as the multiple stepwise linear-regressions performed on diversity in Chapter 4 highlighted northness as accounting for some 22% of the variability in diversity, with south facing slopes containing greater diversity (though northness was not found to be significant in terms of composition). The correlation is borderline significant ($p = 0.04$), and dependent on the low heterogeneity but high diversity found in plots 6 and 10 (both strongly south facing slopes). This may be attributable to the mid-elevation diversity peak already found and discussed in Chapter 4, as heterogeneity in northness is actually lowest in mid-elevations due to the more planar nature of these slopes (the five mid-elevation plots, 1600m – 1900m, have the five lowest values of heterogeneity in northness). Given that no correlation is found between composition and northness, it is likely that the correlation between diversity and heterogeneity in northness is principally driven by the mid-elevation diversity peak rather than the heterogeneity in northness.

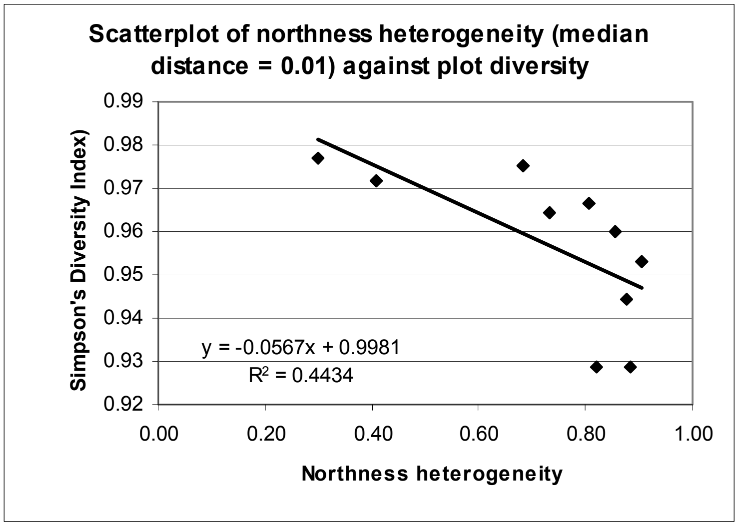


Figure 102 Scatterplot of northness heterogeneity against species diversity for Tambito using a median distance of 0.01.

With no solid data or statistics telling us which variable is the true causal relationship, if there is indeed only one, this section is heavily inconclusive. The significant elevational heterogeneity correlation is however both statistically strong and ecologically understandable given the previously outlined compositional relationship with elevation. To truly understand the causal linkages in the six significant correlations that have been found, more plots are required in strategically located sites, where there are lower levels of co-linearity between the individual heterogeneity variables.

6.2.1.3.3 Multi-variate data analysis

Whilst some heterogeneity variables singularly correlate with diversity, it is likely that a number and combination of factors are indeed important in shaping diversity, both in terms of heterogeneity derivatives themselves and the original terrain derivatives that have already been examined in Chapter 4. Furthermore, confusion over the separation of causal relationships in non-independent variables may also be examined using multi-variate methods.

Prior to performing multi-variate analyses on all variables, attention is paid to the important distinction between slope position heterogeneity and elevational heterogeneity. Multiple stepwise regression is applied to just two variables; slope position (median distance 2) and elevation (median distance 8), in order to examine the extra variability in diversity that is explained by elevation after slope position is taken into account. Elevational heterogeneity is found to explain just 8% extra variability in diversity (despite explaining 53% in the single-variate correlation), indicating that these two variables are to a large extent measuring the same variability. It is important that this is quantified, indicating that slope position and elevation are not only largely co-linear, but co-linear in their explanatory power of diversity.

Having clarified this important issue, three sets of multiple stepwise linear-regressions are performed to fully understand the interactions between heterogeneity in all variables and diversity:

1. Analysis using all heterogeneity variables at all scales
2. Analysis of all heterogeneity variables only at the scale where the greatest correlation with diversity was found

3. Analysis of all heterogeneity variables at the scale where maximum correlation was found alongside the original terrain derivatives already analysed in Chapter 4.

In all three cases the heterogeneity values for the random grid are also included in the analysis in order to check for chance relationships. Given the multi-variate nature of this statistical procedure, there is danger of non-causal relationships by chance providing some explanation of the diversity. Inclusion of any of the random grids in the multiple linear regression models will clearly indicate that non-causal relationships are being selected.

Taking the first set of variables (1), multiple stepwise linear regression is applied to all heterogeneity variables at all scales. The resultant model extracts three significant variables that are significant in explaining diversity. These are slope position (median distance 2 cells) (explaining some 56% of variability), then elevation (median distance 0.2 cells) (explaining a further 23% of variability, and cumulatively covering 78% of all variation), and finally topmodel (median distance 1 cell) (explaining a further 13% of variability), with all three variables combined explaining some 92% of variability ($D = 0.570 + 0.479\text{Slope Position}_{(\text{HET - 2})} + 0.141\ \text{Elevation}_{(\text{HET - 0.2})} - 0.193\text{Topmodel}_{(\text{HET - 1})}$).

Prior to performing detailed discussion of these results, the other two multiple stepwise linear-regressions are analysed. The second model using heterogeneity data only at the scale of maximum correlation for each variable pulls out two variables that significantly contribute to explaining 72% of the variability in diversity.

Heterogeneity in slope position with median distance of 2 cells explains 56% of variability and heterogeneity in northness at a median distance of 0.01 cells (explains a further 17% of variability) ($D = 0.669 + 0.332\text{Slope Position}_{(HET - 2)} - 0.038\text{Northness}_{(HET - 0.01)}$).

Finally, the third model combines the environmental and topographic variables (studied in detail in Chapter 4) with their respective heterogeneities in a multiple-stepwise linear regression (total of 21 variables + 1 random variable). Four variables explain 99% of the variability in this analysis, with heterogeneity in slope position accounting for 56% of the variability in diversity, followed by solar radiation accounting for a further 28% (84% cumulative), heterogeneity in slope position accounting for a further 10% (94% cumulative) and heterogeneity in solar radiation with median distance 0.8 accounting for the final 5% ($D = 0.596 + 0.522\text{Slope Position}_{(HET - 2)} - 0.00002\text{Solar} + 0.00037\text{Slope Position} + 0.101\text{Solar}_{(HET - 0.8)}$).

Depending on the variables used in the multiple stepwise linear-regression different results are achieved, making interpretation difficult. Firstly it is important to note that despite their inclusion, none of the random heterogeneity variables provided any explanation of the diversity. This is not to say that non-causal relationships have not been selected in the three models presented above, but provides a little more confidence in the results during their interpretation.

Looking at the first multiple regression (Figure 103), with all heterogeneity variables at all scales included in the analysis, the additional variability that elevational heterogeneity at short median distances provides is interesting. Despite elevational heterogeneity at median distances of 0.2 cells explaining just 6% when correlated directly with diversity, it explains some 23% of variability in the residual after the multivariate regression with slope position heterogeneity. This may be due to slope position being a more generalized variable, whilst elevation contains more detail. In other words, diversity is generated through a multi-scale combination of small-scale and broader-scale heterogeneity in slope position/elevation, if we assume that their co-linearity is capturing the same variability in diversity. However, multiple-regression on all scales of elevational heterogeneity alone provides no evidence of this, with only heterogeneity at a median distance of 8 cells providing a significant correlation. No other scales explain any of the remaining variability. This draws us to the conclusion that slope position is explaining some important variability independently of elevation. This may be an artifact of the few points used in this analysis (n = 10), and a greater number of plots may clarify these complex interactions between non-independent variables.

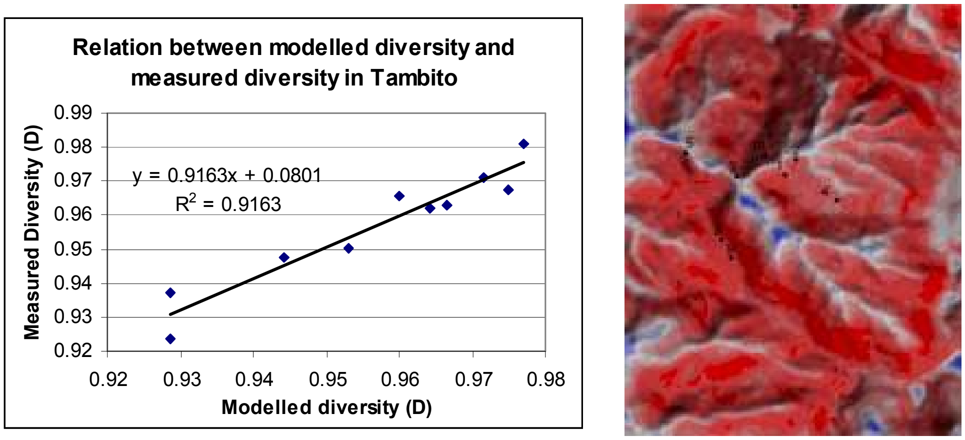


Figure 103 First multiple linear-regression of all heterogeneity variables at all scales. Left figure compares the modeled diversity with the measured diversity in the plots, and the right figure applies the resultant regression model to the entirety of Tambito. Areas in white and

blue are beyond the range of the input data to the regression, hence are based on extrapolation and should be considered potentially less trustworthy in their model fit.

In the second regression (Figure 104), the role of small-scale homogeneity (median distance 0.01) of northness is once again observed, with it explaining some 17% extra variability after the already discussed importance of slope position heterogeneity. This indicates that the role of northness in these correlations is fairly independent of that of heterogeneity of slope position/elevation (17% explained in the residual compared to 22% explained singularly). As discussed, this relationship is somewhat dependent on the high diversity, low heterogeneity found in the south-facing plots 6 and 10, and may simply be a result of the mid-elevation diversity peak.

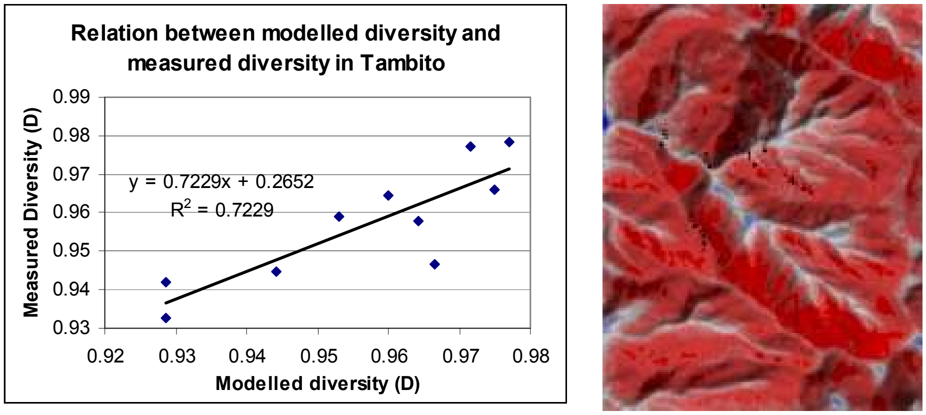


Figure 104 Second multiple linear-regression of heterogeneity variables at only at the scale of maximum correlation. Left figure compares the modeled diversity with the measured diversity in the plots, and the right figure applies the resultant regression model to the entirety of Tambito. Areas in white and blue are beyond the range of the input data to the regression, hence are based on extrapolation and should be considered potentially less trustworthy in their model fit.

Areas heterogeneous in northness are likely to be concentrated around areas with high curvature (already identified as an important driver of diversity in Chapter 4), though no relationship is present (Pearson = -0.09, p = 0.80, n = 10) meaning that the importance of northness is independent of curvature. There is likely to be a clearer relationship with plan curvature, but as mean curvature mixes both plan and profile curvature the relationship is lost. These types of curvature are not studied in this thesis, and therefore are not discussed further.

If the correlation between small-scale northness heterogeneity (median distances < 0.5 cells) is independent of other variables, and a truly causal relationship with diversity it means that a locally diverse set of conditions in northness generates to some extent low diversity. In other words, relatively planar hillsides have greater diversity, though this is more likely due to the aforementioned relationship between heterogeneity in northness and the mid-elevation diversity peak.

Finally, the third multiple-regression analysis combines absolute values of environmental and topographic variables and their respective spatial heterogeneities. Interestingly, it was a combination of the absolute value for slope position and solar radiation receipt and their respective heterogeneities that were pulled out in the regression to explain an impressive 99% of variability in diversity (Pearson = 0.999, p = 0.0001, n = 10) (Figure 105).

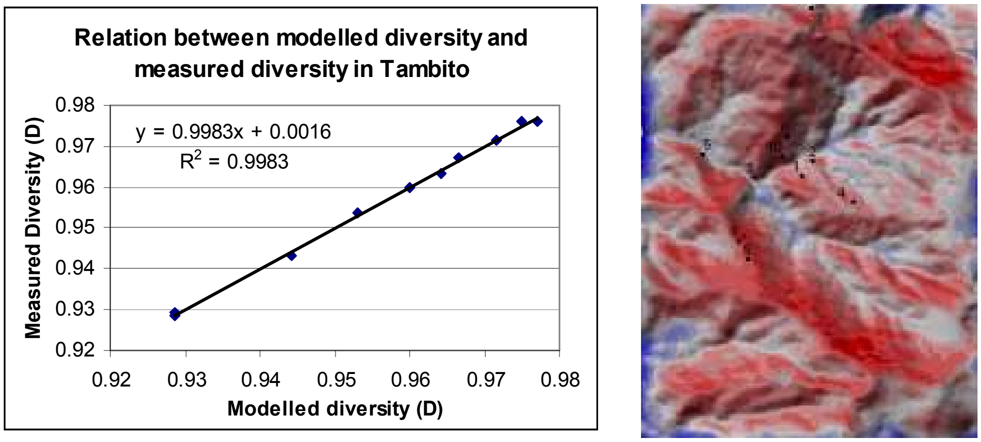


Figure 105 Third multiple linear regression combining both absolute value and heterogeneities of each environmental and topographic variable. Left figure compares the modeled diversity with the measured diversity in the plots, and the right figure applies the resultant regression model to the entirety of Tambito. Areas in white and blue are beyond the range of the input data to the regression, hence are based on extrapolation and should be considered potentially less trustworthy in their model fit.

Interestingly neither slope position nor solar radiation receipt demonstrate any explanatory power in Chapter 4, neither singularly nor in the multi-variate analyses. However, when combined in multiple linear-regressions with their respective heterogeneity values they are shown to be important. Once again slope position is by far the most important variable, but some 28% of the residual is explained by homogeneity in solar radiation receipt. Heterogeneity in solar radiation, despite being strongly controlled by aspect, shows no clear relationship across the elevational gradient (i.e. mid-elevations are not more homogenous in solar radiation, despite the already discussed homogeneity in northness found in the mid-elevation planar slopes). This goes against many ecological concepts about heterogeneity generating diversity, and once again no interpretation of this pattern can be provided.

These analyses provide a confusing set of results, and it is almost certain that many of these are not causal relationships but chance relationships achieved through multiple regression of many variables with so few field plots. Four of the twelve variables exhibit some type of control on diversity (slope position, elevation, northness, solar radiation) on top of the three classification variables (Feature, Network Feature and Topoclass) that show some correlation with diversity when treated on their own. Interpretation is difficult and fairly arbitrary depending on the variables used in the regression analysis. However, generalities are visually evident in the resultant maps of each model presented in Figure 103, Figure 104 and Figure 105. The general pattern of each of the three models is somewhat similar, with low diversity in the valley bottoms, low-moderate diversity in peaks and high ridges, and high diversity in mid-elevations, especially in north, north-east and south-west facing slopes. Under these circumstances, it is difficult to explicitly quantify the degree to which spatial heterogeneity is affecting the diversity in Tambito, with complex combinations of variables all producing a similar mid-elevation diversity peak which could be entirely attributed to a number of other more established ecological processes (the mid-domain effect or the productivity-diversity gradient, for example).

Perhaps as a conclusion to this section few concrete findings can be reported, except that heterogeneity in slope position and elevation are significantly explaining some 50% of the variability in diversity, and that both these variables are co-linear and explaining the same variability. Furthermore, highest heterogeneity in these variables is found in mid-elevations, which have already been found to harbor the highest diversity, potentially due to a number of different explanations outlined in Chapter 4. If elevation is assumed to represent a productivity gradient in Tambito (a notion supported by Letts, 2003), this shows that environmental heterogeneity in Tambito is greatest in mid-productivity levels, a pattern also found in limestone pavements (Lundholm and Larson, 2003). This coincidence of high spatial heterogeneity in mid-elevations and mid-productivity regions adds another factor which may be significant in explaining mid-elevation diversity peaks.

Although complex combinations of variables manage to explain as much as 99% of the variability in diversity, the confidence of these findings is questionable as there are few clear ecological interpretations of the patterns and too few data points. It would be preferable to have a larger number of plots to permit split sample validation of these multiple stepwise linear regressions.

6.3 Tiputini Biodiversity Station

In TBS the extent to which spatial heterogeneity is significant in the maintenance of species diversity is unknown, but theoretically it may be important. Firstly, the extent of habitat association in LRF tree species is questionable and still under debate, though the literature reports 20-80% of species have some kind of association (Webb and Peart, 2000; Harms et al., 2001; Phillips et al., 2003; St-Louis et al., 2004). Furthermore, gap dynamics play an important role in maintenance of forest diversity in LRF, and non-equilibrium theories predict that gaps are recruited principally by chance occupants through low densities in tropical tree species distributions and dispersal limitations (Hubbell et al., 1999). This has important implications for spatial heterogeneity, as the probability of a specialist species recruiting in the successional process after gap formation is enhanced if a diverse local seed pool is available. Under these circumstances there is potentially a strong role for spatial heterogeneity shaping species diversity at least to some extent in LRF. However, practical limitations limit the degree to which this can be tested in TBS due to quality issues in the DEMs. Section 3.7 has already shown that the DEMs poorly represent the conditions on the ground, with neither DEM capturing the more complex topography around the small streams and 20-30m deep valleys. Under these circumstances it is questionable the degree to which this analysis can conclude whether spatial heterogeneity is significant or not in shaping tree diversity, but nevertheless the analysis is presented in detail in a similar fashion to that of Tambito. Unlike in Chapters 4 and 5, the results here are presented for each DEM separately as the different spatial resolutions merit more specific discussion.

6.3.1 TOPO DEM

The spatial heterogeneity analysis for TBS is first performed on the TOPO DEM. The TOPO DEM is a smooth representation of the topography in TBS, in many cases failing to account for the micro-scale topographic variation observed in the field. Under these circumstances it is likely that the model will underestimate the true heterogeneity across the region, but also fail to accurately quantify the spatial distribution. These concerns must be considered throughout the analysis.

6.3.1.1 Spatial heterogeneity results

6.3.1.2 Cross-correlation matrix

As was done for Tambito, a cross-correlation is performed on the resultant heterogeneity grids for median distances of 1 cell (Table 58).

	Elevation	Eastness	Northness	Curvature	Slope	Slope Position	Solar	Toposcale	Topmodel	Topoclass	Feature	Feature (network)
Elevation	-	0.14	-0.05	0.66	0.84	0.65	0.69	0.75	-0.02	0.72	0.54	0.44
Eastness		-	0.01	0.36	0.41	0.02	0.29	0.43	0.36	0.42	0.33	0.53
Northness			-	0.21	0.14	0.00	0.08	0.23	0.36	0.21	0.24	0.33
Curvature				-	0.87	0.30	0.90	0.90	0.37	0.83	0.92	0.82
Slope					-	0.46	0.80	0.93	0.24	0.87	0.75	0.79
Slope Position						-	0.29	0.39	0.01	0.39	0.22	0.21
Solar							-	0.82	0.23	0.77	0.83	0.62
Toposcale								-	0.35	0.90	0.78	0.82
Topmodel									-	0.26	0.32	0.48
Topoclass										-	0.72	0.75
Feature											-	0.75
Feature (network)												-

Table 58 Cross-correlation matrix between all spatial heterogeneity variables with the median distance set at 1 cell in TBS using the TOPO DEM (n = 142,450). Cells are shaded when the correlation coefficient is above 0.80 in order to highlight the most significant correlations.

In general the correlation coefficients between heterogeneity variables are higher than for Tambito. Furthermore, all heterogeneity variables are positively co-correlated using the TOPO DEM in TBS, meaning that high heterogeneity in one variable to some extent is also indicative of high heterogeneity in another variable. This may be due to TBS being an essentially flat landscape with valleys cut through it whereas the topography of Tambito varies at multiple scales because of changes in geology, tectonic features and fluvial features of various river orders (a dendritic scheme, whereas TBS is more trellised in drainage pattern). Northness, topmodel, slope position and eastness are the least cross-correlated heterogeneity variables (in that order), whilst toposcale, curvature and slope are the most cross-correlated variables (also in that order). Specific discussion of these cross-correlations is not provided here, but referred to later in the text.

6.3.1.3 Comparison with plot data

6.3.1.3.1 Control Experiment

As performed for Tambito, twelve random grids are created in Arc/Info (using the RAND command), and the spatial heterogeneity model applied to these grids for all 16 scales. The results of which are compared with the Simpson's diversity measured in the plots (Table 59).

Random Run	**Maximum Pearson**	**Minimum Pearson**	**No. Scales with significant correlation**
Random grid 1	0.70	-0.39	4
Random grid 2	0.09	-0.54	0
Random grid 3	0.10	-0.27	0
Random grid 4	0.84	0.09	8
Random grid 5	-0.26	-0.69	4
Random grid 6	0.51	-0.17	0
Random grid 7	0.15	-0.09	0
Random grid 8	0.43	-0.34	0
Random grid 9	-0.31	-0.69	1
Random grid 10	0.34	-0.13	0
Random grid 11	0.86	-0.11	8
Random grid 12	0.41	-0.19	0

Table 59 Results of the heterogeneity analysis for the 12 random grids using the SRTM DEM in TBS.

Significant correlations are found between heterogeneity in the random grid and Simpson's diversity for five of the 12 random grids for at least one scale per grid, with a total of 25 correlations occurring (on average five scales with significant correlation per correlating random grid). This is an alarming number of correlations, all of which must be assumed to be spurious but nevertheless an artifact of either the heterogeneity model or the TBS diversity dataset.

As discussed in Chapter 4, the diversity found in the plots in TBS is exceptionally high in eight plots, with almost indistinguishable differences between plots (Simpson's Index between 0.976 and 0.996), and the remaining two plots having significantly lower levels of diversity (Plot 4 and 5 with Simpson's diversity indices of 0.95 and 0.84 respectively). This non-normal irregular distribution of diversity values for the ten plots produced a number of significant correlations with terrain characteristics that did not hold true when only the high diversity plots were included in the correlation. In other words, the significant correlations were not robust, and heavily sensitive to the low diversity in two points. This is also somewhat the case in the correlations shown in Table 59 with the random grid heterogeneity analyses, whereby the omission of plots 4 and 5 from the analysis significantly lowers the number of correlations to just one grid at three different scales (Table 60, Figure 106). At least in this case it can be concluded that the high number of potentially spurious correlations found with the random grids are caused by the poor distribution of points rather than problems with the heterogeneity model itself.

Random Run	Maximum Pearson	Minimum Pearson	No. Scales with significant correlation
Random grid 1	0.11	-0.09	0
Random grid 2	0.09	-0.57	0
Random grid 3	0.22	0.02	0
Random grid 4	0.48	-0.65	0
Random grid 5	0.02	-0.67	0
Random grid 6	0.78	0.03	3
Random grid 7	0.38	0.05	0
Random grid 8	0.22	-0.56	0
Random grid 9	0.68	-0.58	0
Random grid 10	0.12	-0.49	0
Random grid 11	-0.21	-0.59	0
Random grid 12	0.34	-0.27	0

Table 60 Results of the heterogeneity analysis for the 12 random grids when Plots 4 and 5 are excluded from the analysis using the TOPO DEM in TBS.

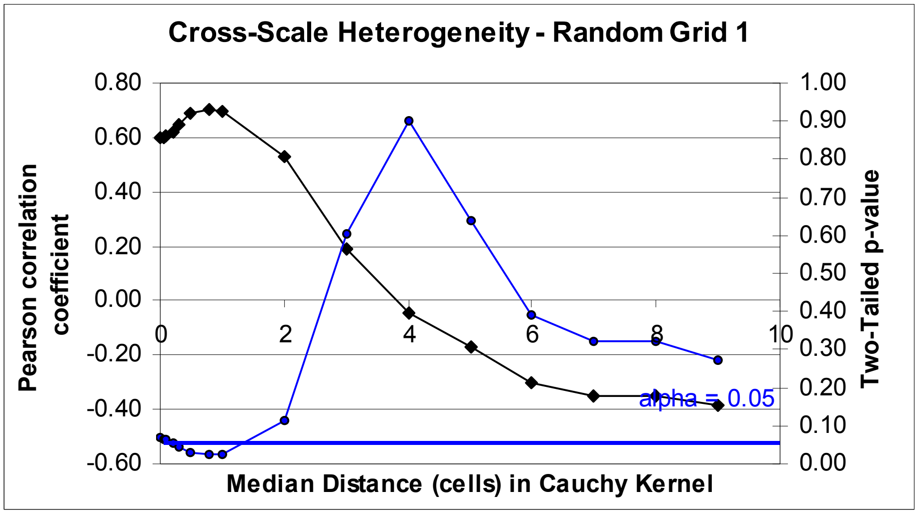


Figure 106 Control experiment of cross-scale heterogeneity for a random grid 6 using the TOPO DEM.

However, one random grid still correlates, despite the exclusion of Plots 4 and 5, meaning that spurious correlations can occur at multiple spatial scales, and must be carefully considered in the analysis and discussion. Though some non-equilibrium based theories of species diversity maintenance predict that stochastic processes generate an auto-correlated but relatively random distribution in diversity, there is no causal reason that heterogeneity in a particular random grid should correlate with plot diversity (for info, the heterogeneity in random grid 6 with a median distance of 1 cell is displayed in Figure 107).

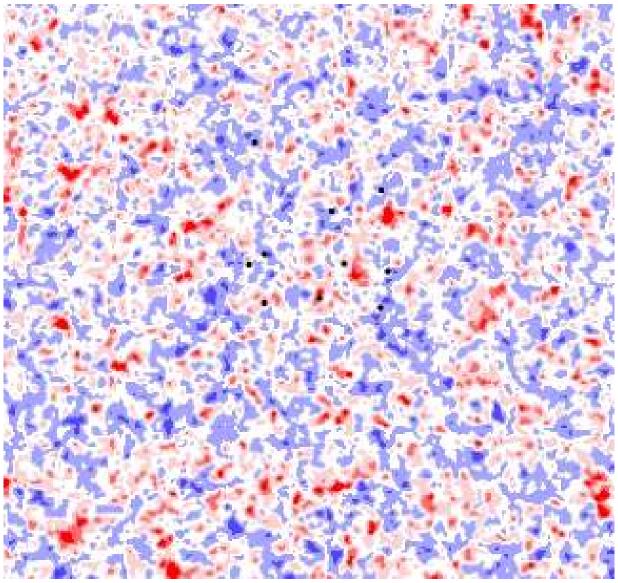
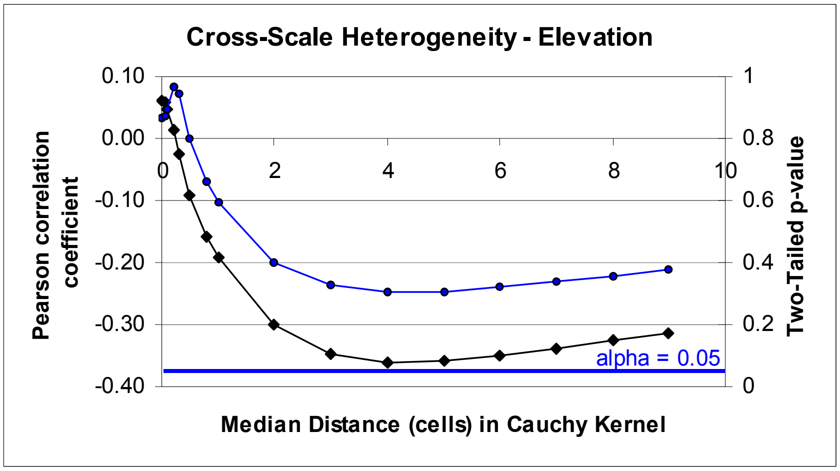


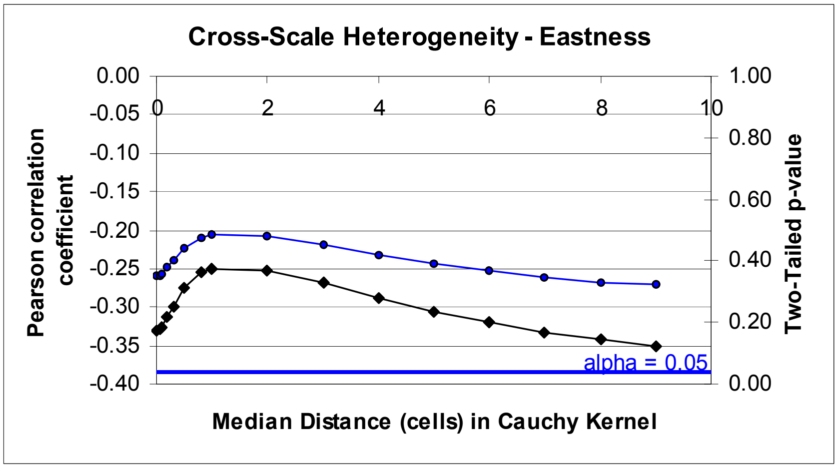
Figure 107 Result of the heterogeneity model for Random Grid 6 for the TOPO DEM in TBS. Represented here is the analysis with median distance of 1 cell (25m), where the correlation with plot diversity was found to be highest. Red indicates low heterogeneity, and blue high heterogeneity, with the plots displayed as the black dots.

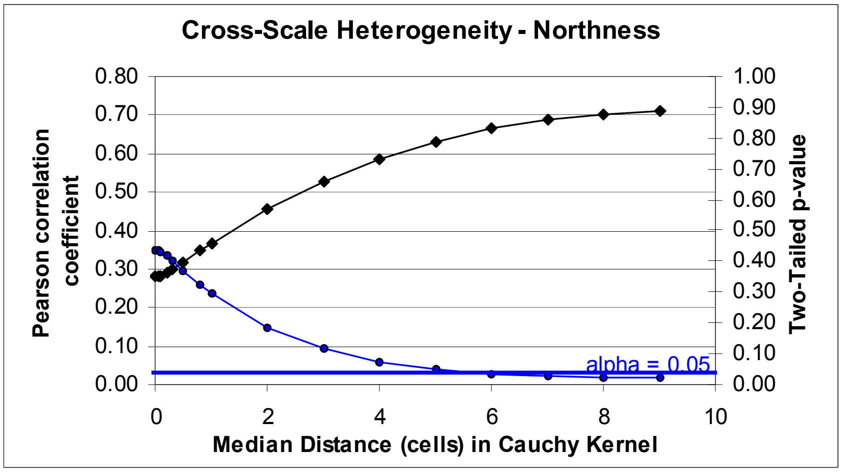
As stated before, it would be beneficial to apply this control experiment multiple times for different sets of random grids, but computational limitations prevent this.

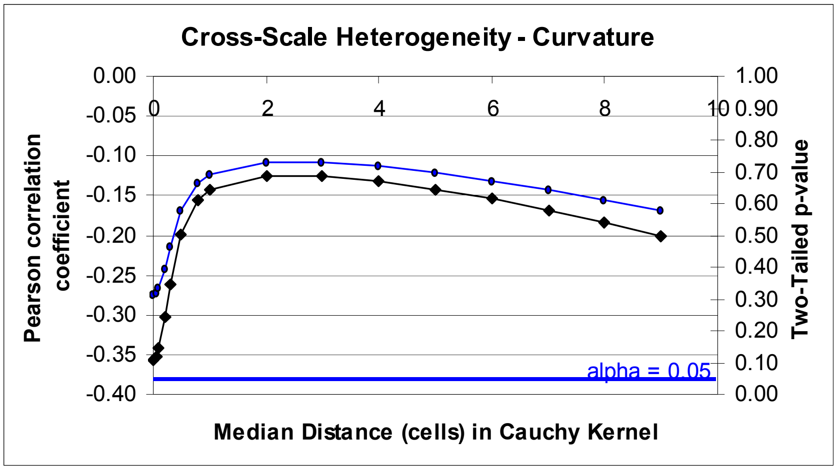
6.3.1.3.2 Individual variables

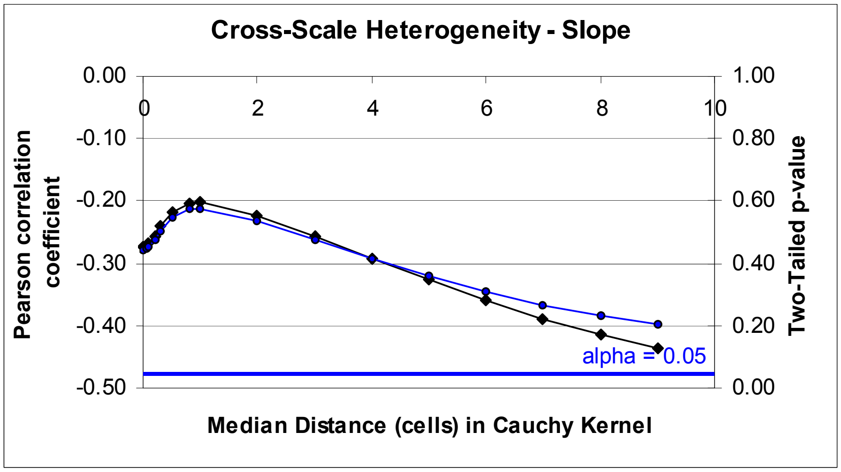
Having highlighted the danger of non-causal relationships occurring in this analysis, the results of the heterogeneity model for each terrain characteristic using the TOPO DEM is presented variable by variable (Figure 107), and the results summarized in a single table (Table 61).

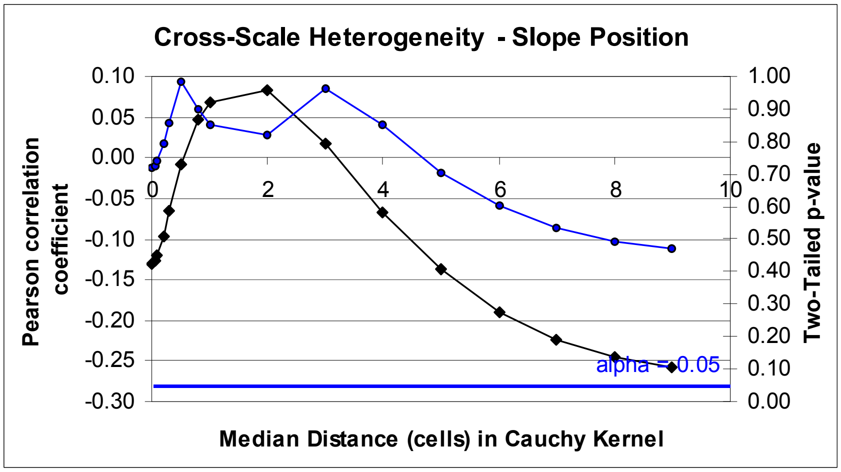


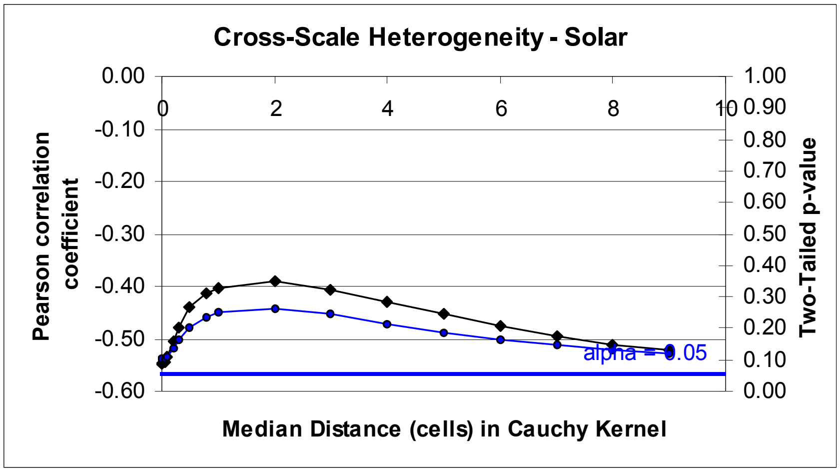


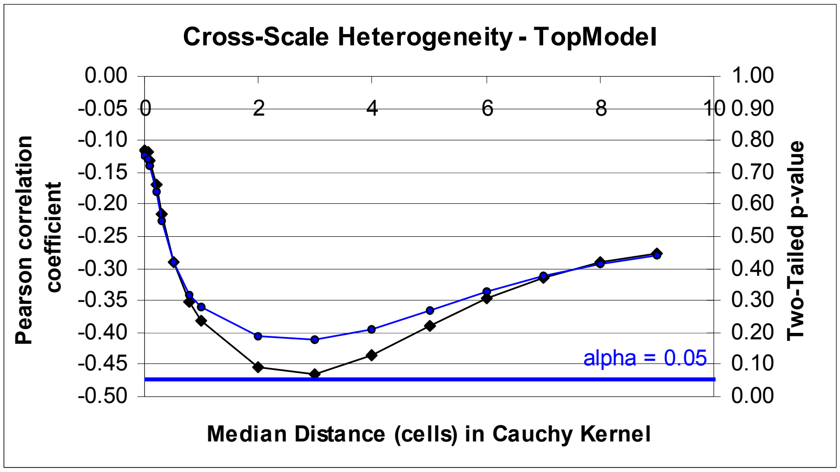



Cross-Scale Heterogeneity - Curvature
Pearson correlation coefficient
0.00
-0.05
-0.10
-0.15
-0.20
-0.25
-0.30
-0.35
-0.40
0
2
4
6
8
10
Two-Tailed p-value
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
alpha = 0.05
Median Distance (cells) in Cauchy Kernel


Cross-Scale Heterogeneity - Slope
Pearson correlation coefficient
0.00
-0.10
-0.20
-0.30
-0.40
-0.50
0
2
4
6
8
10
Two-Tailed p-value
1.00
0.80
0.60
0.40
0.20
0.00
alpha = 0.05
Median Distance (cells) in Cauchy Kernel


Cross-Scale Heterogeneity - Slope Position
Pearson correlation coefficient
0.10
0.05
0.00
-0.05
-0.10
-0.15
-0.20
-0.25
-0.30
0
2
4
6
8
10
Two-Tailed p-value
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
alpha = 0.05
Median Distance (cells) in Cauchy Kernel


Cross-Scale Heterogeneity - Solar
Pearson correlation coefficient
0.00
-0.10
-0.20
-0.30
-0.40
-0.50
-0.60
0
2
4
6
8
10
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
Two-Tailed p-value
alpha = 0.05
Median Distance (cells) in Cauchy Kernel


Cross-Scale Heterogeneity - TopModel
Pearson correlation coefficient
0.00
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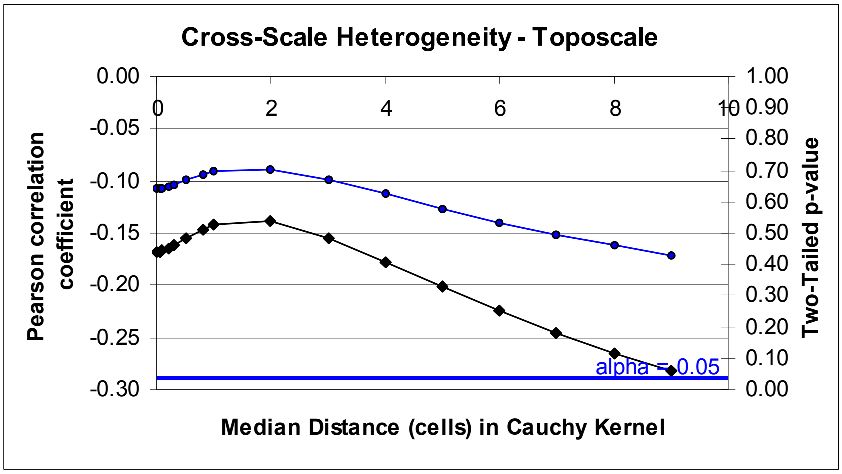
-0.10
-0.15
-0.20
-0.25
-0.30
-0.35
-0.40
-0.45
-0.50
0
2
4
6
8
10
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
Two-Tailed p-value
alpha = 0.05
Median Distance (cells) in Cauchy Kernel


Cross-Scale Heterogeneity - Toposcale
Pearson correlation coefficient
0.00
-0.05
-0.10
-0.15
-0.20
-0.25
-0.30
0
2
4
6
8
10
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
Two-Tailed p-value
alpha = 0.05
Median Distance (cells) in Cauchy Kernel

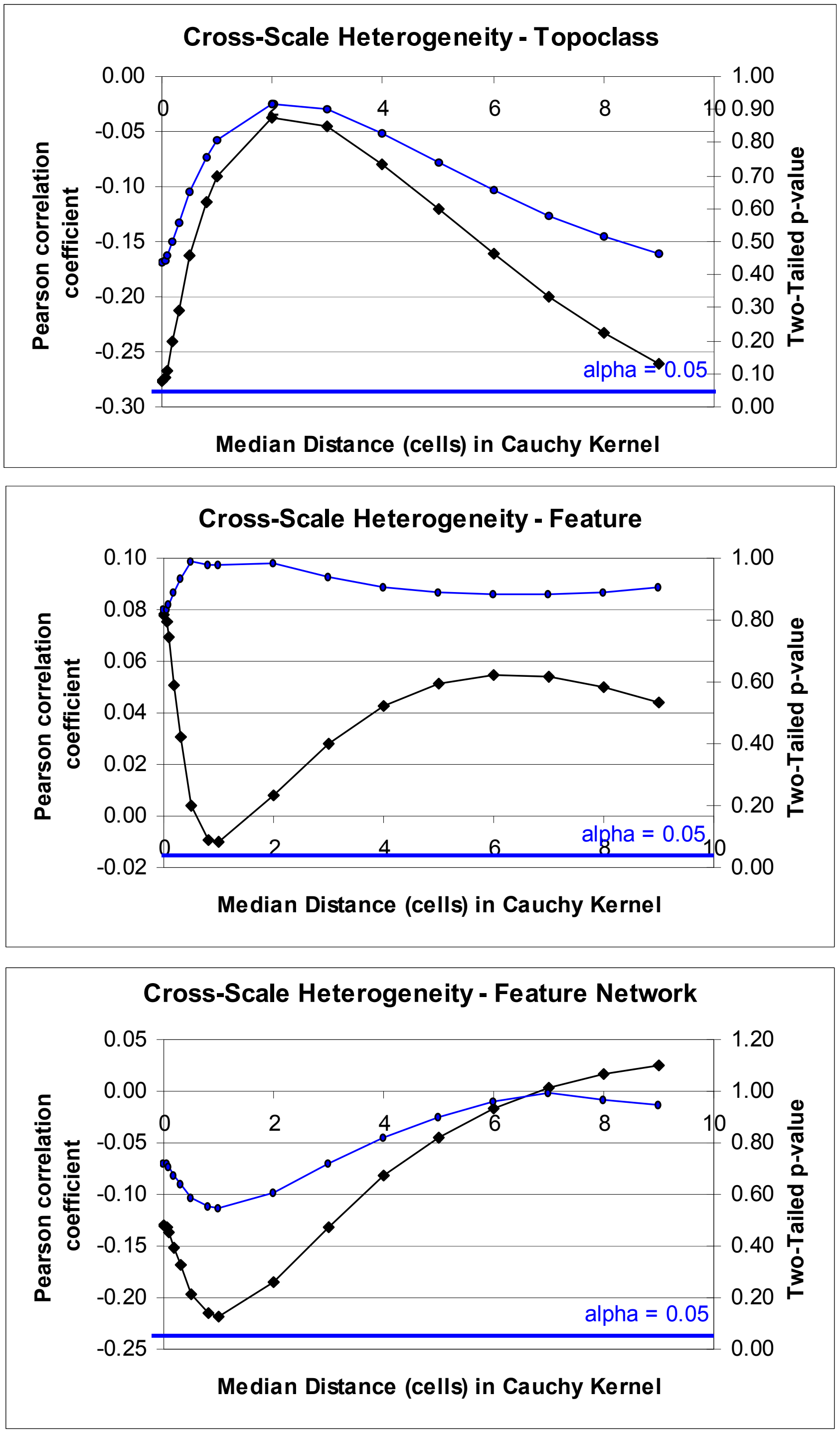


Figure 108 Cross-scale correlations between species diversity (Simpson's) and spatial heterogeneity for each environmental variable in TBS using the TOPO DEM. The black line represents the Pearson correlation coefficient, whilst the blue line indicates the respective p-value. For ease of interpretation, the thick blue line shows the threshold for significant correlations at the alpha = 0.05 level.

Variable	Minimum Pearson Correlation Coeffcient	Maximum Pearson Correlation Coeffcient	Minimum p-value	Significance (alpha=0.05)	Scale of lowest p-value (median distance in cells)
Elevation	-0.36	0.06	0.31	Not-significant	4
Eastness	-0.35	-0.25	0.32	Not-significant	9
Northness	0.28	0.71	0.02	Significant	9
Curvature	-0.36	-0.12	0.31	Not-significant	0.01
Slope	-0.44	-0.20	0.21	Not-significant	9
Slope Position	-0.26	0.08	0.47	Not-significant	9
Solar Radiation	-0.55	-0.39	0.10	Not-significant	0.01
Topmodel	-0.46	-0.12	0.18	Not-significant	3
Toposcale	-0.28	-0.14	0.43	Not-significant	9
Topoclass	-0.28	-0.04	0.44	Not-significant	0.01
Feature	-0.01	0.08	0.83	Not-significant	0.01
Network Feature	-0.22	0.03	0.55	Not-significant	1

Table 61 Summary table of results of multi-scale environmental heterogeneity modeling, examining maximum correlations between species richness and heterogeneity for the ten plots in TBS using the TOPO DEM.

Few significant results are evident, with only heterogeneity in northness correlating for large median distances. However, the results of all these correlations are heavily affected by the low Simpson's diversity of plot 5 (0.84), which is considerably more dominant than the other plots (with Simpson's diversity of 0.97-0.99). The correlations are therefore highly sensitive to this point and when plot 5 is discounted from the analysis, all correlations (including northness) are insignificant. This shows that the correlation with northness is not sufficiently robust, and should not be considered as a concrete result.

Given the lack of correlations for single variables, multiple linear regressions are not performed for this data.

The abject lack of correlations using the TOPO DEM is a result in itself, but the role of spatial environmental heterogeneity on tree species diversity in LRF cannot be rejected due to quality and scale issues in the DEM used to calculate the terrain characteristics and subsequent heterogeneity. As stated many times before in this thesis, the TOPO DEM does not capture the intricate network of small streams found in steep sided but small valleys. These characteristics, likely the principal cause of environmental heterogeneity in most variables in the site, are not captured as the aerial photographs used to produce the cartography only map the canopy level topography, which is significantly smoother than the underlying terrain. Under these circumstances, many topographic features are not captured, and the measurement of heterogeneity in terrain characteristics using this DEM is not sufficiently reliable to make a concrete conclusion.

6.3.2 SRTM DEM

Having examined the results of the heterogeneity modelling using the TOPO DEM, finding no significant correlation but data quality issues hampering this analysis, this section performs the same analysis using the SRTM DEM. Though the SRTM DEM likely contains greater precision than the cartographic DEM, the coarse cell size (92m) renders it even less representative of the micro-scale environmental heterogeneity found in TBS. Nevertheless, the scale at which environmental heterogeneity may be significant in shaping the tree species diversity is unknown and coarse-scale patterns may prove to be significant.

6.3.2.1 Spatial heterogeneity results

6.3.2.2 Cross-correlation matrix

There is much more cross-correlation between heterogeneity variables in TBS using the SRTM DEM expressed using the Pearson correlation coefficient, though this is likely due to the few number of cells used in the analysis (Table 62). It is also important to note that all variables are positively correlated, indicating once more that in TBS an area that is heterogeneous in one variable is also likely to be heterogeneous in others (this was not the case in Tambito), again likely a function of the small and uniform scale of topography variation in TBS compared with the more multi-scale topographic variation found in Tambito. Heterogeneity in the feature classification, solar radiation and slope position variables were the least cross-correlated (in that order), and heterogeneity in curvature, toposcale and eastness were the most cross-correlated variables.

	Elevation	Eastness	Northness	Curvature	Slope	Slope Position	Solar	Toposcale	Topmodel	Topoclass	Feature	Feature (network)
Elevation	-	0.81	0.72	0.96	0.98	0.77	0.89	0.85	0.75	0.85	0.49	0.77
Eastness		-	0.83	0.89	0.82	0.78	0.63	0.93	0.91	0.86	0.71	0.93
Northness			-	0.82	0.74	0.68	0.53	0.89	0.86	0.79	0.76	0.90
Curvature				-	0.96	0.82	0.83	0.92	0.83	0.88	0.65	0.86
Slope					-	0.78	0.90	0.86	0.78	0.88	0.51	0.79
Slope Position						-	0.64	0.80	0.71	0.76	0.55	0.75
Solar							-	0.67	0.56	0.75	0.34	0.57
Toposcale								-	0.91	0.93	0.70	0.94
Topmodel									-	0.84	0.72	0.92
Topoclass										-	0.59	0.86
Feature											-	0.73
Feature (network)												-

Table 62 Cross-correlation matrix between all spatial heterogeneity variables with the median distance set at 1 cell in TBS using the SRTM DEM (n = 10,400). Cells are shaded when the correlation coefficient is above 0.80 in order to highlight the most significant correlations.

6.3.2.3 Comparison with plot data

6.3.2.3.1 Control Experiment

The application of the heterogeneity model to twelve random grids with the dimensions and resolution of the SRTM DEM also provides an alarming result, with 50% of the random grids (six) producing a significant correlation (95% significance level) with Simpson's diversity in the plots for at least one scale (Table 63). For these six correlations, an average of 4.5 scales correlated for each grid (partly as a result of the co-correlation between heterogeneity grids of adjoining scale, Pearson = 0.97, n = 180), involving a total of 27 significant correlations. Once again this highlights the danger of non-causal relationships in the multi-scale correlation analyses.

Random Run	Maximum Pearson	Minimum Pearson	No. Scales with significant correlation
Random grid 1	0.13	-0.14	0
Random grid 2	0.29	0.07	0
Random grid 3	0.39	-0.21	0
Random grid 4	-0.15	-0.50	0
Random grid 5	0.88	-0.03	8
Random grid 6	0.72	0.00	3
Random grid 7	-0.08	-0.27	0
Random grid 8	0.40	-0.02	0
Random grid 9	0.69	0.18	4
Random grid 10	0.08	-0.74	2
Random grid 11	0.65	-0.54	1
Random grid 12	0.82	0.33	9

Table 63 Results of the heterogeneity analysis for the 12 random grids using the SRTM DEM in TBS.

When Plots 4 and 5 are excluded from the correlations for reasons outlined in Section 6.3.1.3.1, four of the 12 random grids still provide a correlation (Table 64), with an average of six different scales correlating significantly per random grid.

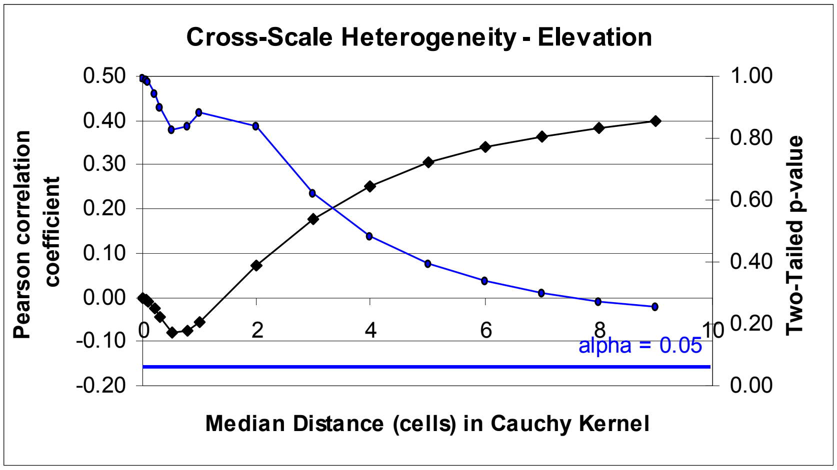
Random Run	Maximum Pearson	Minimum Pearson	No. Scales with significant correlation
Random grid 1	0.65	-0.30	1
Random grid 2	0.70	0.04	4
Random grid 3	0.04	-0.55	0
Random grid 4	-0.05	-0.46	0
Random grid 5	0.59	-0.14	0
Random grid 6	-0.02	-0.17	0
Random grid 7	0.32	-0.32	0
Random grid 8	0.43	0.14	0
Random grid 9	0.92	0.16	10
Random grid 10	0.52	-0.55	0
Random grid 11	0.87	-0.42	8
Random grid 12	0.58	0.17	0

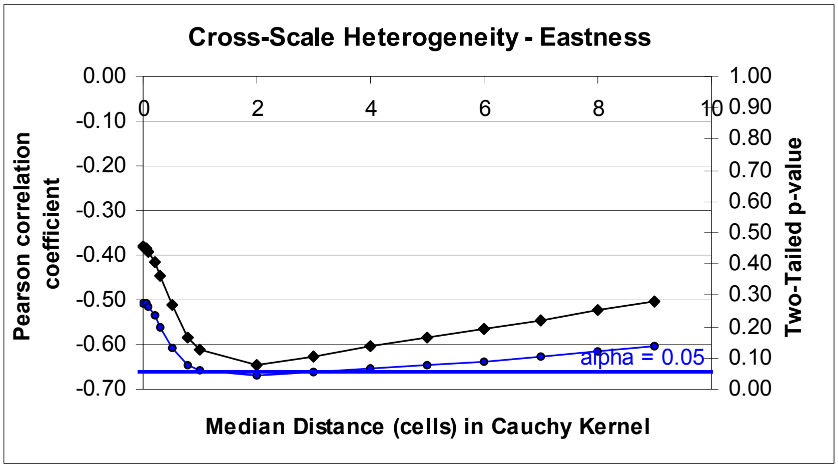
Table 64 Results of the heterogeneity analysis for the 12 random grids when Plots 4 and 5 are excluded from the analysis using the SRTM DEM in TBS.

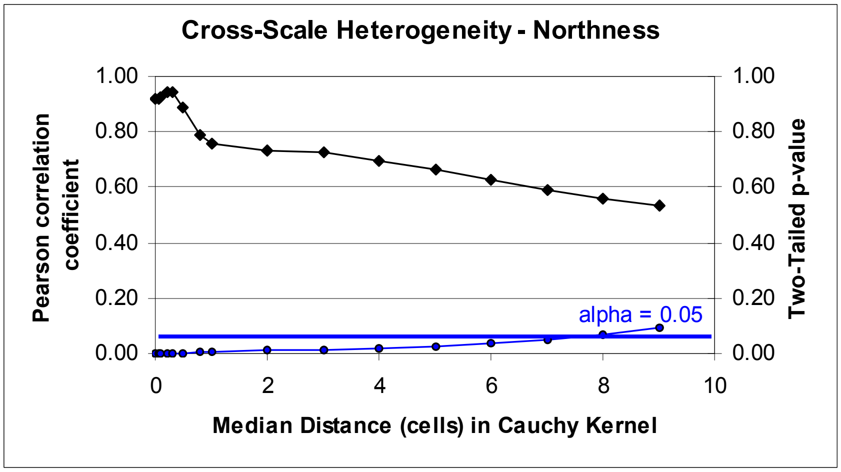
This calls for extreme caution in interpreting the results of the heterogeneity modelling as numerous spurious correlations may be expected, though the reasons for so many significant correlations are unknown. This is a strong limitation to the interpretation of these heterogeneity results in TBS, and is something that requires further study.

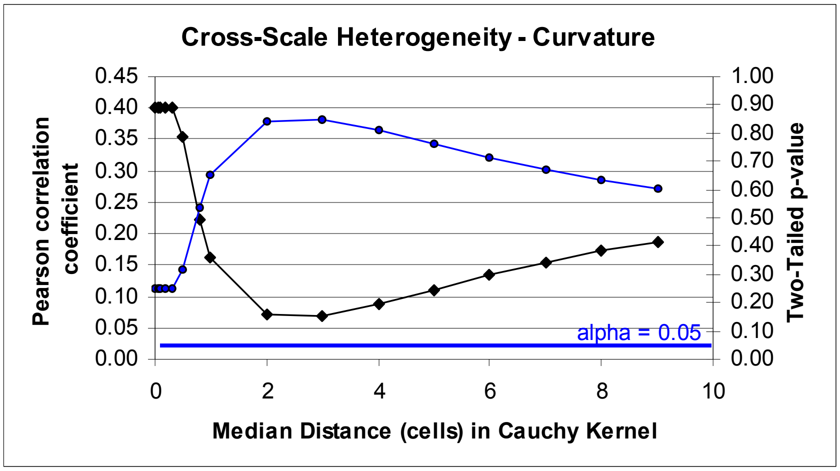
6.3.2.3.2 Individual variables

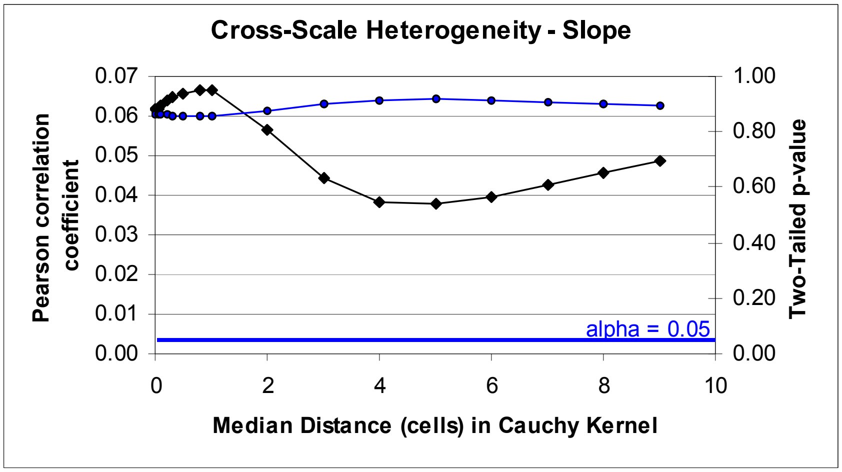
The heterogeneity model is applied for all terrain characteristics from the SRTM DEM, and the multi-scale correlation graphs shown in Figure 109, and a summary of the results is shown in Table 65.

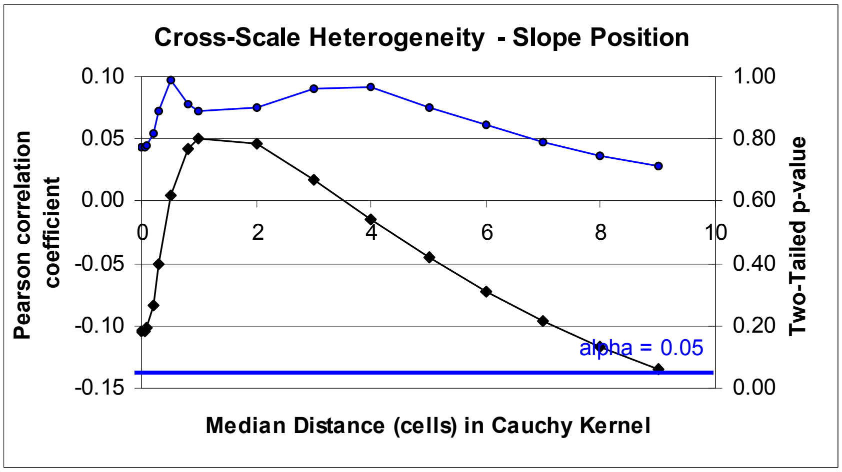

Cross-Scale Heterogeneity - Elevation
Pearson correlation coefficient
Two-Tailed p-value
Median Distance (cells) in Cauchy Kernel
alpha = 0.05
0.50
0.40
0.30
0.20
0.10
0.00
-0.10
-0.20
1.00
0.80
0.60
0.40
0.20
0.00
0
2
4
6
8
10

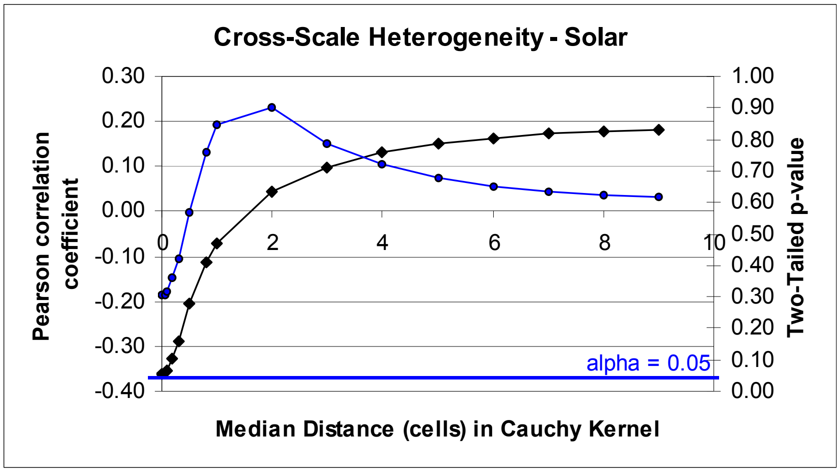

Cross-Scale Heterogeneity - Eastness
Pearson correlation coefficient
Two-Tailed p-value
Median Distance (cells) in Cauchy Kernel
alpha = 0.05
0.00
-0.10
-0.20
-0.30
-0.40
-0.50
-0.60
-0.70
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
0
2
4
6
8
10

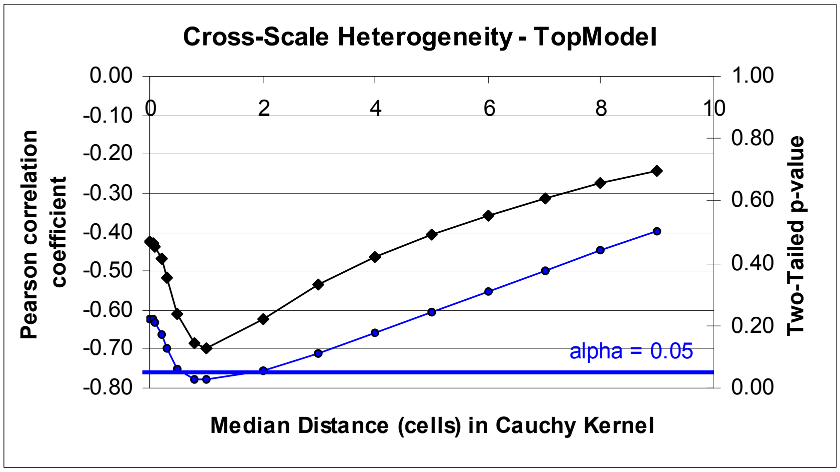

Cross-Scale Heterogeneity - Northness
Pearson correlation coefficient
Two-Tailed p-value
Median Distance (cells) in Cauchy Kernel
alpha = 0.05
1.00
0.80
0.60
0.40
0.20
0.00
1.00
0.80
0.60
0.40
0.20
0.00
0
2
4
6
8
10

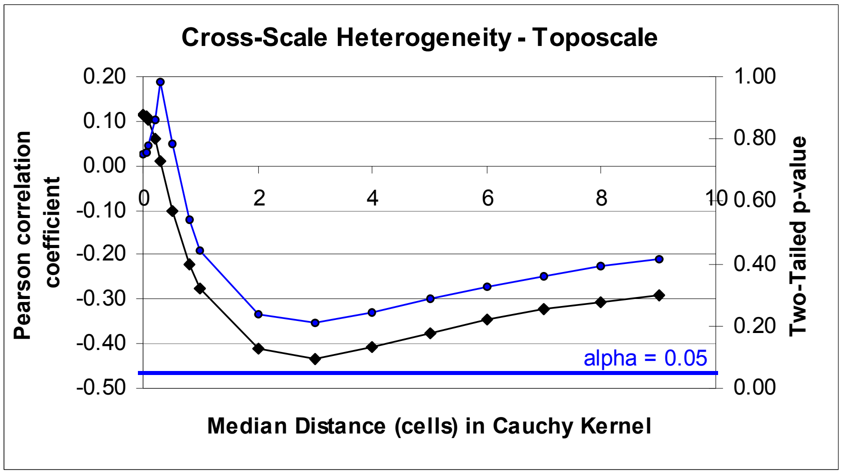

Cross-Scale Heterogeneity - Curvature
Pearson correlation coefficient
Two-Tailed p-value
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
0
2
4
6
8
10
alpha = 0.05
Median Distance (cells) in Cauchy Kernel


Cross-Scale Heterogeneity - Slope
Pearson correlation coefficient
Two-Tailed p-value
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
1.00
0.80
0.60
0.40
0.20
0.00
0
2
4
6
8
10
alpha = 0.05
Median Distance (cells) in Cauchy Kernel


Cross-Scale Heterogeneity - Slope Position
Pearson correlation coefficient
Two-Tailed p-value
0.10
0.05
0.00
-0.05
-0.10
-0.15
1.00
0.80
0.60
0.40
0.20
0.00
0
2
4
6
8
10
alpha = 0.05
Median Distance (cells) in Cauchy Kernel


Cross-Scale Heterogeneity - Solar
Pearson correlation coefficient
Two-Tailed p-value
Median Distance (cells) in Cauchy Kernel
0.30
0.20
0.10
0.00
-0.10
-0.20
-0.30
-0.40
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
0
2
4
6
8
10
alpha = 0.05


Cross-Scale Heterogeneity - TopModel
Pearson correlation coefficient
Two-Tailed p-value
Median Distance (cells) in Cauchy Kernel
0.00
-0.10
-0.20
-0.30
-0.40
-0.50
-0.60
-0.70
-0.80
1.00
0.80
0.60
0.40
0.20
0.00
0
2
4
6
8
10
alpha = 0.05


Cross-Scale Heterogeneity - Toposcale
Pearson correlation coefficient
Two-Tailed p-value
Median Distance (cells) in Cauchy Kernel
0.20
0.10
0.00
-0.10
-0.20
-0.30
-0.40
-0.50
1.00
0.80
0.60
0.40
0.20
0.00
0
2
4
6
8
10
alpha = 0.05

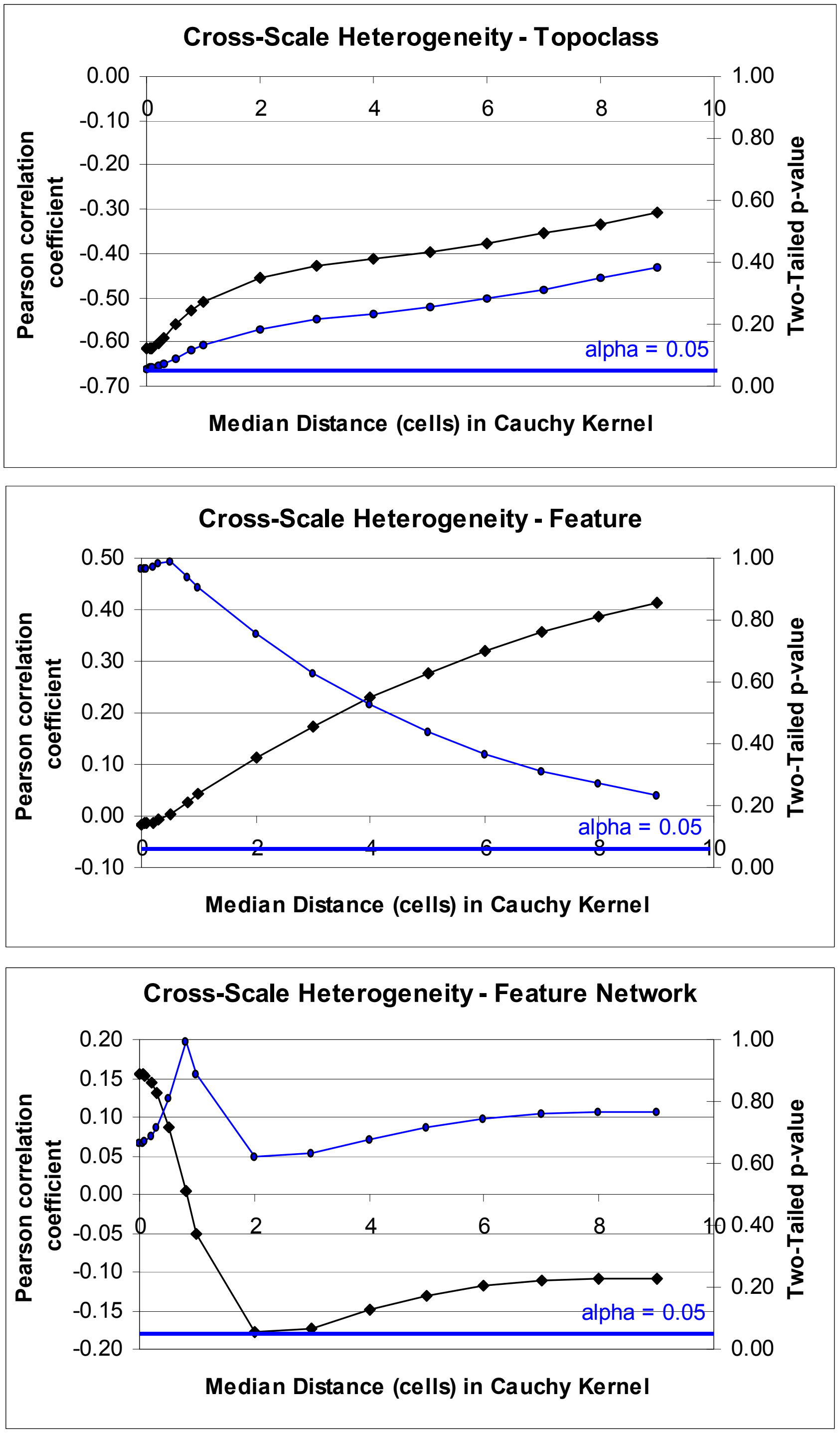


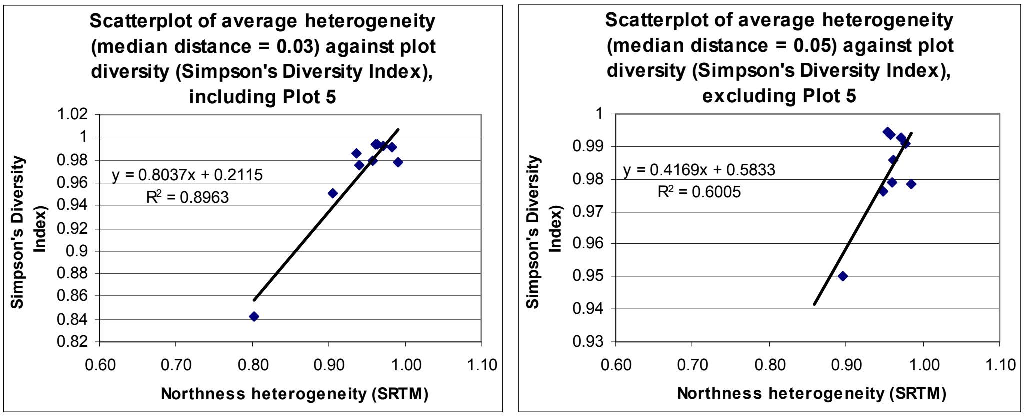
Figure 109 Cross-scale correlations between species diversity (Simpson's) and spatial heterogeneity for each environmental variable in TBS using the SRTM DEM. The black line represents the Pearson correlation coefficient, whilst the blue line indicates the respective p-

value. For ease of interpretation, the thick blue line shows the threshold for significant correlations at the alpha = 0.05 level.

Variable	Minimum Pearson Correlation Coeffcient	Maximum Pearson Correlation Coeffcient	Minimum p-value	Significance (alpha=0.05)	Scale of lowest p-value (median distance in cells)
Elevation	-0.08	0.40	0.25	Not-significant	9
Eastness	-0.64	-0.38	0.04	Significant (inverse)	2
Northess	0.53	0.95	0.00	Significant	0.3
Curvature	0.07	0.40	0.25	Not-significant	3
Slope	0.04	0.07	0.85	Not-significant	0.8
Slope Position	-0.13	0.05	0.71	Not-significant	9
Solar Radiation	-0.36	0.18	0.30	Not-significant	0.01
Topmodel	-0.70	-0.24	0.03	Significant (inverse)	1
Toposcale	-0.43	0.12	0.21	Not-significant	3
Topoclass	-0.62	-0.31	0.06	Not-significant	0.01
Feature	-0.02	0.41	0.23	Not-significant	9
Network Feature	-0.18	0.16	0.62	Not-significant	2

Table 65 Summary table of results of multi-scale environmental heterogeneity modeling, examining maximum correlations between species richness and heterogeneity for the ten plots in TBS using the SRTM DEM.

Significant correlations are found between plot species diversity and spatial environmental heterogeneity in three variables for the SRTM DEM, including eastness (inversely correlated at 1 scale), northness (positively correlated at 13 scales), and topmodel (inversely correlated at 2 scales). As discussed earlier, many of these correlations are heavily affected by the low Simpson's diversity in Plot 5 and to a lesser extent in Plot 4. When these plots are excluded from the correlation, eastness and topmodel no longer provide any significant correlation ($p>0.05$ in both cases), whilst northness still correlates but with a reduced Pearson coefficient of 0.77 ($p = 0.01$) (Figure 110).


Scatterplot of average heterogeneity (median distance = 0.03) against plot diversity (Simpson's Diversity Index), including Plot 5

Scatterplot of average heterogeneity (median distance = 0.05) against plot diversity (Simpson's Diversity Index), excluding Plot 5

Figure 110 Scatterplot of heterogeneity in the northness variable against plot diversity, using the SRTM DEM for TBS when plot 5 is included (left) and excluded (right).

Lowest species diversity is found in areas homogenous in northness, with low diversity Plots 4 and 5 both having markedly low levels of heterogeneity in northness at low median distances. However, these two plots are in close proximity to the river, within the flat flood plain that neighbours the main River Tiputini channel with frequent flooding, and it is unlikely that the low diversity in these plots is brought about by homogeneity in northness. Rather the low diversity in these plots has already been attributed to the frequent flooding outlined in Chapter 4.

Beyond the correlation with northness, the significant correlations with topmodel and eastness are not sufficiently robust to merit specific discussion. Given the lack of a clear result in the single variate analysis presented here, the multiple linear regression is not performed as the interpretation of results is difficult and would be highly inconclusive. The lack of correlation between heterogeneity and diversity for the SRTM DEM may originate from the resolution of the original DEM, which captures general topographic patterns but fails to identify much of the micro-scale heterogeneity present in TBS.

6.4 Conclusions

This chapter has examined the role of spatial environmental heterogeneity on tree species diversity in a montane environment (Tambito) with extensive environmental gradients over short distances and in a lowland environment (TBS) with less extensive gradients but nevertheless a degree of environmental heterogeneity at the micro-scale.

In Tambito, heterogeneity in elevation is concluded to be of importance in shaping tree species diversity with greater diversity found in more spatially heterogeneous sites, though the precise cause of this is open to discussion. This observation is supported in theory by the habitat association that has already been identified in tree species composition across the elevational gradient (Chapter 4). If species are associated to specific altitudinally controlled habitats, regions with a great neighbouring diversity in these habitats are likely to contain more species, due to them representing a mixing-zone with a diverse pool of seeds arriving to the site through distance-dependent dispersal. There are likely also important biotic interactions in heterogeneous sites, including the important effects of herbivory (and associated host-specificity) that have not been discussed explicitly here, but nevertheless important to acknowledge.

However, issues of co-linearity between variables complicate greatly the analysis. These problems occur not only *between* heterogeneity variables (i.e. heterogeneity in elevation is co-linear with heterogeneity in slope position) but also between heterogeneity and other basic factors such as elevation. An important finding of this chapter has been the identification of a peak in elevational heterogeneity in mid-elevations. Given that Letts (2003) has found productivity to decrease with greater elevation this also represents a productivity gradient, indicating that highest heterogeneity is found in mid-productivity levels, a finding reported only once in the literature across the productivity gradient in limestone pavements (Lundholm and Larson, 2003). In this case study it makes it impossible to isolate the causal factor for the mid-diversity peak observed in the plot data, with plausible explanations including the mid-domain effect, species-area relationships, productivity-diversity relationships and the role of spatial environmental heterogeneity. Indeed, further testing of the heterogeneity model and associated analyses in other regions may indicate that this peak in heterogeneity in mid-elevations (or mid-catchment more precisely) is a property shared by many landscapes, brought about by geomorphological processes originating from the erosional processes of rivers especially in tectonic environments.

Finally, it is also important to note that heterogeneity using the method applied here is not a universal concept for this kind of landscape, with numerous examples of heterogeneity in one variable signifying homogeneity in another. This means that the selection of environmental variable for quantifying heterogeneity is of great importance, and must be carefully considered.

In TBS the results of the heterogeneity modelling were not satisfactory, and no significant correlations can be concluded using either of the DEMs. Quality issues with the topographic data means that spatial heterogeneity cannot be discounted as a driver of tree species diversity maintenance, as the DEMs may not be capturing the topographic variation relevant to spatially distributing species composition and diversity. Neither DEM accurately captures the intricate network of valleys and ridges, and it may be this environmental variation and the spatial heterogeneity of this variation that to some extent shapes tree species diversity. However, perhaps it can be conclusively stated that broad scale heterogeneity (which is suitably captured in both DEMs) does not appear to shape tree species diversity at the micro-scale.

However, contrary to the findings in Tambito, regions heterogeneous in one topographic variable are also likely to be heterogeneous in another variable, with high levels of positive co-linearity in heterogeneity for most variables. This indicates that heterogeneity in lowland rain forests at the scale used in this study is a more universal phenomenon in the landscape, and is less sensitive to the type of variable used.

Though the results presented here show little evidence of significant patterns between spatial environmental heterogeneity and diversity in lowland rain forests, further studies should apply the models over high resolution and more precise DEMs in well-studied diversity plots. Furthermore the worrying number of correlations found between diversity and heterogeneity of random grids must be further examined, especially in the case of the SRTM DEM. The uncertainty in the validity of the correlations with terrain characteristics that the control experiments highlighted significantly weakened the degree to which concrete conclusions could be achieved in TBS.

In general, the analyses shown here represents the first application of a model that quantifies spatial environmental heterogeneity in tropical forests, and compares it to tree species diversity. The results are far from conclusive, yet some important patterns have been identified and further study is undeniably warranted. Firstly, spatial environmental heterogeneity could be quantified in a broad range of ways, and different models should be developed and tested to examine the degree to which the results are dependent on the statistical method used to quantify heterogeneity, as well as the distance function applied to define the spatial weighting. Secondly, more concrete conclusions could be achieved with a greater number of diversity plots, minimizing the potential effect of single data points which significantly affected the results in TBS, for example.

Chapter 7

7 Final Conclusions

This thesis has attempted to understand micro-scale spatial variation in tree diversity, composition and structure in two contrasting sites using terrain-based characteristics that through different mechanisms determine some of the essential resources for plants (light, water and temperature principally). The approach adopted is centered on testing equilibrium-based theories for diversity maintenance in tropical forests.

The results have been mixed. Firstly, plot-based measurement of tree diversity, composition and structure showed significant between-plot variability in each of the two study sites. In the steep topographic gradients of the tropical montane (cloud) forest at Tambito, plot richness varied from 30 to 52 species, with an average abundance of 4.1 individuals per species. Similarly, for the topographically more subtle lowland rainforest TBS site, plot richness was found to vary between 31 and 82 species, with an average abundance of just 2.1 individuals per species. These results alone present sufficient evidence to state that tree diversity and composition is significantly variable over space in both of these environments (Objective 1), and also that both sites studied here have remarkable levels of diversity.

When spatial patterns in composition are examined in detail, a very clear elevational gradient is evident in the TMCF site in Tambito, with 36% of variability in composition explained by elevation. Although elevation itself is not a variable that is likely to affect composition, it represents a gradient in temperature, wetness, cloud cover and likely other variables. This compositional gradient is attributed to species adaptations to specific climatic bands. Similarly in TBS, a compositional gradient is also identified along the short elevational gradient (explaining just 16%), though this pattern is also observed with greater distance from the main river channel (which correlates with altitude since the river occupies the lowest land), and with greater geographic (Cartesian) distance between plots (all three variables co-linear). The elevational gradient itself is too small to represent a temperature gradient in TBS, but is indicative of flooding frequency, also partly captured with the distance from river variable. However, these factors may also represent a gradient of forest and soil age, driven by long-term migration of the river channel across its floodplain. Ultimately the compositional gradient observed may indeed be a combination of these factors.

These results indicate that physical (as opposed to biotic) habitat association in composition does occur in both sites to different extents, but that the majority of compositional variability between plots remains unexplained by the terrain-based variables used here (Objective 2). The remaining unexplained variability in composition may be driven by a combination of abiotic factors not measured here, biotic factors as well as non-equilibrium based processes of forest dynamics. This is an interesting result, and indeed the first example of the identification of micro-scale habitat associations in composition using quantified terrain-based analysis in tropical forests. The levels of habitat associations observed here may be sensitive to sampling strategy, and indeed the use of different sized plots (with associated different scale terrain-based characteristics) will likely cause variation in the habitat associations found here (35% in Tambito and 16% in TBS). Further research with larger plots, and multi-scale terrain analyses would provide better results.

When patterns in diversity are examined (Objective 3), this study has found a mid-elevation peak in diversity in Tambito at around 1850m, and also a strong pattern between richness and mean topographic curvature, with greatest richness being found on convex slopes. The peak in diversity in mid-elevations is attributed to a combination of the mid-domain effect and an area-based hypothesis, and a simple model is produced to illustrate this (Section 4.2.2.1.2). The identification of higher richness on convex slopes is principally attributed to a greater diversity of light environments, brought about by a combination of vertical and lateral light penetration of the canopy, though this pattern may also be explained by greater exposure to cloud-based water and nutrient inputs on convex slopes, or the poor soils expected on leached convex slopes. In the lowland forest site at TBS, few richness or diversity patterns were found except for significantly lower diversity in two sites alongside the river and which are thus regularly subjected to flooding (sometimes for prolonged periods of time). The remaining variability in diversity in the TBS site is unexplained by the terrain characteristics used in this study, though issues with DEM quality mean that the existence of a link between tree diversity and terrain characteristics cannot be discounted.

Tree structure has been shown to vary significantly between sites in Tambito, yet surprisingly little of this variability is explained by terrain characteristics (Objective 5). Particularly surprising is the lack of patterns across the elevational gradient, with no evidence of a progressive increase in stem density, decrease in DBH or decrease in tree height with greater elevation. These results are contradictory to many empirical studies found in the literature (presented in Section 2.4). Just one significant correlation was found in Tambito, with 67% of variability in the DBH/Height ratio being explained by the topmodel wetness index variable, indicative of soil moisture. This pattern is attributed to an investment by trees in increased girth relative to height in order to achieve greater stability and lessen the likelihood of treefall through uprooting, which is more likely on wetter, therefore less stable soils. In TBS, a significant difference is found in tree height between the three highest elevation plots and the lower-elevation plots, with these groups possibly differentiated in terms of flooding regime with plots below 220m elevation being subjected to occasional flooding and having significantly lower average tree stature than the three higher elevation plots. This pattern may indeed be indicating two unique forest structures, no doubt reflecting the two types of Amazonian lowland forest discussed in the literature; *terra firme* and *varzea* forest.

Finally, models of spatial environmental heterogeneity have been applied to examine the role of characteristics in surrounding areas on diversity and composition at each of the plots, as brought about by spatial interactions such as seed dispersal (Objective 4). In Tambito, spatial heterogeneity in elevation is shown to explain some variation in diversity (explaining 53% of variability). This is an important finding, showing how both absolute elevation combined with spatial heterogeneity in elevation both contribute significantly to micro-scale diversity patterns in Tambito. In TBS, many complications contributed to a confusing set of results, for which no concrete conclusion can be reached. These problems included questionable quality in the original DEMs for the study site, many surprising and spurious correlations with control (random) analyses, and the poor distribution of diversity levels in the ten plots. DEM quality could be addressed through identifying alternative topographic data sources with higher resolution, which may capture topographic variation at a more relevant scale for the processes which drive spatial variability in tree diversity. The heterogeneity model seems to work where the terrain gradient (heterogeneity) is high, but fall subject to statistical constraints (inclusion of random effects) where the gradients are low (as in TBS). In general, the spatial heterogeneity analyses have shown promise in explaining some variability in diversity, and indeed furthering our understanding of the processes behind diversity maintenance, but fall short of providing solid results and merit further study.

Amongst these results are some important findings that further our understanding of micro-scale variation in diversity in tropical forests. Whilst terrain-based characteristics that determine the spatial variation in essential resources in tropical forests have explained some variability in composition, diversity and structure, a great deal of variability remains unexplained. This leads to the possibility that a combination of equilibrium and non-equilibrium (physical) processes (such as gap dynamics) is shaping the micro-scale variability in diversity alongside a suite of biotic (competition etc) interactions that also determine resource availability. This thesis has also presented innovative methodologies for examining the relationship between environment and diversity at the micro-scale, and the application of these methods in other sites with greater volume of ground-based diversity data may yield further insights.

There have been significant complications in reaching concrete conclusions in this research due to the low number of ground-based plots used to examine the relationships between topography and composition, diversity and structure. The original experimental design was to use high-resolution aerial imagery to monitor the spatial distribution of diversity, and use this larger dataset to compare canopy diversity with topography, at least for TBS where there was available imagery. Unfortunately the analysis of high-resolution imagery was complicated by many factors (shading, image coverage, suitable methods) and was not included in this PhD (though Appendix 1 provides an overview of what was achieved in this line of research). Within the time available for this thesis just ten plots could be generated for each study site, and making concrete conclusions with this data has been difficult, especially in TBS where two extremely low diversity plots alongside the river had great influence on the statistical significance of the linear regressions.

The analysis has also been complicated by strong co-linearity between some of the different terrain characteristics, making it difficult to separate true correlations from spurious relationships. Whenever possible, ecological interpretation of the results has been used to explain the most likely process *behind* such relationships (e.g. understanding the relationship between composition and elevation / geographic distance / distance from river in TBS), but in some cases this has not been possible. More data points (plots) would help illustrate more clearly the true correlations, alongside some more advanced statistical methods, though this is left for further study.

Whilst this research has provided some interesting results and conclusions, as in most research studies it has opened up many more questions. Specifically, the following topics should be further investigated in future research studies:

1. Full testing of different spatial heterogeneity measures as potential explanations of spatial variation in tree species diversity, and analysis of the sensitivity of the results to the different methods
2. Detailed analysis of the diversity gradient with greater distance from the main river channel, including soil surveying to confirm if this is in reality a pattern brought about by a disturbance from river flooding (short-term) or the result of longer term non-equilibrium adjustment along a primary successional gradient
3. Repetition of the analyses in other sites, and with greater number of ground-based diversity plots
4. Repetition of the analyses in lowland forest using higher-quality DEMs, possibly derived from ground based surveying or LIDAR / RADAR.

Perhaps the best strategy for following-on this research would be to apply the models to large, long-term plots such as the 50-Ha plot found in Yasuni National Park near the TBS site presented in this thesis, where abundant tree diversity data is available.

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8 Appendix 1

Acquisition and processing of digital high resolution aerial imagery over tropical forests

This Appendix shows some of the preliminary results achieved from a pilot study at using high resolution images to "monitor" tree canopy diversity.

The regular presence of cloud and steep topographic characteristics of the montane tropical forest found in Reserva Tambito make aerial photography an unrealistic means of assessing biodiversity. Logistically it is very complicated to take the necessary data in Reserva Tambito, so aerial photography is only to be applied to Tiputini Biodiversity Station.

Data Collection

Images were acquired using two complementary approaches, at both high and low altitude, designed to provide images with different spatial coverages and resultant differences in resolution. The first approach uses aircraft based aerial photography to acquire high altitude/low resolution images for the whole of the TBS field site. Within the Tiputini Biodiversity Station the second approach concentrated on the acquisition of high resolution (but low spatial coverage) images of the forest canopy, especially over ground-based diversity plots through the use of a tethered helium balloon.

Instruments and technical specifications

The instruments used for the photo acquisition vary depending on the aerial or tethered techniques, but all take full colour photos (red, green, blue) from digital cameras.

The aircraft based acquisition of aerial photos is not limited by weight, and so two cameras were used to ensure varying image resolutions and qualities. These were a Canon Digital Video camera, and a Kodak DCS420 digital camera. The Canon digital video takes 30 frames per second in DV format to a 1-hour DV tape. Individual frames of size 768 x 567 pixels were extracted from the resultant video. The recorded video was viewed externally by a small LCD TV monitor from within the aircraft to ensure that the imagery was properly acquired.

The digital camera used in the aerial photography was a Kodak DCS420 professionally calibrated digital aerial photography camera, which takes images of size 1524 x 1012 pixels. This camera was attached to a frame rate generator to automatically takes photos at a given time interval. The imagery is written to a PCMCIA memory card, and requires a minimum of 4 seconds between photos to completely save the imagery to memory. The camera will hold a maximum of 201 images in memory, before it must be downloaded to computer. These limitations were important when planning the flight path for image acquisition. Figure 1 shows the instrumental setup of the apparatus.

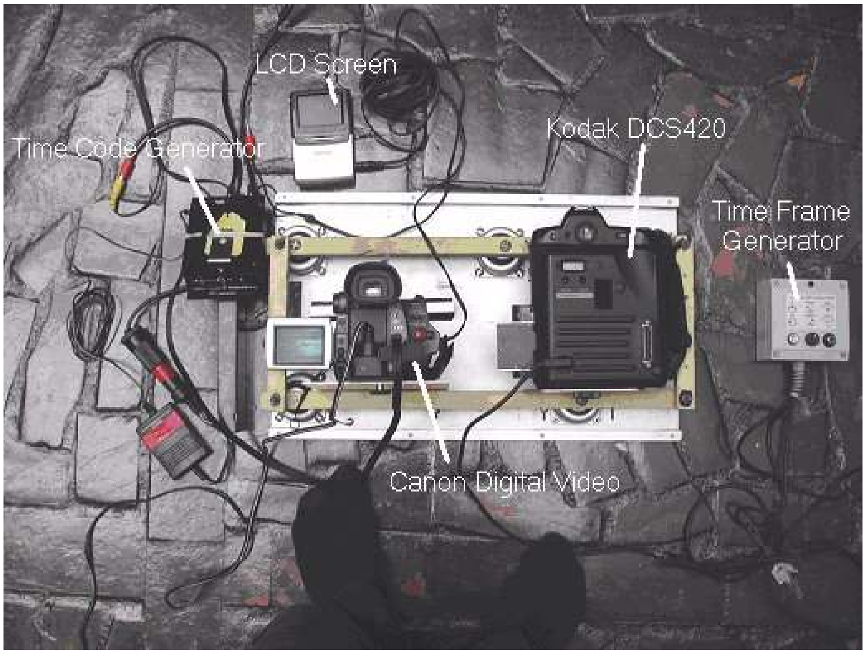


Figure 111 Instrumental setup for aerial photography acquisition

Camera calibration

Each camera was subjected to a calibration experiment to determine the relationships between the distance of the sensor from the target and the spatial resolution and spatial coverage. With this information it was also possible to calculate the time required between frames (frame-rate) to ensure a 33% overlap in images, and also the elevation at which blurring was likely to occur. This information is important for flight planning, in order to ensure that the imagery covers the entire TBS study region. The results of these calibrations are shown in Figures 112-115.

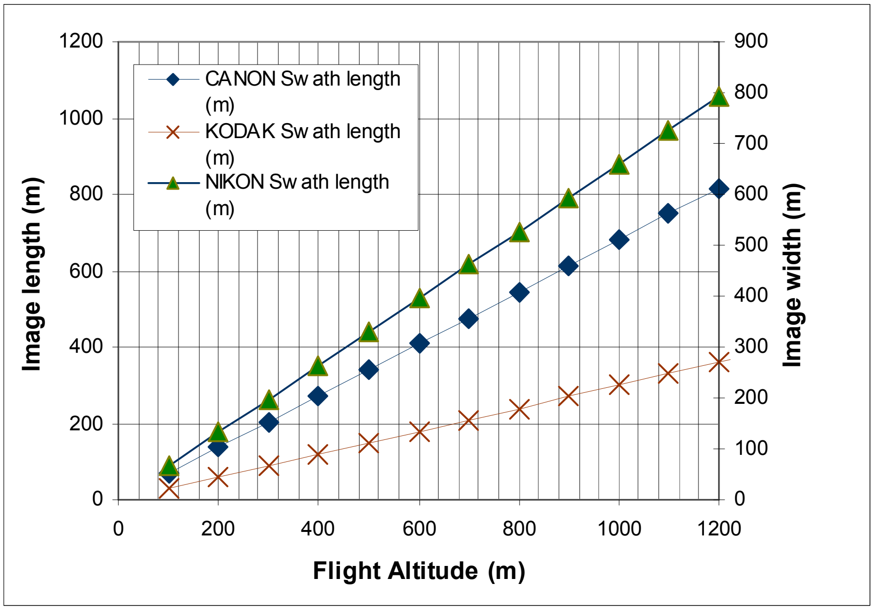


Figure 112 Ground spatial coverage of images from the three different cameras depending on elevation of the sensor above the ground surface.

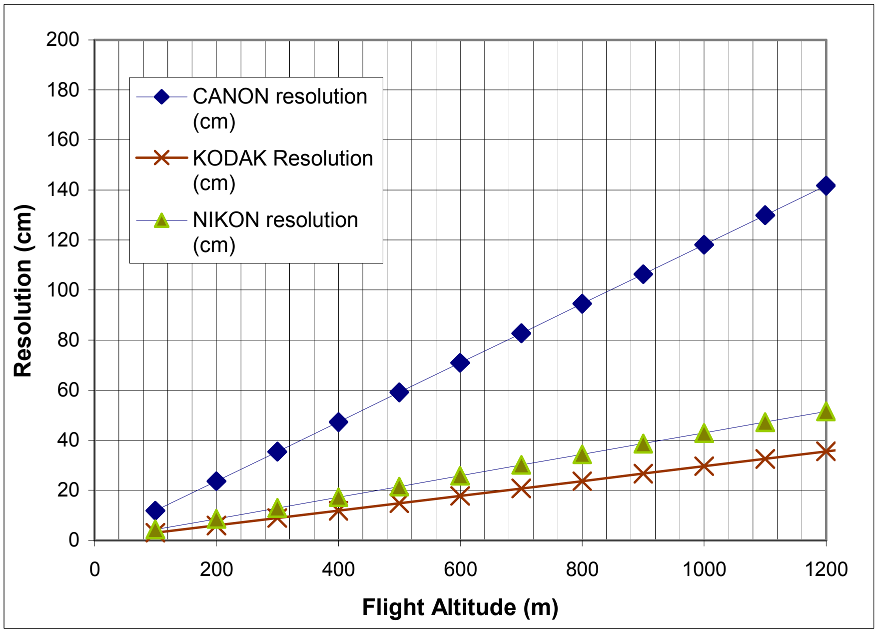


Figure 113 Resolution of images from the three different cameras depending on elevation of the sensor above the ground surface.

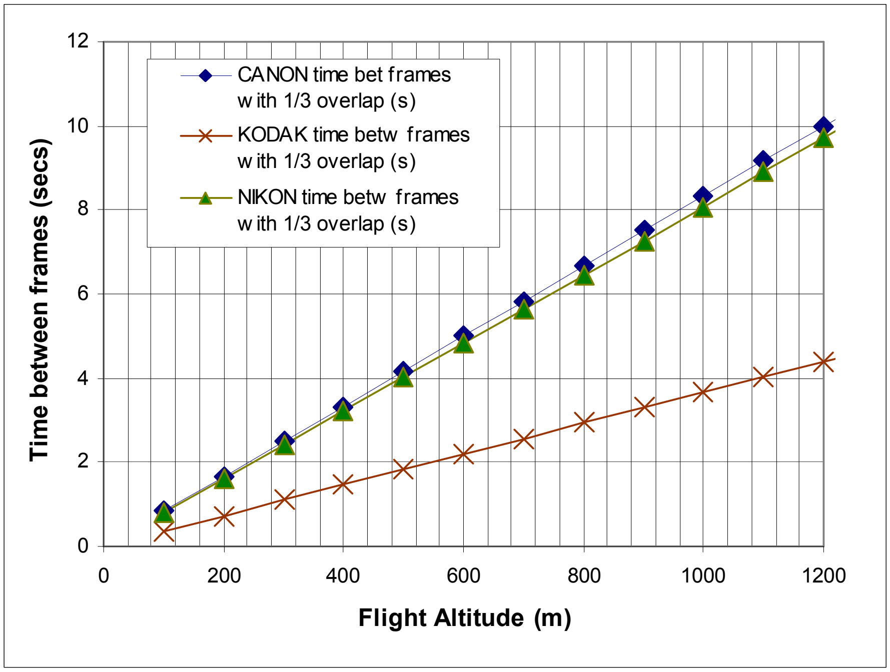


Figure 114 Required time between frames to ensure 1/3 overlap in images depending on elevation of the sensor above the ground surface.

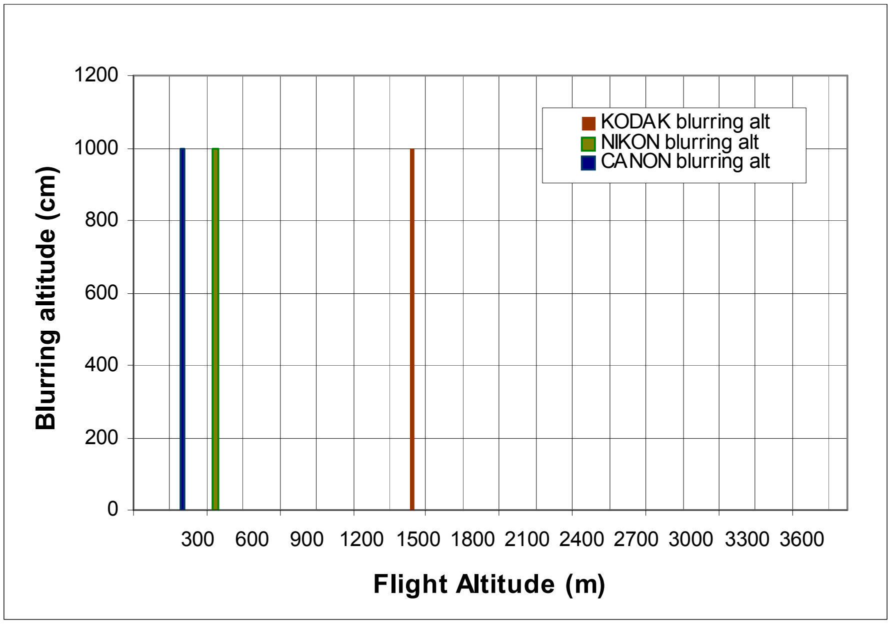


Figure 115 Elevation at which blurring is expected to occur for each of the three cameras. This was calculated based on the spatial resolution of the pixels, the exposure of the camera

and the speed of the aeroplane (fixed at 200km/h). If during the exposure time the aeroplane movement exceeds the equivalent of 1 ground pixel, it was assumed that blurring would be present in the image.

Aerial photo acquisition

Based on these calibrations, a flight path was constructed which involved image acquisition at three elevations, producing images with spatial resolution of approximately 30cm (1200m elevation), 15cm (600m elevation) and 10cm (300m elevation) with the Kodak DCS420. The 1200m and 600m swaths were designed to produce continuous stereo images with 33% overlap. The flight path was loaded as a background file in the Trimble ProXL GPS, and used in flight to navigate. The planned and the actual flight path are shown in Figure 116.

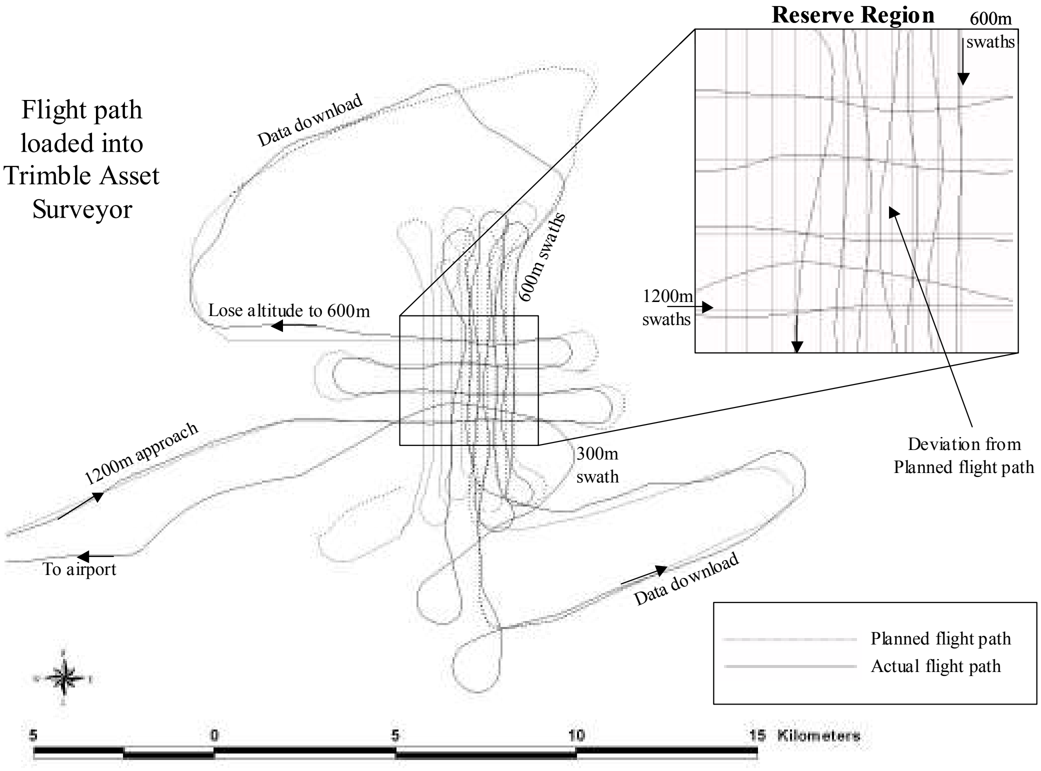


Figure 116 Planned and actual flight path for aerial image acquisition over TBS, March 2002.

The images were taken during one single flight on the 11th March, 2003. The sky was around 80% clear, with just a few isolated clouds at approximately 1100m elevation above the ground surface. As can be seen in Figure 116, turbulence meant that the planned flight path could not be exactly maintained, and fuel limitations mean that only seven out of eleven of the 600m swaths were completed. Due to the cloud height, the planned 1200m imagery was actually taken at approximately 1100m elevation above the ground surface. All images were of reasonable quality, and a large percentage of the reserve was covered with at least one resolution of aerial imagery.

Helium balloon photo acquisition

The helium balloon based photo acquisition is limited by weight. The helium balloon carries some 7 cubic metres of helium, and is capable of a maximum payload of approximately 3kg. This limitation means that only the one sensor can be safely attached, accompanied by servos and remote control receivers and transmitters. In this case a high-resolution Nikon Coolpix 990 digital camera is used, with a 28mm lens and resolution of 3.3 mega-pixels with an image size of 2048 x 1536 pixels. The camera is attached to the balloon, and the balloon held on a cable of up to 200m length.

There is no form of propulsion so the path of the balloon is at the whim of the wind. The balloon requires a large clearing to avoid snagging on tree branches, so the balloon can only be flown from the river, or from some especially large gaps in the forest floor (Figure 117). This restricted the potential coverage of the balloon imagery. The photos were taken by means of a remote control servo attached to the camera platform. Figure 118 and Figure 119 show the strategy used for the balloon within the forest, and an image of the camera apparatus.

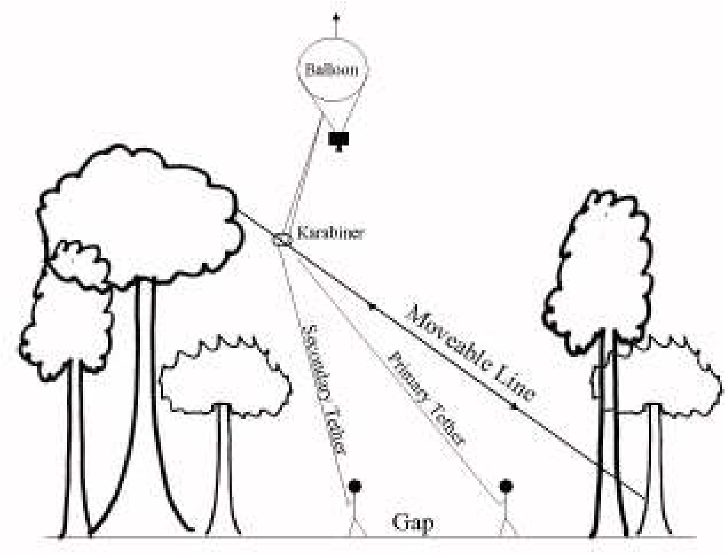


Figure 117 Method for helium balloon image acquisition from forest gaps

Figure 118 The helium balloon in flight

Figure 119 Instrumental setup of tethered balloon photo acquisition

At full balloon height (200m) the camera provides images with a pixel size of 5.6cm and a spatial coverage of 115m x 86m. Images were taken along the river covering almost continuously some 3 km of river, and extending as far as 100m into the surrounding forest. The balloon was also flown from a canopy tower, capturing high resolution images of plot 6, and from a gap in the center of the 1Ha Pitman plot, capturing approximately 80% of the plot with high resolution imagery.

Georeferencing of images

The method for georeferencing the images vary between the balloon and the aircraft. The aerial photos were georeferenced using GPS data through an iterative approach, starting with the 1200 m imagery. First of all in-flight GPS data and camera characteristics derived from the calibration were used to approximately georeference the images. The orientation of the image is calculated based on the change in position from the GPS for the second prior to and after image acquisition. The GPS height is used to calculate the spatial coverage, and geographic positions of the corner points are calculated, and used as control points in the georeferencing. Starting with the image closest to the accommodation cabins, identifiable features were selected in the crudely georeferenced image. The easiest feature to identify were buildings, but these were only present in this one 1200m images. Logs and outcroppings in the riverbank were also easily identifiable in the image and in the field. Inland and away from buildings it was more difficult. Some features that were used included large gaps, flowering trees, large leafless ceibas, and some especially prominent palms. The approximate coordinates of each identified feature was entered into a Garmin12 GPS unit, and this location then visited in the field. Once the precise point was found, the Trimble ProXL GPS unit was left taking a geographic position for at least 10 minutes. In each image at least 5 GPS points were taken, whenever possible covering the corners and a central point. ERDAS Imagine was used to georeference the images, using bilinear interpolation.

Once the first image was georeferenced accurately, adjoining images were georeferenced firstly based on a crude stitching to the 33% overlap with the first image. This crudely georeferenced image was then used to locate features in the field, and the final georeferenciation of the image performed using bilinear interpolation of the GPS points. This “dispersive” method was used to georeference all 1200m images. The root mean square error was approximately 3-5 pixels (equivalent to 1-2m).

Once the 1200m images had been georeferenced, they were mosaiced together to form a single image of the study site. This mosaic was then used as a base map with which to georeference the 600m and 300m imagery, also using bi-linear interpolation.

In this case common features were identified for control points, using at least 10 per image.

The helium balloon images were more easily georeferenced due to the clarity in the photos. Features were located on the ground, and ERDAS Imagine used to georeference each image. Only high quality images were georeferenced. The approximate accuracy of the georeferencing using this method is 1m.

Table 66 summarises the number of images acquired, how many of which were georeferenced and their approximate ground coverage, and shows the georeferenced imagery available for the study site.

Altitude of image acquisition (metres above ground level)	Total Number of Images Acquired	Total Number of images Georeferenced	Average Resolution of Images (cm)	Area coverd by images (Ha)
1200	60	33	33.6	1006
600	154	46	21.4	300
300	18	14	8.4	24
100-200 (balloon)	679	30	7.6	51

Table 66 Summary of image acquisition and georeferencing results.

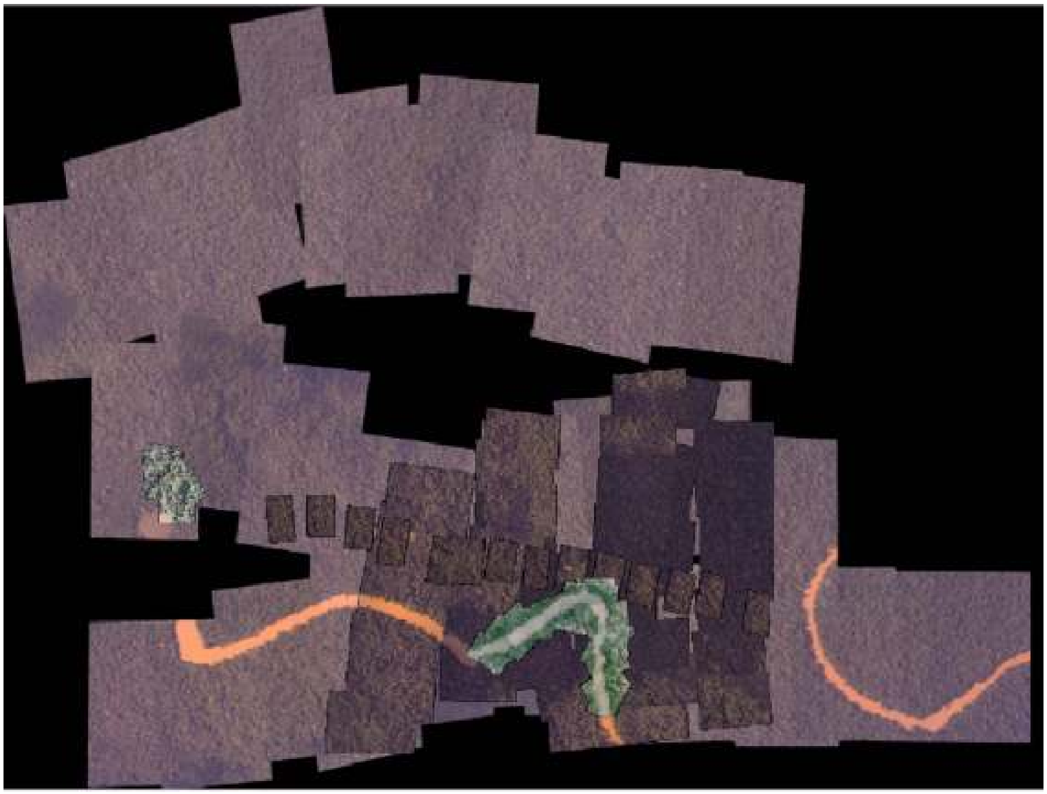


Figure 120 Georeferenced imagery for TBS at all resolutions

Image Analysis

Firstly, object-oriented remote sensing techniques were used on the 1500m imagery to separate out individual tree forms, in order to provide a vector coverage of each canopy tree. This analysis was performed using eCognition Version 2. eCognition makes a segmentation of an image into shapes based on the colour and texture of the image. These shapes attempt to maintain internal homogeneity, but represent the external heterogeneity of the image. The scale of these objects can be adjusted using the arbitrary scale parameter, and the segmentation can be manipulated by weighting the importance of each spectral band, and the relative weight between colour and shape.

The second phase of analysis in eCognition is a hierarchical classification. A number of levels are produced using the multi-resolution segmentation, of increasing levels of detail using the scale parameter. Within each level, rules are produced based on the spectral and textural properties of each shape, including neighbourhood functions, to create a classification of key objects. At each level, the multiresolution segmentation is tailored to the specific classification needs. In the case of this work, classification hierarchies were constructed to classify the image into shade / canopy hole, tree canopy, and river (the classification hierarchy is shown in Figure 121).

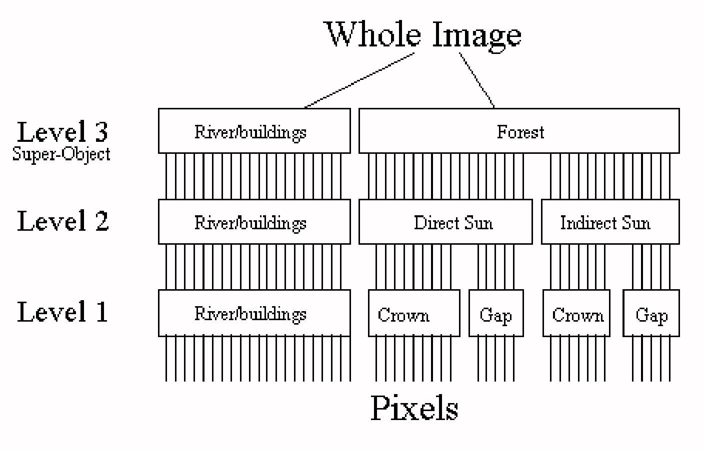


Figure 121 Classification hierarchy constructed in eCognition.

Once individual shapes classified as "tree crown" were identified, the image data for each shape was extracted, including mean, max, min, mode and standard deviation of pixels for each of the three bands, along with shape-based characteristics such as "roundness", perimeter, and area. The attribute values for each tree crown were then subjected to a clustering analysis (using Ward's method), and 100 arbitrary "canopy forms" extracted from this analysis.

Finally, a grid-based analysis of canopy form richness was performed using DIVA-GIS (http://diva-gis.org), to provide a map of possible canopy diversity.

Results and Discussion

The classification process was applied to a 1500m image, producing a realistic classification or image regions representing tree crowns (Figure 122). When this classification was combined with the image segmentation, and multi-variate statistical analysis a map of diversity in tree crown canopy forms was produced (Figure 123).

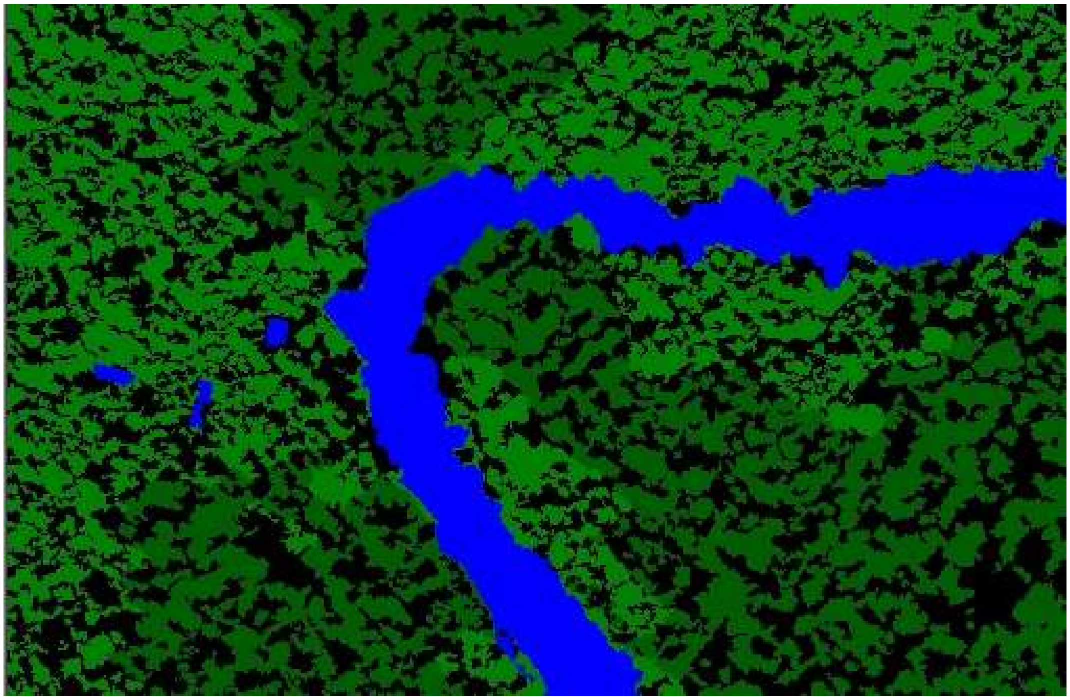


Figure 122 Results of the hierarchical classification of eCognition, identifying river (blue), gaps / shade (black) and tree crowns (green).

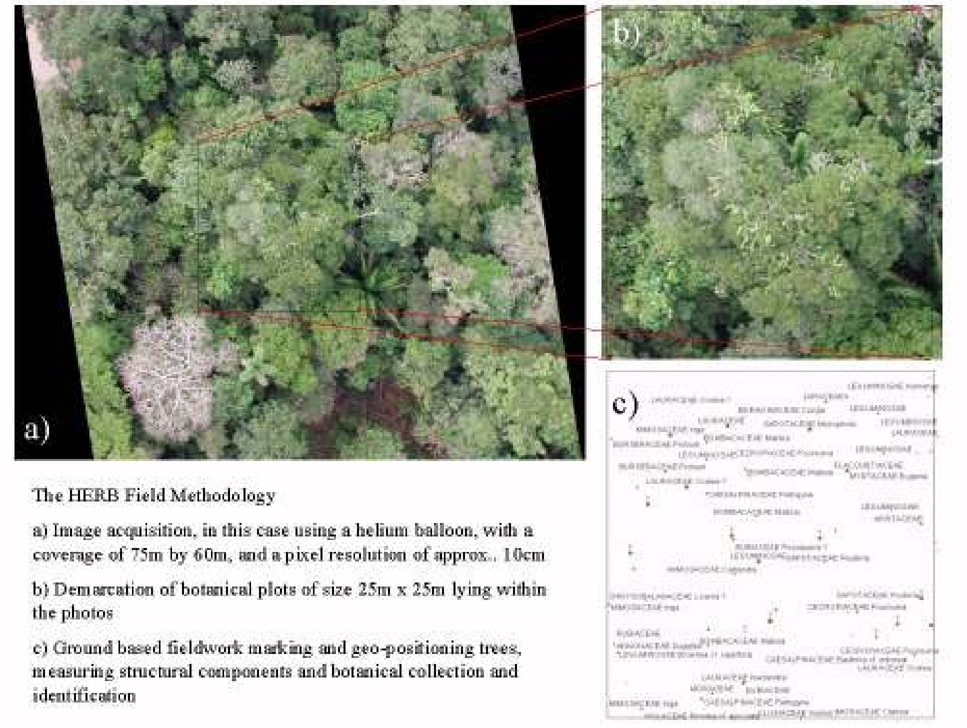
Figure 123 Modelled canopy diversity, derived from object-oriented analysis of canopy forms.

The analysis has not been rigorously performed, rather has been performed as a pilot test to examine the potential of this kind of analysis in measuring tree canopy diversity over large areas. The results are promising, but the methods require detailed study which is considered beyond the possibilities of this PhD thesis. Several problems were identified:

1. The scale-dependent image segmentation failed to account for different sized tree crowns, resulting in a segmentation that, depending on the scale parameter selected, clumped or separated individuals trees into single or multiple objects
2. The statistical methods behind the classification of tree forms requires greater rigor, and detailed development

3. Validation of the image analysis is required, and the ten diversity plots established for this study were not suitable for validation of these images (see Figure 124).

Fieldwork in 2003 attempted to gather ground-based measurements of canopy tree diversity using the matching of individual crowns visible in the imagery with crowns identified from the ground, but this proved highly difficult.



The HERB Field Methodology

a) Image acquisition, in this case using a helium balloon, with a coverage of 75m by 60m, and a pixel resolution of approx.. 10cm

b) Demarcation of botanical plots of size 25m x 25m lying within the photos

c) Ground based fieldwork marking and geo-positioning trees, measuring structural components and botanical collection and identification

Figure 124 Plot 1 (25m x 25m) from the air, in an image taken using the helium balloon. As can be seen, few trees penetrate the canopy, with just 5-10 of the 80 trees identified on the ground actually visible in this high-resolution image.

For the reasons briefly outlined above, and others not-mentioned the image-based measurement of tree diversity was dropped from the research for this thesis, and is not included in main text. However, it still merits further study.

9 Appendix 2

Heterogeneity model for quantitative variables

```
/*  Integrated model for studying the spatial heterogeneity of the environment from a
biological standpoint
/*
/*  The model requires :
/*        a kernel file, in ASCII format (or several if you wish to perform a multi-scale
analysis - file format = kernel_50x50_"scale".asc)
/*        input environmental variable (can be integer, floating)
/*
/*  The model makes the following steps:
/*        * Reclassifies the environmental variable to between 25 and 30 classes
/*        * For each reclassified map, creates seperate binary grids for each class
/*        * Calculates the probability of receiving seeds from each environmental class
in the surrounding area (defined by the kernel)
/*        * Combines the probabilities of receiving each class through calculation of the
Shannon Index to
/*                produce a grid of environmental diversity
/*        * Normalises the final diversity map (mean_div_rel) and adjusts for edge
effect (mean_div_adj)
/*
/*  The model also carries out validation on your data, writing a text file with the rsq
correlation.
/*
/*
/*
/*  by Andy Jarvis
/*        2003
/*  a.jarvis@cgiar.org

/*  Model variables

&terminal 9999

&s inputvariable = d:\datosproyecto\ecuador\dem_comparison\srtm\mean_curv_dd
&s thresholdlow = 25
&s thresholdhigh = 30
&s kernel = kernel_50x50
&s killer = no

/*  Validation variables

&s samplesites = d:\datosproyecto\ecuador\dem_comparison\srtm\plot_richness

&s kernelfiles := [listfile kernel*.asc -file]

&if [null %kernelfiles%] &then &type There are no kernel ASCII files
   &else
```

```
  &do
   &s num := [token %kernelfiles% -count]
   &do k := 1 &to %num%
    &sv name = [extract %k% %kernelfiles%]
    &sv scale = [substr %name% 14 3]

/*  This section reclassifies the maps into %thresholdhigh% classes, so that the
focalsum calculation can work

describe %inputvariable%
&sv mapmin = %grd$zmin%
&type %mapmin%
&sv mapmax = %grd$zmax%
 &do j := %thresholdlow% &to %thresholdhigh%
   &type Classifying map into %j% classes
      &do i := 1 &to %j%
      &sv interval1 = [calc %mapmax% - %mapmin%]
      &sv interval = [calc %interval1% / %j%]
      &sv countless = [calc %i% - 1]
      &if [EXISTS tempclass%i% -grid] &then kill tempclass%i% all
      tempclass%i% = con (%inputvariable% <= [calc %i% * %interval% +
%mapmin%], con (%inputvariable% > [calc %interval% * %countless% +
%mapmin%], %i%, 0), 0)
       &end

      &do i := 1 &to %j%
      &if %i% = 1 &then &sv list = tempclass%i%
      &else &sv list = %list%, tempclass%i%
      &end
      &if [EXISTS intermed -grid] &then kill intermed all
      intermed = sum (%list%)
      &do i := 1 &to %j%
      kill tempclass%i% ALL
      &end
      &if [EXISTS classes_%j% -grid] &then kill classes_%j% all
      classes_%j% = con (isnull(intermed), 0, intermed)

      &type Separating into component class maps
      &do i := 1 &to %j%
      &if [EXISTS class_%j%_%i% -grid] &then kill class_%j%_%i% all
      class_%j%_%i% = con(classes_%j% == [calc %i%], 1, 0)
      &end
 kill classes_%j% all

/* This section of the model makes the spatial heterogeneity calculation on each class

&type Running focalsum model
 &do i := 1 &to %j%
  &if [EXISTS het_%j%_%i% -grid] &then kill het_%j%_%i% all
```

```
    het_%j%_%i% = focalsum (class_%j%_%i%, weight, %kernel%_%scale%.asc,
DATA)
  &end

  &do i := 1 &to %j%
    &if %i% = 1 &then &sv thelist = het_%j%_%i%
    &else &sv thelist = %thelist%, het_%j%_%i%
  &end

  &type Combining class layers

  &if [EXISTS het_sum_%j% -grid] &then kill het_sum_%j% all
  het_sum_%j% = sum (%thelist%)

/* This section calculates the Shannon Index for diversity, normalises and adjusts for
density

  &type Creating temporary frequencies
  &do i := 1 &to %j%
    &if [EXISTS tem%i% -grid] &then kill tem%i% all
    tem%i% = (het_%j%_%i% / het_sum_%j%) * (het_%j%_%i% / het_sum_%j%)
  &end

  &do i := 1 &to %j%
    &if %i% = 1 &then &sv thelist2 = tem%i%
    &else &sv thelist2 = %thelist2%, tem%i%
  &end

  &type Creating sum-squared layer

  &if [EXISTS het_sum2_%j% -grid] &then kill het_sum2_%j% all
  het_sum2_%j% = sum (%thelist2%)

  &do i := 1 &to %j%
    kill tem%i%
  &end

  &type Calculating relative diversity layer
  &if [EXISTS rel_div_%j% -grid] &then kill rel_div_%j% all
  rel_div_%j% = (1 - het_sum2_%j%)

  &type Calculating adjusted diversity layer
  &if [EXISTS adj_div_%j% -grid] &then kill adj_div_%j% all
  adj_div_%j% = (rel_div_%j% * het_sum_%j%)

  &type normalizing final maps

  describe adj_div_%j%
  &sv divmin = %grd$zmin%
  &sv divmax = %grd$zmax%
```

```
  &if [EXISTS adj_div_%j%_n -grid] &then kill adj_div_%j%_n all
  adj_div_%j%_n = (adj_div_%j% - %divmin%) / (%divmax% - %divmin%)

  describe rel_div_%j%
  &sv divmin2 = %grd$zmin%
  &sv divmax2 = %grd$zmax%
  &if [EXISTS rel_div_%j%_n -grid] &then kill rel_div_%j%_n all
  rel_div_%j%_n = (rel_div_%j% - %divmin2%) / (%divmax2% - %divmin2%)

&do i = 1 &to %j%
    kill het_%j%_%i%
    kill class_%j%_%i%
&end
&end

&do i := %thresholdlow% &to %thresholdhigh%
   &if %i% = %thresholdlow% &then &sv thelist3 = rel_div_%i%_n
   &else &sv thelist3 = %thelist3%, rel_div_%i%_n
   &if %i% = %thresholdlow% &then &sv thelist4 = adj_div_%i%_n
   &else &sv thelist4 = %thelist4%, adj_div_%i%_n
&end

&type Calculating means

/*  THis section puts the different maps for each class number together

&if [EXISTS div_rel -grid] &then kill div_rel all
div_rel_%scale% = sum(%thelist3%) / (%thresholdhigh% - %thresholdlow% + 1)

&if [EXISTS div_adj_%scale% -grid] &then kill div_adj_%scale% all
div_adj_%scale% = sum(%thelist4%) / (%thresholdhigh% - %thresholdlow% + 1)

/*  Cleans up your directory of temporary files

&do i := %thresholdlow% &to %thresholdhigh%
   kill het_sum_%i% all
   kill het_sum2_%i% all
   kill adj_div_%i% all
   kill adj_div_%i%_n all
   kill rel_div_%i% all
   kill rel_div_%i%_n all
   &if [EXISTS intermed -grid] &then kill intermed all
&end

/*  Performs the validation using your sample sites map

model_comparison_%scale%.txt = sample (%samplesites%, div_adj_%scale%,
div_rel_%scale%)
correlation %samplesites% div_rel_%scale%
        &sv rsqtable = [open rsq_results.txt openstat -append]
```

```
        &if %openstat% ne 0 &then
        &do
       &type could not open rsqtable (Close arc/info and start again)
         &return
        &end
        &else
      &type %openstat%
      &do
         &if %k% = 1 &then
         &do
         &sv writeres = [write %rsqtable% 'Scale          Rsquared']
         &sv writeres = [write %rsqtable% %scale%'    '%.correlation_out%]
         &end
         &else
         &sv writeres = [write %rsqtable% %scale%'    '%.correlation_out%]
         &sv closestat = [close %rsqtable%]
       &end

&end
&end
&return
```

10 Appendix 3

Heterogeneity model for categorical variables

```
/*  Integrated model for studying the spatial heterogeneity of the environment from a
biological standpoint
/*
/*  The model requires :
/*        a kernel file, in ASCII format (or several if you wish to perform a multi-scale
analysis - file format = kernel_50x50_"scale".asc)
/*        input environmental variable (can be integer, floating)
/*
/*  The model makes the following steps:
/*        * Reclassifies the environmental variable to between 25 and 30 classes
/*        * For each reclassified map, creates seperate binary grids for each class
/*        * Calculates the probability of receiving seeds from each environmental class
in the surrounding area (defined by the kernel)
/*        * Combines the probabilities of receiving each class through calculation of the
Shannon Index to
/*                produce a grid of environmental diversity
/*        * Normalises the final diversity map (mean_div_rel) and adjusts for edge
effect (mean_div_adj)
/*
/*  The model also carries out validation on your data, writing a text file with the rsq
correlation.
/*
/*
/*
/*  by Andy Jarvis
/*        2003
/*  a.jarvis@cgiar.org

/*  Model variables

&terminal 9999

&s inputvariable = d:\datosproyecto\ecuador\dem_comparison\srtm\featu_dd

/*  Validation variables

&s samplesites = d:\datosproyecto\ecuador\dem_comparison\srtm\plot_richness

&s kernelfiles := [listfile kernel*.asc -file]

&if [null %kernelfiles%] &then &type There are no kernel ASCII files
   &else
   &do
     &s num := [token %kernelfiles% -count]
     &do k := 1 &to %num%
       &sv name = [extract %k% %kernelfiles%]
```

```
    &sv scale = [substr %name% 14 3]

/*  This section reclassifies the maps into %thresholdhigh% classes, so that the
focalsum calculation can work

describe %inputvariable%
&sv mapmin = %grd$zmin%
&type %mapmin%
&sv mapmax = %grd$zmax%


      &type Separating into component class maps
      &do i := 1 &to 6
      &if [EXISTS class_%i% -grid] &then kill class_%i% all
      class_%i% = con(%inputvariable% == [calc %i%], 1, 0)
      &end

/* This section of the model makes the spatial heterogeneity calculation on each class

&type Running focalsum model
 &do i := 1 &to 6
  &if [EXISTS het_%i% -grid] &then kill het_%i% all
  het_%i% = focalsum (class_%i%, weight, %name%, DATA)
 &end

 &do i := 1 &to 6
  &if %i% = 1 &then &sv thelist = het_%i%
  &else &sv thelist = %thelist%, het_%i%
 &end

 &type Combining class layers

 &if [EXISTS het_sum -grid] &then kill het_sum all
 het_sum = sum (%thelist%)

/* This section calculates the Shannon Index for diversity, normalises and adjusts for
density

 &type Creating temporary frequencies
 &do i := 1 &to 6
  &if [EXISTS tem%i% -grid] &then kill tem%i% all
  tem%i% = (het_%i% / het_sum) * (het_%i% / het_sum)
 &end

 &do i := 1 &to 6
  &if %i% = 1 &then &sv thelist2 = tem%i%
  &else &sv thelist2 = %thelist2%, tem%i%
 &end

 &type Creating sum-squared layer
```

```
  &if [EXISTS het_sum2 -grid] &then kill het_sum2 all
  het_sum2 = sum (%thelist2%)

  &do i := 1 &to 6
    kill tem%i%
  &end

  &type Calculating relative diversity layer
  &if [EXISTS rel_div -grid] &then kill rel_div all
  rel_div = (1 - het_sum2)

  &type Calculating adjusted diversity layer
  &if [EXISTS adj_div -grid] &then kill adj_div all
  adj_div = (rel_div * het_sum)

  &type normalizing final maps

  describe adj_div
  &sv divmin = %grd$zmin%
  &sv divmax = %grd$zmax%
  &if [EXISTS adj_div_n -grid] &then kill adj_div_n all
  adj_div_n = (adj_div - %divmin%) / (%divmax% - %divmin%)

  describe rel_div
  &sv divmin2 = %grd$zmin%
  &sv divmax2 = %grd$zmax%
  &if [EXISTS rel_div_n -grid] &then kill rel_div_n all
  rel_div_n = (rel_div - %divmin2%) / (%divmax2% - %divmin2%)

&do i = 1 &to 6
    kill het_%i%
    kill class_%i%
&end


&type Calculating means

/*  THis section puts the different maps for each class number together

&if [EXISTS div_rel_%scale% -grid] &then kill div_rel_%scale% all
div_rel_%scale% = rel_div_n

&if [EXISTS div_adj_%scale% -grid] &then kill div_adj_%scale% all
div_adj_%scale% = adj_div_n

/*  Cleans up your directory of temporary files

&if [EXISTS adj_div -grid] &then kill adj_div all
&if [EXISTS het_sum -grid] &then kill het_sum all
```

```
&if [EXISTS het_sum2 -grid] &then kill het_sum2 all
&if [EXISTS rel_div -grid] &then kill rel_div all
&if [EXISTS adj_div_n -grid] &then kill adj_div_n all
&if [EXISTS rel_div_n -grid] &then kill rel_div_n all
&if [EXISTS intermed -grid] &then kill intermed all

/*  Performs the validation using your sample sites map

model_comparison_%scale%.txt = sample (%samplesites%, div_adj_%scale%,
div_rel_%scale%)
correlation %samplesites% div_rel_%scale%
        &sv rsqtable = [open rsq_results.txt openstat -append]
        &if %openstat% ne 0 &then
        &do
       &type could not open rsqtable (Close arc/info and start again)
         &return
        &end
        &else
      &type %openstat%
      &do
         &if %k% = 1 &then
         &do
         &sv writeres = [write %rsqtable% 'Scale         Rsquared']
         &sv writeres = [write %rsqtable% %scale%'    '%.correlation_out%]
         &end
         &else
         &sv writeres = [write %rsqtable% %scale%'    '%.correlation_out%]
         &sv closestat = [close %rsqtable%]
       &end

&end
&return
```

11 Appendix 4

Submitted to Novedades Colombiana

PLANTS OF TAMBITO I. DICOTILEDONOUS. A PRELIMINARY LIST

Carlos E. González and Andrew Jarvis

Resumen

Se presenta una lista preliminar de las plantas dicotiledóneas registradas desde 1998 hasta el 2002 en la reserva Tambito, Cauca, Colombia (2º 30' N- 76º 59' W). Se reportaron 585 especies distribuidas en 86 familias. Se organizaron según su hábito de crecimiento: hierbas (52 especies), arbustos (132 especies), árboles (301 especies), trepadoras (59 especies) y epífitas (5 especies). Las familias de mayor número de especies fueron Rubiaceae, Gesneriaceae, Melastomataceae y Piperaceae. Esta es una lista preliminar centrada en ofrecer una estimación inicial de las especies en Tambito. El patrón numérico demuestra que se deben hacer esfuerzos de colecta en lianas, epífitas y trepadoras además de nuevas identificaciones a los grupos menos conocidos taxonomicamente para completar el inventario de dicotiledóneas. Iguales esfuerzos de deben hacerse en Helechos, monocotiledones y grupos de plantas criptógamas.

Palabras claves: Flora, Bosque de Niebla, Tambito, Cordillera Occidental, Cauca, Colombia

Abstract

This study presents a preliminary list of dicotiledonous plants that have been registered 1998 – 2002 in Reserva Tambito, Cauca, Colombia (2º 30' N- 76º 59' W). Some 585 species are reported, in 86 families. The species included in this list were classified into herbs (52 species), shrubs (132 species), trees (301 species), climbers (59 species) and epiphytes (5 species). The most speciose familes are Rubiaceae, Gesneriaceae, Melastomataceae and Piperaceae. This is a preliminary list aimed to provide an initial estimate of the plant species in Tambito. It is suggested that more collections are made in lianas, epiphytes and climbers to further complete the inventory of dicotiledonous plants, and that similar studies should be made for monocotiledonous and cryptogams (including mocees and ferns) species.

Key words: Flora, Cloud Forest, Tambito, Western Andes, Cauca, Colombia

Introduction

This is the first compilation of Tambito´s plant species, which presents a preliminary list of dicotiledonous plants. A series of future lists are in preparation under a Florula project (II: Monocotiledonous III: Ferns and similars IV: Mosses and affines). Previous studies in Tambito suggest that there might be as many as 640 species collected (including monocotiledonous), in 269 genera and 110 families including monocotiledonous (González C.E, 2000). This paper produces a rigorous review of collections in Tambito between 1998 and 2002, providing a more conclusive figure for the number and taxonomy of the species now registered in Tambito. Additionally we make suggestions for the focus of future botanical collection in Tambito.

Materials and Methods

Study Site

Reserva Tambito, Cauca, Colombia (2º 30' N- 76º 59' W) lies on the western slopes of the western cordillera of the Andes. The altitudinal range rises from 1053 to 2860 m.a.s.l.. The total area of the reserve is 2150 hectares, with areas of secondary and primary forest, and some pasture area around the Tambito cabin. Annual rainfall ranges from 3900mm around the cabin, to as much as 6560mm at 2000m.a.s.l. (Jarvis, 2000). Relative humidity averages at over 90%, with daily variation between 60 and 100% (Jarvis, 2000). It is a private nature reserve which forms the Pacific Enviromental Studies Centre to the University of Cauca, Popayan.

Field data collection

Botanical collections were made from 1998 – 2002, many as part of the fieldwork for HERB Project and Project Negret (King's College London). The areas covered were web distributed around the twin catchments, between 1300 and 2500 m.a.s.l.. Lack of access to the higher elevations prevented collections above 2500m.a.s.l..
Samples were collected and preserved temporarily in alcohol according to the traditional method of botanical sample preservation. The samples were then dried for 48 hours at 90ºF, and stored in the CAUP herbarium in the Natural History Museum of Popayan. Identification of the samples were made to species level whenever possible, though many identifications

stop at genus. Some samples remain unidentified to family, and so have been omitted from this list.

Results and Discusion

Table 1 shows the species which have been registered, and are seperated into families. For each species additional information is provided with regard to the Holdridge life zone in which the species was found, in addition to the plant form and information on the collection number for the herbarium.

In total, 585 species have been identified, in 86 families. Some 301 of these are tree species, whilst 132 are shrubs, 59 are climbers, 52 are herbs and 5 are epiphytes. Only 60-65% (around 326 species) of identifications are confirmed; 4% (around 22 especies) remain unidentified and 21 especies are being investigated as new species for science (4 have already been described). Some of the species which are unidentified might also be undescribed species. Melastomataceae and Rubiaceae are generally poorly identified families. Tree families like Lauraceae and Myrtaceae were found to be less taxonomically documented. Genera like *Nectandra*, *Ocotea*, *Miconia*, *Piper*, *Besleria*, *Solanum*, *Ficus*, *Palicourea* and *Psychotria* have the highest probabilities for finding new undescribed or non identified species.

These figures show the weaknesses in collections, and highlight the need for further study in lianas, epiphytes and climbers. For both these groups the species richness is likely to be significantly higher. Some data about rare or endemic species are marked, but must be considered more thoroughly in subsequent analyses.

Figure 1 shows the species composition with respect to families. The most speciose familes are Rubiaceae (67 species), Gesneriaceae (64 species), Melastomataceae (59 species) and Piperaceae (36 species). A total of 38% of all registered species are in these four families.

Conclusions

This preliminary list provides a basic documentation of the dicotiledonous flora found in Tambito. It demonstrates the exceptional level of plant diversity in Tambito, and throws down the challenge to further study and document the biological resources within the Reserve and the surrounding area. This kind of information is crucial to comply with the Convention on Biological Diversity, where basic inventory of biological resources is essential to construct relevent and effective national conservation policies.

It is hoped that this paper will contribute to the establishment of a Florula project for Tambito (González, 2002), which integrates the results of biological research in Tambito over the past years. Amongst these findings are new species to science (Gonzalez, 2002), and significant advances in knowledge of the ferns (Casañas, 2002) and palms (Cortes, 1996). This preliminary list could be lengthened and finalised under such a project, and extended into the surrounding Munchique National Park and Choco Biogeographic region.

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Tables and Figures

Figure 1 Number of species per family for Reserva Tambito.

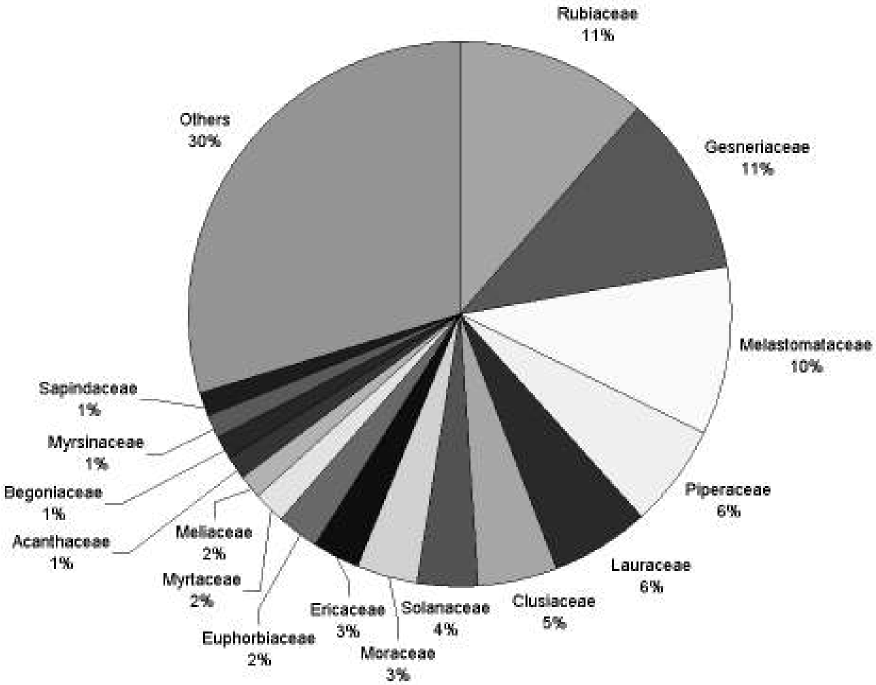

Table 1 Taxonomic list

Life Zone (Lf): Refers to the ecological forest type. bh-pm (1300-1600 m) = Premontane Wet Forest; bh-mb (1600-2000 m) = Lower Montane Wet Forest; bll-mb (2000-2500 m) = Lower Montane Rain forest; bll-m (> 2500 m) = Upper Montane Rain forest. According to classification (Holdridge, 1967)

* = **Refering to endemic or rare species**

Plant form: hb = Herb; tr = Tree; sh = Shrub; cl = Climber; ep= Epiphytic

Elevation range: Refers to the records of altitudinal range

Reference of collection (Only main collector): **CG** Carlos González**,** **RS** Ramón Serna, **SD** Sandra Díaz, **RR** Rosalba Ruiz, **OC** Olga Casañas, **RSA** Roberto Sánchez, **LA** Liza y Aleja, **BR** Bernardo Ramírez, **FG** Fernando González; **MB** Martha Burbano; **HB** HERB

Taxon	Life zone	Lf	Elevation	Collection	Herbarium
Acanthaceae					
Aphelandra acanthus Nees	bh-mb	sh	1800	CG 3359	CAUP
Aphelandra *sp nov*	bh-mb/pm	hb	1655-1850	CG 3383	CAUP
Justicia chlorostachya Leonard	bh-pm	hb	1600	OC 135	CAUP
Justicia	bh-mb	hb	1800	CG 3359	CAUP
Lepidagathis lanceolata (Nees.) Wasshausen	bh-pm	hb	1350-1600	BR 7724	CAUP PSO
Odontonema *cf*	bh-pm	sh	1300	CG 1482	CAUP
Pseuderanthemum	bh-pm	hb	1600	RS 844	CAUP
Trichantera gigantea (Bonpl.) Nees	bh-pm	tr	1600	RS 1065	CAUP
Actinidaceae					
Saurauia brachybotrys Turcz	bh-pm	tr	1450-1600	LG 036	AFP CAUP
Saurauia micayensis Killip & Soejarto	bh-mb	tr	1600-2000	CG 3187	CAUP
Saurauia aff omnichlophila *R.E. Schult.*	bll-mb	sh	2300	CG 1254	CAUP
Amaranthaceae					
Alternanthera cf *elongata* (W. ex R.) Schinz	bh-pm	hb	1600	RS 996	CAUP
Iresine diffusa Humb. & Bonpl ex Willd	bh-pm	hb	1600	RS 997	CAUP
	bh-pm	tr	1300	CG 3154	CAUP
	bh-pm	tr	1200		

Anacardiaceae	bh-pm		1480	RS 1182	CAUP
Toxicodendron striatum (Ruiz & Pavon) Kuntze	bh-mb	tr	1686-1966		
Ochoterenaea	bh-pm	tr	1500	CG 1383	CAUP
Annonaceae		tr		CG 3132	CAUP
Guatteria	bh-pm		1450	SD 367	CAUP
Guatteria		hb			
Malmea	-		-	CG 0000	CAUP
Apiaceae		cl			
Hydrocotyle	bh-pm/mb		1300-2000	-	CAUP
Apocynaceae	bh-mb	tr	1500-1966		
Mandevilla	bh/ll-mb	tr	1856-2200	CG 3197	CAUP
Aquifoliaceae	bh-pm	tr	1650	CG 3143	CAUP
Ilex	bh-pm	tr	1450-1600	CG 3248	CAUP
Ilex		tr		CG 3008	CAUP
Ilex cf pernervata Cuatrec	bh-pm		1500	CG 1145	CAUP
Ilex cf karstenii Loes	bh-mb	tr	1650		
Ilex cf laurina HBK	bh-pm	tr	1500	CG 1908	CAUP
Araliaceae	bh-mb	tr	1856	CG 1921	CAUP
Dendropanax cf caucanus (Harms.) Harms	bh-mb	tr	1950	CG 1886	CAUP
Dendropanax macrophyllum Cuatrec	bh-mb	cl	1856	CG 3271	CAUP
Oreopanax cf arboreus (L.) Dec ex Plank	bh-pm	cl	1200-1300	CG 3280	CAUP
Oreopanax peltatus Linden		cl		CG 3283	CAUP
Schefflera	bh-pm		1450	CG 2933	CAUP
Schefflera	bh-pm	sh	1450		
Schefflera trifolium	bh-mb	sh	1600	RS 1056	CAUP
Asteraceae	bh-pm	tr	1580	RS 1078	CAUP
Ambrosia cumanensis HBK	bh-mb	sh	1600-2000	CG 1150	CAUP
Austroeupatorium inulaefolium (Kunth.) K & H	bh-pm	cl	1450	RS 847	CAUP
*Critoniopsis cf occidentalis (*Cuatrec.) H. Rob	bh/ll-mb	cl	1580-2400	RR 1371	CAUP
Lepidaploa lehmanii (Hieron.) H. Robinson		tr		RS 1068	CAUP
Mikania banisteriae DC	bll-mb		2200	CG 1400	CAUP
Munnozia hastifolia (Poepp.) H. R & Brettel		hb			
Pollalesta aff macrophylla * (Sch. Bip) Aris	bh/ll-mb		1400-2200	CG 1262	CAUP
Balanophoraceae		hb			
Langsdorffia hypogea Matinus	bh-pm/mb		1500-1700	-	CAUP
Balsaminaceae	bh-pm	cl	1300		
Impatiens cf balsamina L.	bll-mb	cl	2300	CG 1328	CAUP
Begoniaceae	bh-mb	hb	1800	CG 1358	CAUP
Begonia tiliifolia C. DC	bll-mb	cl	2300-2500	CG 1292	CAUP
Begonia cf *maynensis* A. DC.	bll-mb	cl	2100	CG 3107	CAUP
Begonia geminiflora L.	bh-pm	cl	1550	CG 1225	CAUP
Begonia secunda L.	bh-pm	cl	1300	CG 1423	CAUP
Begonia killipiana * Smith & Schubert		cl		CG 1154	CAUP
Begonia urticae L. var. *urticae*	-		-	CG 1513	CAUP
Begonia rossmanniae A. DC.		cl			
Begonia aff *guaduensis* Kunth	bh-mb		1950	CG 3257	CAUP
Bignoniaceae	bh-mb	tr	1600		
Schlegelia cf roseiflora Ducke	bh-pm	tr	1300	CG 1104	CAUP
Bombacaceae	bll-mb	tr	2300	CG 1149	CAUP COL
Matisia bolivarii Cuatrec	bh-pm/mb	tr	1350-1400	CG 1750	CAUP
Matisia aff dolychopoda sp nov	bll-mb	tr	2300	CG 1323	CAUP
Matisia	bh-mb	tr	1856	CG 1344	CAUP
Matisia		tr		CG 1181	CAUP
Matisia cf cordata Bonpl.	bh-pm		1400	CG 3268	CAUP
Quararibea cf	bh-mb	sh	1700		
Spirotheca rhodostyla Cuatrec		sh		CG 2884	CAUP
Boraginaceae	bll-mb		2500	CG 2863	CAUP
Cordia cf cylindrostachia (Ruiz & Pavón) R & S		tr			
Tournefortia gigantifolia Killip	bh-pm		1450-1600		CAUP
Brunelliaceae	bh-pm	tr	1300		
Brunellia cf glabra Cuatrec.	bh-pm/mb	tr	1650-1686	CG 3544	CAUP
Burseraceae	bh-pm	tr	1450	CG 3155	CAUP
Protium	bh-mb	tr	1700	CG 3057	CAUP
Protium	bh-pm	tr	1500	CG 1902	CAUP
Protium		tr		CG 1897	CAUP
Protium	bh-pm		1300	CG 3094	CAUP
Trattinikia		tr			

Indet	bh-mb		1900	CG 3160	CAUP
Caesalpinaceae	bh-mb	sh	1710		
Brownea	bh-pm	sh	1450	CG 1425	CAUP
Campanulaceae	bll-mb	sh	2400	OC 324	CAUP
Burmeistera cf *oblongifolia* E. Wimm.	bll-mb	sh	2000	RS 1063	CAUP
Burmeistera cf *cylindrocarpa* Zahlbr.	bh/ll-mb	sh	1600-2400	CG 1301	CAUP
Burmeistera cf *ceratocarpa* Zahlbr.	-	sh	-	CG 1269	CAUP
Centropogon cf *papillosus* E. Wimm.		sh		CG 1424	CAUP
Centropogon congestus Gleason	bh-pm		1400-1500	-	-
Centropogon grandis (l.f.) Presl	bh-pm	hb	1400-1600		
Siphocampylus scandens (Kunth.) G. Don		sh		CG 1363	CAUP
Capparaceae	bh-mb		1600-1800	CG 1452	CAUP
Cleome	bh/ll-mb	tr	1500-2200		
Podandrogyne cf. polychroma Woodson (Colc)		tr		CG 3265	CAUP
Caprifoliaceae	bh-pm		1300	CG 1183	CAUP
Viburnum lehmanii Killip & Smith	bh-pm	sh	1400		
Viburnum pichinchense Benth.		tr		CG 2887	CAUP
Caricaceae	bh-pm/mb		1300-1856	CG 3166	CAUP
Carica microcarpa Jacq	bh-pm	tr	1580		
Jacaratia aff chocoensis Gentry & Forero	bll-mb	tr	1950	CG 3249	CAUP
Cecropiaceae	bll-mb	tr	2200	RS 1001	CAUP
Cecropia garciae Standl.	bh-mb	tr	1686	CG 1277	CAUP
Cecropia cf *telealba* Cuatrec.		tr		CG 3302	CAUP
Cecropia bullata C. Berg & P. Franco	bll-mb		2100	CG 3387	CAUP
Cecropia	bh/pm/mb	tr	1600-1800		
Cecropia	bh/ll-mb	tr	1950-2000	RSA 2437	AFP
Celastraceae	bll-mb	tr	2100-2300	CG 3192	CAUP
Celastrus colombianus Cuatrec		tr		CG 3145	CAUP
Gymnosporia gentryi Lundell	bh-pm/mb		1580-1700	CG 1312	CAUP COL
Perrottetia maxima Cuatrec	bh-mb	tr	1900-2000		
Perrottetia * sp nov	bh-pm	tr	1400	CG 3067	CAUP
Chloranthaceae		tr		CG 3133	CAUP
Hedyosmum bonplandianum Kunth	bh/ll-mb		1500-1850	CG 1394	CAUP
Hedyosmum cuatrecazanum Occhioni	bh-pm	tr	1300-1600		
Hedyosmum racemosum (Ruiz & Pavón) G Dn		tr		CG 3084	CAUP
Chrysobalanaceae	bll-mb		2250	CG 3171	CAUP
Hirtella cf *americana* Cuatrec		tr			
Licania aff *cuatrecasasii* Prance	bh-mb		1600-1686	CG 3232	CAUP
Chletraceae	bh-pm	tr	1500-1600		
Chletra fagifolia Kunth	bh/ll-mb	tr	1600-2000	CG 3389	CAUP
Clusiaceae	bh-mb	tr	1600	CG 3101	CAUP
Calophyllum brasiliense Camb.	bh-mb	tr	1650	RS 831	CAUP
Clusia alata Pl. & Tr.	bh-pm	tr	1300	RS 889	CAUP
Clusia bernardoi * Pipoly & Cogollo	bh-mb	tr	1650	CG 3030	CAUP
Clusia bracteosa Cuatrec.	bh-pm	tr	1400-1600	CG 3218	CAUP
Clusia cf. *crenata* Cuatrec.	bh-mb	tr	1750	CG 3037	CAUP
Clusia discolor Cuatrec or T. Parviflora cf1279	bh-mb	tr	1856	CG 1754	CAUP
Cluisa aff *dixonii* Little	bll-mb	tr	2300	CG 3200	CAUP
Clusia cf *ellipticifolia* Cuatrec.	bh-pm	tr	1200	CG 2877	CAUP
Clusia aff inesiana or *longistyla* Cuatrec.	bh-mb	tr	1600-1800	CG 1255	CAUP
Clusia loranthacea Planchon & Triana	bh-pm	tr	1490	CG 1353	CAUP
Clusia pentandra Cuatrec.	-	tr	-	CG 1911	CAUP
Clusia hirsuta * Hammel sp nov	-	tr	-	LA 017	CAUP
Clusia	bll-mb	tr	2300	CG 1768	CAUP
Clusia	bh/ll-pm/mb	tr	1200-2200	CG 1508	CAUP
Clusia	bh-mb	tr	1600-1966	CG 1172	CAUP
Clusia	bh-pm	tr	1300	CG 3016	CAUP
Chrysoclamis cf *bracteolata* Cuatrec.	bh-pm	tr	1600	CG 3105	CAUP
Chrysoclamis colombiana (Cuatrec.) Cuatrec	bh-pm/mb	tr	1400-1800	CG 1496	CAUP
Chrysoclamis cf *tenuifolia*	bll-mb	tr	2100	CG 1101	CAUP
Chrysoclamis	bh-pm	tr	1600	CG 3100	CAUP
Chrysoclamis	bh-pm	tr	1450	CG 1432	CAUP
Tovomita weddelliana Planchon ex Triana	bll-mb	tr	1900-2000	CG 1129	CAUP
Vismia cavanillesiana Cuatrec.		tr		LA 031	CAUP
Vismia baccifera (L.) Tr. ex Pl.	bll-mb		2300	CG 3382	CAUP
Vismia lauriformis (Lamb.) Choisy		cl			
Vismia mandur Hieron.	-		-	CG 1227	CAUP COL

Cornaceae	bll-mb	cl	2300		
Cornus periviana J.F. Macbr.		cl		-	-
Cucurbitaceae	-		-	CG 1287	CAUP
Gurania macrophylla (Collect)		tr			
Melothria pendula L.	bll-mb		1966	-	-
Cunnoniaceae	bh-pm/mb	tr	1650		
Weinmannia		tr		CG 3120	CAUP
Elaeocarpaceae	bll-mb		2000	CG 3013	CAUP
Sloanea cf *brevispina* Smith	bll-mb/m	sh	2580-2640		
Sloanea cf *echinocarpa* Uittien	bh-mb	hb	1800-2000	CG 1505	CAUP
Ericaceae	bh-pm	sh	1400	FG 3184	CAUP COL
Antropterus cf *verticillatus*	bll/h-mb	sh	1900-2000	CG 2937	CAUP
Bejaria mathewsii Fielding & Gardner	bh-mb	sh	1600	CG 2956	CAUP
Cavendishia bracteata (Ruiz & Pavon. ex JH)	bh-mb	sh	1600	CG 1119[a]	CAUP
Cavendishia	bh-pm	sh	1700	CG 1119	CAUP
Gaultheria cf	bll-mb	sh	2200	RS 808	CAUP
Psammisia cf	bh-mb	sh	1600	CG 3202	CAUP
Macleania cf *recumbens* A.C. Sm	bh-pm	hb	1400	CG 1233[a]	CAUP
Macleania	bll-mb	hb	2000	RS 1146	CAUP
Satyria	bll-mb	cl	2400	CG 1495	CAUP
Psammisia	bll-mb	cl	2400	CG 1420	CAUP
Psammisia	bll-mb	hb	‘2000	CG 1216	CAUP
Psammisia sodiroi Hoerold	bll-mb	hb	2300	CG 1202	CAUP
Themistoclesia cf *cuatrecasasii* A. C. Smith	bll-mb	tr	2400	BR 7755	CAUP
Pernettya		tr		CG 1240	CAUP
Sphyrospermum buxifolium Poepp & Endl.	bh-pm		1450-1500	CG 1245	CAUP
Themistoclesia	bh-pm	tr	1580		
Themistoclesia		tr		CG 1387	CAUP
Erythroxilaceae	bh-pm		1300	RS 846	CAUP
Erythroxilum lucidum Kunth	bh-pm	tr	1600		
Erythroxilum cf *macrophyllum* Cav	bll-mb	tr	2200	CG 3162	CAUP
Euphorbiaceae	bh-pm	tr	1600	RS 794	CAUP
Acalypha macrostachya Jacq.	bh-mb	sh	1750	CG 1221	CAUP
Acalypha platyphylla Müll. Arg.	-	tr	-	CG 1128	CAUP
Alchornea coelophylla Pax & K. Hoffmann	bll-mb	tr	2200-2500	CG 3214	CAUP
Alchornea aff *glandulosa* Endl. & Poepp.	bh/bll-mb	tr	1600-2200	CG 3264	CAUP
Alchornea triplinervia Müell	bh/ll-mb	tr	1300-2200	RS s.n	AFP
Alchornea sp nov	bh-pm	tr	1300	CG 3210	CAUP
Euphorbia goudotii Boiss	bh-pm	tr	1600-1850	CG 3180	CAUP
Hyeronima oblonga (Tul.) Müll. Arg.	bh-pm	tr	1300	CG 3156	CAUP
Hyeronima	bh-mb	tr	1856	CG 3535	CAUP
Mabea cf. *occidentalis* Benth.	bh-mb	tr	1856	CG 3168	CAUP
Richeria grandis Vahl.		tr		CG 3313	CAUP
Sapium cf *marmieri* Huber.	bh-mb	tr	1856	CG 3250	CAUP
Sapium	bh-pm/m	hb	1350-1966		
Tetrorchidium macrophyllum Müll. Arg	bh-mb		1856	CG 3262	CAUP
Fabaceae	bh-pm		1400	CG 3102	CAUP
Andira	-	tr	-	CG 3072	CAUP
Dussia cf *lehmannii* Harms.		tr		CG 3548	CAUP
Dussia cf	bh-pm		1450	-	-
Desmodium	bh-mb	tr	1650-1856		
Crotalaria	bh/ll-mb	tr	1950	LA 034	CAUP
Flacourtiaceae		tr		CG 3029	CAUP
Banara guianensis Aublet.	bh/ll-mb		2200	CG 3278	CAUP
Casearia arborea (L.C. Rich.) Urban	bh-mb	hb	1650	168	CAUP
Casearia cajambensis Cuatrec.		tr		CG 1940	CAUP
Casearia silvestris Sw.	bh-pm		1200	CG 3018	CAUP
Casearia		sh			
Pleuranthodendron lindenii (Turcz.) Sleumer	bh-pm		1350-1600	-	CAUP
Gentianaceae	bh/ll-mb	sh	1800-2300		
Irlbachia alata (Aublet.) P. Maas	bll-mb	sh	2300	CG 1940	CAUP
Gesneriaceae	bh-mb	sh	1580-1600	CG 2834	CAUP
Alloplectus bolivianus (Britton.) Wiehler	bll-mb	sh	2200-2500	CG 1313	CAUP
Alloplectus icthyoderma Hanst	bh/ll-mb	sh	1200-2200	RS 853	CAUP
Alloplectus medusaeus L.E. Skog	bh/ll-mb	sh	1400-2000	CG 2832	CAUP
Alloplectus aff *panamensis* Morton	bh/ll-mb	cl	1650-2100	CG 1751	CAUP
Alloplectus schultzei Mansfeld	bh-mb	cl	1400-1600	CG 1369	CAUP

Alloplectus tetragonoides Mansfeld	bh-mb	sh	1800	CG 3356	CAUP
Alloplectus tetragonus (Oerst.) Hanst	bh-mb	sh	1700	CG 2867	CAUP
Alloplectus teuscheri (Raymond.) Wiehler	bll-mb	sh	2100	CG 3276	CAUP
Alloplectus weirii Wiehler	bh/ll-mb	sh	1600-2300	CG 2846	CAUP
Alloplectus sp nov	bll-mb	hb	2150	CG 3240	CAUP US
Alloplectus sp nov	bh-mb	sh	1900	CG 2838	CAUP
Alloplectus sp nov	bh/ll-mb	sh	1800-2200	CG 1257	CAUP
Besleria quadrangulata L.E. Skog	bll-mb	sh	2300	CG 1444	CAUP
Besleria reticulata Fritsch	bll-mb	sh	2300-2500	CG 2843	CAUP
Besleria miniata C.V. Morton	bh-mb	sh	1450-1800	CG 1215	CAUP
Besleria aff *riparia* C.V. Morton	bh/ll-mb	sh	1400-2100	CG 1207	CAUP
Besleria sp nov	bll-mb	sh	2100	CG 3391	CAUP
Besleria sp.nov	bh-mb	cl	1500-1700	CG 2966	CAUP
Besleria sp nov	bh/ll-mb	cl	1500-2100	CG 2871	CAUP
Besleria villosa Fritsch	bh-pm	cl	1600	CG 2848	CAUP
Besleria cf *tambensis* C.V. Morton	bll-mb	cl	2200	CG 2844	CAUP
Besleria	bh-pm	cl	1200-1400	CG 1461	CAUP
Besleria	bh-mb	cl	1600-1800	CG 1179	CAUP
Capanea affinis Fritsch	bh/ll-mb	cl	1800-2400	CG 2870	CAUP
Capanea grandiflora (Kunth) Decne & Planch.	bh-pm/mb	cl	1300-2100	CG 1451	CAUP COL
Columnea angustata (Wiehler) Skog	bh-pm/mb	cl	1600	CG 1336	CAUP COL
Columnea anisophylla DC.	bh-pm	cl	1400-1600	CG 3547	CAUP COL
Columnea dimidiiata (Benth.) Kuntze	bh-mb	cl	1400-1900	CG 2836	CAUP COL
Columnea fuscihirta Kvist & Skog	bh-pm/mb	cl	1400-1700	CG 1893	CAUP COL
Columnea gigantifolia Kvist & Skog	bh-mb	cl	1800	CG 1765	CAUP COL
Columnea lehmannii Mansfeld	bh/ll-mb	cl	1800-2250	CG 2866	CAUP COL
Columnea medicinalis (Wiehler.) Kvist & Skog	bh-mb	cl	2180	CG 3000	CAUP COL
Columnea minor (Hook.) Hanst var nov 1	bh-mb	cl	1600	CG 2941	CAUP COL
Columnea minor (Hook.) Hanst var nov 2	bll-mb	cl	2300-2500	CG 2942	CAUP COL
Columnea nicaraguensis Oerst var nov 1	bh-mb	hb	1580-1800	RS 1013	CAUP COL
Columnea nicaraguensis Oerst var nov 2	bll-mb	hb	2000	CG 1166	CAUP
Columnea cf *picta* H. Karst.	bh-mb	hb	1700-1900	CG 2996	CAUP
Columnea strigosa Bentham	bh/ll-pm/mb	hb	1500-2100	CG 1412	CAUP
Columnea aff *villosissima* Kvist & Skog	bll-mb	hb	2000-2100	CG 2849	CAUP
Columnea sp nov	bh-mb	sh	1700	CG 2847	CAUP
Cremosperma hirsutissimum var *hirsutissimum*	bh-pm	sh	1300-1450	CG 2960	CAUP
Cremosperma hirsitissimum var album K & S	bll-mb	sh	2300	CG 2990	CAUP
Cremosperma humidium Kvist & Skog	bh-pm	sh	1300	CG 157	CAUP COL
Cremosperma cf *nobile* C.V. Morton	bh-pm	cl	1200	CG 1293	CAUP
Diastema affine Fritsch	bh-mb	sh	1300-1600	CG 2934	CAUP
Drymonia cf *aciculata* Wiehler	bh/ll-mb	sh	1400-2000	CG 2928	CAUP
Drymonia serrulata (Jacq.) Mart	bh/ll-mb	sh	1300-2100	CG 1354	CAUP
Drymonia cf *sulphurea* Wiehler	bh-mb	hb	1700	CG 2850	CAUP
Drymonia turrialvae Hanst.	bh-pm	hb	1400	CG 1447	CAUP
Drymonia warscewicziana Hanst.	bll-mb	hb	2500	CG 1752	CAUP
Gasteranthus corrallinus (Fritsch) Wiehler	bh-pm/mb	hb	1300-2000	CG 1762	CAUP
Gasteranthus delphinioides (Scem.) Wiehler	bh-pm	sh	1300-1600	-	CAUP
Gasteranthus leopardus M. Freiberg	bh-pm	sh	1300-1600	CG 1361	CAUP
Hepiella ulmifolia (Kunth.) Hanst	bh-pm	cl	1600	-	CAUP
Kohleria inaequalis Benth var *inaequalis*	bh-pm/mb	cl	1400-1700	CG 1289	CAUP
Kohleria inaequalis Benth. Var *ocellata*	bh-pm/mb	cl	1500-1800	RS 1002	CAUP
Kohleria spicata Oerst	bh-mb	cl	1600-1800	CG 1753	CAUP
Monopyle inaequalis C.V. Morton	bh-mb	tr	1800	CG 1473	CAUP COL
Monopyle cf *macrocarpa* Benth		cl		CG 2998	CAUP COL
Paradrymonia	bh/ll-mb		1500-2350	CG 2997	CAUP COL
Paradrymonia		tr			
Paradrymonia sp nov	bh-mb		1600-2000	CG 3226	CAUP
Hippocastanaceae		tr			
Billia columbiana Planch. & Linden ex Tr & Pl.	bll-mb		2500	CG 3006	CAUP
Hippocrateaceae		tr			
Salacia cf gigantea Loes.	bh-mb		1650-1800	178	CAUP
Hydrangeaceae	bh-mb	hb	1750-1950		
Hydrangea		hb		CG 3022	CAUP
Icacinaceae	bh-pm		1400	CG 3191	CAUP
Calatola colombiana Slearm	bh-pm	hb	1200		
Citronella silvatica Cuatrec.		hb		CG 3564	CAUP
Lamiaceae	bh-mb		1684	CG 1522	CAUP

Hyptis	bh-pm	tr	1300		
Salvia	bh-mb	tr	1600	CG 3064	CAUP
Lauraceae	bh-mb	tr	1600	CG 3181	CAUP
Beilschmiedia?	bh-mb	tr	1600	CG 1098b	CAUP
Endlicheria	bh-pm/mb	tr	1300-1600	CG 1391	CAUP
Nectandra aff *longifolia* (Ruiz & Pavon) Nees	bh-mb	tr	1400-2000	NG 018	CAUP
Nectandra aff *membranacea* (Sw.) Griseb.		tr		CG 3399	CAUP
Nectandra aff *mollis* (Kunth.) Nees	bh-pm/mb		1400-1600	CG 3123	CAUP
Nectandra reticulata (Ruiz & Pavón) Mez	bh-mb	tr	1500-1966	CG	CAUP
Nectandra aff *purpurea* (Ruis & Pavón) Mez	bh-mb	tr	1684	CG 1920	CAUP
Nectandra	bh-mb	tr	1600	CG 3098	CAUP
Nectandra	bh-mb	tr	1600	CG 3063a	CAUP
Nectandra	bh-pm	tr	1500	RS 1046	CAUP
Nectandra	bll-mb	tr	2200	CG 3542	CAUP
Nectandra	bh-pm	tr	1750	CG 3092	CAUP
Nectandra	bh-pm	tr	1400-1856	CG 3301	CAUP
Nectandra	bh-mb	tr	1400-1600	CG 3188	CAUP
Nectandra?	bh-mb	tr	1650	CG 3255	CAUP
Nectandra?	bh-mb	tr	1600	CG 3526	CAUP
Ocotea aff *babosa* C.K. Allen	bh-mb	tr	1966	CG 3186	CAUP
Ocotea aff *duqei* Korstom.	bh-pm/mb	tr	1350-1966	RS 874	CAUP
Ocotea oblonga (Meissner) Mez	bh-mb	tr	1684	CG 3134	CAUP
Ocotea aff *simulans* C.K. Allen	bh-mb/pm	tr	1600-1966	CG 3395	CAUP
Ocotea	bh-mb	tr	1600	CG 3065	CAUP
Ocotea	bll-mb	tr	1966	CG 3274	CAUP
Ocotea	bh-mb	tr	1500	RS 872	CAUP
Ocotea	bh-pm	tr	1650	CG 3144	CAUP
Persea aff *caerulea* (Ruis & Pavón) Mez	bh-mb	tr	1600	-	CAUP
Persea aff *hexanthera* Kupp		tr		CG 3012	CAUP
Persea americana Mill.	bh-pm	tr	1300	CG 1095	CAUP
Persea	bll-mb	tr	2200	CG 1759	CAUP
Pleurothyrium cf	bh-mb	tr	1856	CG 3165	CAUP
Rhodostemonadaphne cf	bll-mb	tr	2200	CG 3303	CAUP
Indet		tr		CG 3272	CAUP
Indet	bh-pm		1500-1686	CG 3233	CAUP
Indet	bll-mb	sh	1900-2000		
Indet	bh/ll-mb	tr	1856-2200	CG 3074	CAUP
Lecythidaceae	bll-mb	tr	2200	CG 3294	CAUP
Eschweilera		tr		CG 3270	CAUP
Eschweilera	bh-pm		1550	CG 3235	CAUP
Eschweilera aff *coriaceae*		ep			
Eschweilera aff *caudiculata* Kunth	bll-mb		2500	OC 393	CAUP
Lentibulariaceae	bh-pm	ep	1500		
Utricularia jamesoniana Oliver	-	ep	-	CG 2861	CAUP
Loranthaceae	bh-pm	-	1600	BR 7732	PSO
Gaiadendron punctatum (Ruiz & Pavón) Don	bh-pm	ep	1450	BR	PSO
Ixocanthus hutchinsonii Kunth		ep		CG 1104	CAUP
Orycthanthus asplundii Kunth	bh-pm		1450	LA 27	CAUP
Phorandendron cf piperoides (Kunth) Trell.		hb			
Struthanthus	bh-pm		1600	RS 1072	CAUP
Lythraceae	bh-pm	sh	1500		
Cuphea racemosa (L.f.) Sprengel		cl		CG 3525	CAUP
Malpighiaceae	bh-pm		1600	RS	AFP
Bunchosia cf	bh-pm	hb	1400		
Stigmaphyllon bogotense Triana & Planchon		tr		RS 1070	CAUP
Malvaceae	bh-mb		1400-1800	CG	CAUP
Sida rhombifolia L.		cl			
Wercklea feroz (Hook. F.) Fryxell	bh-pm		1600	CG 3076	CAUP
Marcgraviaceae	bh/ll-mb	hb	1856-2200		
Marcgravia cf *browneii* (Tr. & Pl.) Krug & Urb	bh-mb	tr	1800	MB 039	CAUP
Melastomataceae	bh-pm	tr	1600	CG 3225	CAUP
Aciotis cf	bll-mb	sh	2300	CG 2946	CAUP
Axinaea cf lehhmanii Cogn ex Chair	bh-pm	sh	1650	RS 792	CAUP
Axinaea cf.	bll-mb	tr	2200-2400	CG 1349	CAUP
Arthrostema aff *macrodesmum* Gleason	bh-pm	tr	1450-1680	CG 3028	CAUP
Arthrostema cf	-	cl	-	CG 3220	CAUP
Blakea alternifolia (Gleason) Gleason	bh-pm	tr	1700	CG 3040	CAUP

Blakea punctulata (Triana) Wurdack	bh-mb/pm	tr	1400-2000	CG 2876	CAUP
Blakea cf *squamiger* L. Uribe	bh-mb	tr	1750-1966	OC 675	CAUP
Blakea	bh-mb	tr	1400-1500	CG 3198	CAUP
Bellucia calliptrata Gleason	bh-pm	sh	1684	CG 3116	CAUP
Centronia phlomoides Tr.	bh-pm	tr	1500	CG 1454	CAUP
Centronia	bh-mb	tr	1686-1966	CG 3082	CAUP
Clidemia	bh-pm	tr	1600	CG 3103	CAUP
Conostegia cf. *cuatrecasasii* Gleason	bh-pm	tr	1600	CG 3266	CAUP
Conostegia aff. *icosandra* (Sw.) Urban	bll-mb	tr	2150	CG 3024	CAUP
Graffenrieda colombiana	bll-mb	tr	2200	CG 3531	CAUP
Henrrietella L.	bh-mb	sh	1100	CG 1197	CAUP
Huilaea mutissina	bh-mb	hb	1200	CG 1167	CAUP
Killipia quadrangularis Gleason	bh-pm	hb	1650-1684	CG 1351	CAUP
Killipia	bll-mb	tr	2400	CG 1356	CAUP
Leandra	bh-pm	tr	1800	CG 3043	CAUP
Leandra	bll-mb	tr	2200	CG 406	CAUP
Miconia aff *aegrotans* Naud.	bh-pm	tr	1966	CG 1878	CAUP
Miconia agregata Gleason	bh-pm	sh	1856	CG 3365	CAUP
Miconia aeruginosa Naudin.	bh-pm/mb	sh	1650-1966	CG 3111	CAUP
Miconai aff. *brachygyna*	bh-pm	tr	1750	CG 3111^{a}	CAUP
Miconia aff *caudata (*Bonpl.) DC	bh-pm	tr	1950	CG 3119	CAUP
Miconia cf. *dolichopoda* Naud.	bll-MB	tr	2450-2550	CG 3199	CAUP
Miconia floribunda (Bonpl.) C.CD.	bh-pm	tr	1684-1950	CG 3291	CAUP
Miconai aff. *haughtii*	bh-pm	tr	1686-1700	CG 1760	CAUP
Miconia aff. *laetivirens* L. Uribe	-	tr	-	CG 3073	CAUP
Miconia cf *lehmannii* Cogniaux	bh-pm	-	1856	CG 3209	CAUP
Miconia aff *longifolia* 8^{a}ubl.) C.DC.	bh-pm	tr	1500	CG 3109	CAUP
Miconia aff. *triplinervis* Ruiz & Pavon	bh-pm	tr	1800	CG 3258	CAUP
Miconia	bh-pm	sh	1800	CG 3104	CAUP
Miconia	bh-pm	sh	1800	CG 1896	CAUP
Miconia	bh-pm	sh	1800	CG 1434	CAUP
Miconia	bll-mb	sh	2300	CG 1180	CAUP
Miconia	bh-pm	sh	1450	CG 1281	CAUP
Miconia	bh-pm	tr	1800	CG 1202	CAUP
Miconia	bh-pm	tr	1250	LA 032	AFP,CAUP
Miconia	bh-pm	sh	1600	CG 1777	CAUP
Miconia	bh-pm	tr	1500	CG 1342	CAUP
Miconia	bh-pm	tr	1600	CG 3362	CAUP
Miconia?	bll-mb	tr	2100	CG 1889	CAUP
Miconia		sh	1700	CG 1884	CAUP
Miconia		tr		CG 3555	CAUP
Miconia	bh-pm	tr	1856	CG 3122	CAUP
Pterolepis trichomata (Rottb.) Cogn	bh-pm	tr	1856-1950	CG 1935	CAUP
Tibouchina	bh-pm	tr	1300	CG 3260	CAUP
Tibouchina	-	sh	-	CG 3247	CAUP
Topobea	-	-	-	CG 1915	CAUP
Topobea	-	-	-	CG 3518	CAUP
Indet	-	-	-	CG 3311	CAUP
Indet	-	-	-	CG 3140	CAUP
Indet		-		CG 3073	CAUP
Indet	bh-pm		1686-1950	CG 1132	CAUP
Indet	bh-pm	tr	1350-1686		
Indet	bh-pm	tr	1600-1650	CG 3070	CAUP
Meliaceae	bh/ll-pm/mb	tr	1600-2200	CG 3080	CAUP
Carapa guianensis Aubl.	bh/ll-pm/mb	tr	1600-2500	CG 3011	CAUP
Guarea cf *glabra* Vahl.	bh-pm	tr	1686	CG 3039	CAUP
Guarea cf *guidonia* L. (Sleum)	bll-mb	tr	2200	CG 3516	CAUP
Guarea cf *kunthiana* A. Juss.	bh/ll-pm	tr	1900-1950	CG 3079	CAUP
Guarea	bh-pm	tr	1600-1750	CG 3364	CAUP
Guarea		tr		CG 3281	CAUP
Guarea	bh-pm		1500	CG 3189	CAUP
Ruagea cf *pubescens* H. Karst.	bh-pm	tr	1300		
Trichilia	bh/ll-pm	tr	1856-1966	CG 3096	CAUP
Mimosaceae	bh-pm	tr	1300	CG 3400	CAUP
Inga chartaceae	bh-pm	tr	1600	CG 3245	CAUP
Inga densiflora Benth	bh-pm	tr	1450-1500	CG 3158	CAUP
Inga exalata T.S. Elias	bh-pm	tr	1500	CG 2886	CAUP

Inga		tr		CG 1392	CAUP
Inga	bh-pm		1300-1600	CG 3108	CAUP
Inga	bh-pm	tr	1400-1800		
Inga	bh/ll-pm	sh	1800-1900	CG 3158	CAUP
Monimiaceae	bll-mb	sh	2300	CG 3195	CAUP
Mollinediia tomentosa (Benth.) Tull	bh-pm	sh	1450-1856	CG 3115	CAUP
Siparuna cf *gesnerioIdes* (Kunth) A..DC.	bh-pm	sh	1400-1500	CG 1300	CAUP
Siparuna laurifolia (Kunth) A. DC.		sh		CG 3259	CAUP
Siparuna cf *lepidota* A. DC.	bh-pm		1750	CG 1492	CAUP
Siparuna	bh-pm	tr	1300		
Siparuna	bh-pm	tr	1500	CG 3215	CAUP
Moraceae	bll-mb	tr	2200	CG 1917	CAUP
Brosimum cf.	bh-pm	tr	1686	CG 3087	CAUP
Clarisia cf.	bh/ll-pm	tr	1950-2000	CG 3237	CAUP
Ficus cf *gigantocyse* Dugand	bh-pm	tr	1300	CG 3058	CAUP
Ficus cuatrecassana	bh-pm	tr	1400	CG 3295	CAUP
Ficus	bh-pm	tr	1500-1600	CG 3176	CAUP
Ficus	bh-pm	tr	1400-1500	CG 1924	CAUP
Ficus	bh-pm	tr	1600	HB 169	CAUP
Ficus	bh-pm	tr	1600	LA 40	CAUP
Ficus	bh-pm	tr	1300	RS 882	CAUP
Ficus	bh-pm	tr	1400-1600	CG 1517[a]	CAUP
Ficus	bh/ll-pm	tr	1750-2000	CG 1517	CAUP
Ficus	bh-mb	tr	1950	CG 2987	CAUP
Ficus	bh-pm	tr	1300	CG 3124	CAUP
Ficus	bh-mb	tr	1950	CG 3293	CAUP
Helicostylis tovarensis (Klotzsch & Karst.) Berg	bh-pm	tr	1300	CG 3152	CAUP
Naucleopsis cf	bh-pm	tr	1500-1600	CG 3292	CAUP
Perebea xantochyma Dugand		tr		CG 3153	CAUP
Pseudolmedia laevigata Trecul.	bh-pm		1500	HB 147	CAUP
Sorocea pubivena (Akker & Berg) C.C. Berg	bh/ll-pm/mb	tr	1500-2000		
Indet	bh-pm	tr	1700	CG 3090	CAUP
Myristicaceae	bh-pm/mb	tr	1600	CG 3023	CAUP
Compsoneura aff. *rigidifolia* W. Rodriguez		tr		CG 1435	CAUP
Otoba gordonifolia A.C (Gentry)	bll-mb		2200	RS 773	CAUP
Otoba lehmannii (A.C. Smith) Gentry	bh-mb	tr	1600-1856		
Otoba novogranatensis Moldenke	bh-pm/mb	tr	1600-2000	CG 3229	CAUP
Myrsinaceae	bh-pm	tr	1600	CG 3044	CAUP
Ardisia	bh/ll-mb	tr	1684-2200	CG 3538	CAUP
Cybianthus aff *montanus* Lundell (Agost)	bh-pm/mb	tr	1500-1686	NG 05	CAUP
Cybianthus occigranatensis (Cuatrec.) Agosti	bh-pm	tr	1500	CG 3056	CAUP
Cybianthus	bh-pm	tr	1300	CG 3066	CAUP
Geissanthus cf *mezianus* Agost		tr		CG 3099	CAUP
Geissanthus cf	bh-mb		1856	CG 3164	CAUP
Myrsine coriaceae (Sw) R. Br. Ex Roem. & Sh	bh-pm	tr	1400-1500		
Myrsine	bh-pm	tr	1300-1600	CG 3242	CAUP
Myrtaceae	bh-mb	tr	1950	CG	CAUP
Myrcianthes rhopaloides (Kunth) Mc Vaugh	bh-pm/mb	tr	1650	CG 3536	CAUP
Psidium guianensis Sw.	bh-pm	tr	1450	CG 3282	CAUP
Eugenia cf	bll-mb	tr	2300	CG 3046	CAUP
Eugenia cf	bh-pm	tr	1300	CG 1907	CAUP
Eugenia cf	bh-pm-mb	tr	1300-1686	CG 3300	CAUP
Eugenia cf	bh-pm	tr	1300-1350	CG 3169	CAUP
Myrcianthes	bh/bll-mb	tr	1950-2000	CG 3174	CAUP
Myrcia	bh-pm	tr	1650	CG 3163	CAUP
Indet		tr		CG 3118	CAUP
Indet	bh-pm		1300	CG 3045	CAUP
Indet		tr			
Indet	bh-mb		1200-1800	CG 3178	CAUP
Ochnaceae	bll-mb	sh	2300		
Ouratea		sh		CG 1428	CAUP
Onagraceae	bh-pm		1300-1600	CG 1220	CAUP
Fuchsia macrostigma Bentham		hb			
Fuchsia cf *sessilifolia*	bh-pm		1400	BR 7727	CAUP
Oxalidaceae	bh-pm	hb	1500		
Oxalis	bh-pm	hb	1350	CG 3548	CAUP
Papilionaceae		sh		FG 2944	CAUP

Desmodium	bll-mb		2500	CG 1485	CAUP
Zornia curvata Mohl	bh-pm	cl	1450-1550		
Indet	bh-mb	cl	1700	CG 1763	CAUP
Passifloraceae	bh-pm	cl	1200-1300	CG 1458	CAUP
Passiflora cumbalensis Karsten		cl		CG 1414	CAUP
Passiflora antioquensis H. Karst.	bh-mb		1800	CG 3546	CAUP
Passiflora	bh-mb/pm	cl	1600-2000		
Passiflora	bh-pm/mb	hb	1600	CG 1439	CAUP
Piperaceae	bh-pm	cl	1300	CG	CAUP
Peperomia alberthssmithii Trell & Yunker	bll-mb	sh	2350	CG 1163	CAUP
Peperomia alwynii Callejas & Betancur	bh/ll-mb	sh	1655-2100	CG 2915	CAUP
Peperomia angularis C. DC.	bh-pm	hb	1100	ML 02	CAUP
Peperomia caliginigaudens Trell & Yunker	bh-pm/mb	sh	1800	CG 2952	CAUP
Peperomia hernandifolia (Vahl) A. Dietr.	bll-mb	sh	2100	CG 2924	CAUP
Peperomia lancifolia Hooker	bll/h-mb/pm	sh	1600-2300	CG 2868	CAUP
*Peperomia obtusifolia (*L.) A. Dietr. Cf	bll-mb	cl	1900	CG 2977	CAUP
Peperomia peltoidea Kunth	bh-mb	hb	1800	CG 3150	CAUP
Peperomia striata Ruiz & Pavón	bh-pm	hb	1620	CG 2944	CAUP
Pperomia swartziana Miquel	bh-mb	hb	1800	CG 2991	CAUP
Peperomia	bh-pm	cl	1100	CG 2982	CAUP
Peperomia	bh-pm	hb	1000	CG 2978	CAUP
Peperomia	bll-mb	hb	2100	CG 2925	CAUP
Peperomia	bh-pm	cl	1300-1600	CG 2927	CAUP
Peperomia	bh-pm	cl	1300-1400	CG 1271	CAUP
Peperomiia	bh-mb	hb	1900	CG 2270	CAUP
Peperomia	bh-pm	cl	1200	CG 1343	CAUP
Peperomia	bh-pm	sh	1450	CG 1433	CAUP
Peperomia	bh/ll-pm/mb	hb	1700-2100	CG 1932	CAUP
Peperomia	bh-mb	sh	1900	LA 010	AFP,CAUP
Piper carpunya Ruiz & Pavón	bh/ll-mb	sh	1800-2000	CG 2862	CAUP
Piper crassinervium H.B.K.	bh-pm	cl	1450	CG 3127	CAUP
Piper curvinervium Callejas y Betancur	bh/ll-mb	cl	1900-2200	CG 3557	CAUP
Piper dryadum C.DC.	bh-pm	hb	1700	LA 09	AFP,CAUP
Piper echinocaule Yunck	bh-mb	sh	1900	CG 2858ª	CAUP
Piper lanciifolium C.DC.	bh/ll-mb	sh	1800-2200	CG 2852	CAUP
Piper pilibracteum Trell & Yunck	bh-pm	sh	1400	CG 3217	CAUP
Piper trianae C.DC.	bh-mb	sh	1800	CG 3552	CAUP
Piper turnidinodum Yunck	bh-mb	sh	1800	CG 3565	CAUP
Piper	bll-mb	sh	2100	CG 2972	CAUP
Piper	bh-pm	sh	1400	JG 017	CAUP
Piper		sh		CG 2949	CAUP
Piper	bll-mb		2250	CG 2674	CAUP
Piper	bh-mb	tr	2000		
Piper		tr		CG 1321	CAUP
Polygalaceae	bll-mb		2000-2100	CG 1430	CAUP
Monnina pulcra Chodat	bh-mb	tr	1500-1900		
Monnina		tr		CG 1774	CAUP,COL
Proteaceae	bh-pm		1300	CG 3097	CAUP,COL
Panopsis sp nov	bll-mb	tr	2500		
Panopsis sp nov		cl		CG 3167	CAUP
Rosaceae	bh-pm		1600	CG	CAUP
Prunus integrifolia (Presl.) Walp.	bh-pm	sh	1200-1300		
Rubus robustus C. Presl.	bh/ll-pm/mb	hb	1400-2400	MB 037	CAUP
Rubiaceae	bh-mb	tr	1400-1600	CG 2931	CAUP
Amphidasya	bh-pm/mb	hb	1300-1700	CG 1487	CAUP
Borreria	bh/ll-pm/mb	tr	1750-2000	CG	CAUP
Cinchona cf *pubescens* Vahl.	bh-pm	tr	1550	CG 3173	CAUP
Coccocypselum	bh-pm	tr	1400	CG 3212	CAUP
Dioicodendron dioicum cf (Sch. & Kr.) Steye	bh/ll-pm/mb	tr	2200	RS 1148	CAUP
Elaeagia utilis (Goud) cf	bh-pm	tr	1684	CG 1490	CAUP
Elaeagia cf *pastoensis*	bll-mb	tr	2200	CG 3222	CAUP
Elaeagia	bh-pm	tr	1600	CG 3071	CAUP
Elaeagia	bll-mb	tr	1900-2000	CG 3299	CAUP
Elaeagia	bh/ll-pm/mb	tr	1400-2500	CG 1380	CAUP
Elaeagia	bh-pm	tr	1450-1650	CG 3121	CAUP
Elaeagia	bh-pm	tr	1650	CG 3252	CAUP
Faramea calyptrata C.M. Taylor	bh-pm	tr	1600	CG 3041	CAUP

Faramea aff *chlorophylla* Muell-Arg	bh-pm	hb	1490	CG 3014	CAUP
Faramea oblongifolia Standl.	bll-mb	sh	2300	MB 011	CAUP
Faramea	bll-mb	tr	2400-2500	LA 014	CAUP
Galium cf *hypocarpium* (L.) Endl. Ex Griseb.	bh-pm	tr	1350	CG 1278	CAUP
Gonzalagunia dependens Ruiz & Pavón	bh-mb	tr	1800	CG 1246	CAUP
Guettarda crispiflora Vahl.	bh-pm	sh	1550	CG 1341	CAUP
Guettarda turnefortiopsis Standl.	bh-pm	sh	1600	CG 3358	CAUP
Hamelia?	bh-pm	sh	1490-1500	CG 3203	CAUP
Hoffmannia sprucei Standl.	bh-pm	sh	1550-1700	CG 1106	CAUP
Hoffmannia	bh-pm	tr	1400-2000	LA 020	AFP,CAUP
Hoffmannia	bh-pm	tr	1300	CG 1413	CAUP
Hoffmannia	bh-pm	tr	1400	CG 3062	CAUP,MO
Isertia pittieri (Standl.) Standl	bh-pm	tr	1600	CG 3170	CAUP
Ladenbergia macrocarpa (Vahl.) Klotzsch	bll-mb	sh	2200	CG 1488	CAUP
Ladenbergia magnifolia (R. & P.) Kl.	bh/ll-pm/mb	tr	1950-2000	CG 1148	CAUP
Ladenbergia	bh/ll-mb	sh	2000-2400	CG 3219	CAUP
Palicourea crocea (sw.) R. & S.	bll-mb	tr	2300	CG 3112	CAUP
Palicourea cutrecasasii Standl. & Steyerm	bh-pm	sh	1600	CG 2973	CAUP
Palicourea gibbosa Dwter	bh-pm	sh	1600	CG 1171	CAUP
Palicourea lasiantha K. Krause.	bll-mb	sh	2200	JG 034	CAUP
Palicourea killipii Standl.	bll-mb	sh	2300	CG 1401	CAUP
Palicourea	bh/ll-mb	sh	2000	CG 3310	CAUP
Palicourea	bh-pm	sh	1480	CG 1415	CAUP
Palicourea	bh-pm	sh	1600	CG 1427	CAUP
Palicourea	bh-pm	sh	1600	CG 1397	CAUP
Palicourea	bh-pm	sh	1600	RS 1111	CAUP
Palicourea	bll-mb	sh	2400	RS 1164	CAUP
Palicourea	bh-pm	sh	1500	RS 850	CAUP
Palicourea	bll-mb	sh	2300	CG 1306	CAUP
Palicourea	bh-pm	sh	1500	CG 1453	CAUP
Palicourea	bh-pm	tr	1500	CG 1416	CAUP
Palicourea	bh-mb	sh	1950	CG 1900	CAUP
Palicourea	bh-pm	sh	1350-1650	CG 3086	CAUP
Posoqueria	bh-pm	sh	1500	CG 3286	CAUP
Psychotria allenii Standl.	bll-mb	sh	2400	CG 3052	CAUP
Psychotria aff *beteriana* D.C.	bll-mb	sh	2350	CG 1151	CAUP
Psychotria gentryi (Dwyer) C.M. Taylor	bll-mb	sh	2100	CG 1417	CAUP
Psychotria cf *officinalis* (Aubl.) Raeusch.	bh-pm	sh	1600	CG 1189	CAUP
Psychotria	bh-pm	sh	1300	CG 1498	CAUP
Psychotria	bh-mb	sh	1950	CG 1107	CAUP
Psychotria	bh-mb	sh	1900	CG 3175	CAUP
Psychotria	bh-pm	sh	1300	CG 3296	CAUP
Psychotria	bh-pm/mb	tr	1300-1750	CG 1876	CAUP
Psychotria	bh-pm	tr	1100	CG 3151	CAUP
Psychotria	bh-pm	tr	1600	CG 3522	CAUP
Rondeletia aff *colombiana* Rusby	-	hb	-	CG 2936	CAUP
Rondeletia cf *glabrata* Klotzsch	bll-mb	tr	2200	NG 012	CAUP
Rondeletia	bh-pm	tr	1600	CG 3246	CAUP
Spermacoce	bll-mb	tr	2200	CG 3308	CAUP
Indet	bh-pm/mb	tr	1600-1850	CG 3309	CAUP
Indet		tr		CG 3231	CAUP
Indet	bll-mb		2200-2500	CG 3052	CAUP
Indet		tr			
Indet	bh-pm		1600	CG 1168	CAUP
Rutaceae		tr			
Zanthoxylum	bh-pm/mb		1600	CG 3527	CAUP
Sabiaceae	bh-pm	tr	1300		
Meliosma	bh-pm	tr	1600	CG 1130	CAUP
Sapindaceae	bh-pm	tr	1600	CG 3177	CAUP
Allophylus mollis (H.B.K) Radlk	bh-pm	tr	1500-1600	RS 878	CAUP
Allophylus	bh-pm/mb	tr	1500-1650	RS 1059	CAUP
Allophylus	bh-pm	cl	1500-1600	HB 361	CAUP
Cupania cinerea Poepp	bh-pm	tr	1500-1600	CG 1152	CAUP
Talaisia		tr		CG 1143	CAUP
Serjania	bh-pm		1300-1600	CG 1377	CAUP
Tapirira cf *guianensis* Aubl.	bh/ll-pm/mb	tr	1600-2200		
Indet	bll-mb	tr	1950	CG 1119	CAUP

Sapotaceae		tr		CG 3519	CAUP
Pouteria cf *maguirei* (Aubre) Penn.	bh-pm/mb		1500-1650	CG 3131	CAUP
Pouteria parcki (Ducke)		tr			
Pouteria cf *wurdackii* Aublet	bh-pm		1400	CG 3035	CAUP
Simaroubaceae	bh-mb	sh	1650-1966		
Picramnia cf magnifolia J.F. Macbr.	bh-pm	tr	1600	CG 3390	CAUP
Solanaceae	bh-pm	tr	1400	CG 3138	CAUP
Brugmansia cf *alba* L.	bh-pm	sh	1650	CG 3521	CAUP
Cestrum	bh-pm	sh	1450-1580	CG 2940	CAUP
Cestrum	bh-pm/mb	sh	1500-1600	RS 1026	CAUP
Cestrum	bll-mb	sh	2300	LA 037	CAUP
Cestrum	bh-pm	sh	1600	CG 3545	CAUP
Cuatresia	bh-mb	sh	1900	CG 1250	CAUP
Markea pilosa S. Knapp.	bh-pm	cl	1450-1580	CG 1123	CAUP
Physalis	bh-pm-mb	sh	1950-2000	CG 1471	CAUP
Physalis	bh-pm	sh	1400	RS 881	CAUP
Solandra	bh-pm	tr	1450	CG 3113	CAUP
Solanum aturense Dunal	bh-pm	cl	1600	CG 1370	CAUP
Solanum nudum Dunal	bh-pm	sh	1400-1500	LA 023	AFP,CAUP
Solanum	bll-mb	cl	2000	RS 1000	CAUP
Solanum	bll-mb	sh	2100	CG 3314	CAUP
Solanum	bll-mb	sh	2300	CG 2860	CAUP
Solanum	bll-mb	sh	2400	CG 1418	CAUP
Solanum	bh-pm/mb	sh	1950	CG 1259	CAUP
Solanum		cl		CG 1291	CAUP
Solanum	bh-pm		1600	CG 3205	CAUP
Solanum	bh/ll-mb	tr	1600-2300		
Trianae		tr		CG 3539	CAUP
Staphyleaceae	bh-mb		1600-1850	CG 1489	CAUP
Huertea cf *glandulosa* R. & P.		tr			
Turpinia occidentalis (Sw.) G. Don.	bh-mb		1850	CG 3376	CAUP
Styracaceae		tr			
Styrax tesmannii Perkins	bh/ll-pm/mb		1500-2300	CG 3251	CAUP
Theaceae		cl			
Freziera sessiliflora A. Gentry	bh-pm		-	CG 1286	CAUP
Tropaeolaceae		tr			
Tropaeolum deckerianum Maritz & Karsten	bh-pm		1600	-	-
Ulmaceae	bh-pm	cl	1450		
Trema micrantha 8L.) Blume	bh-pm	hb	1450	RS 999	CAUP
Urticaceae		hb		RS 156	CAUP
Pilea daguensis Killip				LA 022	AFP,CAUP
Urera	bh-mb	tr	1600-1966		
Urtica	bh-pm	tr	1600		
Verbenaceae	bh-pm	hb	1450	CG 3137	CAUP
Aegiphila novogranatense Moldenke		hb		RS 1080	CAUP
Citharexylum aff *kunthianum* Moldenke	bh/ll-mb		1900-2100	RS 1081	CAUP
Stachitarpheta cayenensis Vahl.	bll-mb	hb	2000		
Verbena litoralis Kunth		hb		CG 3559	CAUP
Violaceae	bh-pm		1600	CG 1429	CAUP
Viola		tr			
Viola				RS 966	CAUP
Vochysiaceae					
Vochysia aff *duquei* Pilg					

12 Appendix 5

PLANTS OF TIPUTINI BIODIVERSIY STATION I. DICOTILEDONOUS. A PRELIMINARY LIST

Carlos Gonzalez and Andy Jarvis

This is a preliminary list of tree plot collections at Tiputini Biodiversity Station. The collection was made in ten 25m x 25m distributed evenly around TBS, and one 1-Ha plot which was adapted to the HERB tree plot methodology after Pitman (2002) established the plot.

The collections can be found in the University San Francisco of Quito herbarium, and copies in the National Herbarium, Quito and the herbarium of the Universidad Catolica. Photos have been takn f most individuals, and are available from the authors upon request.

The tree database includes 2375 individuals which have been marked, measured and identified. Of these, some 603 species have been separated, and this list reports these findings. The database is in a continual state of improvement, and it is stressed that the identifications made here are preliminary.

Taxon	No individuals	Elevation (m)	Collection	Photo Gallery
Anacardiaceae				
Astronium cf	1	219	CG 3672	-
Spondias cf *mombin* L.	1	261	CG 4413	1516A/B
Spondias cf *venulosa* (Endl.) Endl	1		CG 4550	-
Spondias cf	1	199-200	CG 3604	55A
Tapiria cf *guianensis*	1	261	CG 4423	1502A/B
Anacardium cf (sp novnigelperu)	1	227	CG 4252	1172A/B
Indet	1	227	CG 4112	697A/B
Annonaceae				
Crematosperma cauliflorum aff	1	-	CG 4442	1648A/B
Duguettia spixiana Mart.	6	227	CG 4204	916A/B
Duguettia	3	200-210	CG 4197	938A/B
Duguettia				1294A/B
Guatteria cargadero cf	3	220	CG 4225	988A/B
Guatteria	1	227	CG 4093	641A/B
Guatteria cf	1	219	CG 3679	-
Guatteria cf	1	261	CG 4436	-
Guatteria	1	238	CG 4493	1652A/B
Annona cf	1	223	CG 4302	1754A/B
Rollinia	1	227	CG 4172	850AA/BB
Xylopia	1	261	CG 4424	1503A/B
Indet	1	196	CG 3753	240A/B
Pseudomolmea	1	217	CG 3759	268A/B
Indet	1	200	CG 3805	342A
Indet	1	227	CG 4372	-
Indet	1	227	CG 4070	672A
Indet	2	227	CG 4158	744A/B
Indet	1	227	CG 4142	778A/B
Indet	3	227	CG 4178	857A/B
Indet	1	227	CG 4323	1319A/B
Indet (Guatteria?)	1	217	CG 3777	235A
Indet	1	227	CG 4220	970A/B
Indet	1		CG 3596	22A/B
Apocynaceae				
Aspidosperma	1	219	CG 4362	1463A/B
Aspidosperma			CG 3644	40A/B

Couma	1	261	CG 4419	-
Couma	1	227	CG 4046	605A/B
Couma	1	227	CG 4177	864A
Himathantus	1	199	CG 3606	-
Lachmellea	1	227	CG 4199	918A/B
Lachmellea	1	227	CG 4245	1037A/B
Aquifoliaceae				
Ilex	1	217	CG 3795	-
Ilex cf *inundata*	1	220	CG 3891	518A/B
Ilex	1	220	CG 3926	532A/B
Araliaceae				
Dendropanax arboreus (L.) Dec & Pl	4	227	CG 4067	673A/B
Dendropanax caucanus (Harm.) Har	3	219-261	CG 3676	2098/99
Dendropanax	1	220	CG 3882	3409/11
Arecaceae				
Astrocarium chambira Burret	6	217-220	CG 3796	290A/B
Astrocarium murumuru Mart.	1	200	CG 3849	394A
Euterpe precatorae	4	219-261	CG 4348	-
Geonoma maxima cf	17	227	CG 4057	-
Iriarthea deltoidea Ruiz & Pavon	25	199-227	CG 3625	49A/B
Oenocarpus bataua Mart.	1		CG 4552	-
Socratea exorrhiza (Mart.) H. Wendl.	2	200-227	CG 3847	360A/B
Wettinia maynensis Spruce	1	217	CG 3904	256A/B
Indet sp1	10	199-21	CG 3699	151A/B
Bignoniaceae				
*Jacaranda copaia (*Aublet) D. Don	4	219-261	CG 4278	1482A/B
Memora cladothica Sandwith	11	227	CG 4208	655A/B
Tabebuia serratifolia (Vahl.) G. Nich			CG 4468	1593A/B
Tabebuia cf	-	219	CG 4337	1434A/B
Indet	-	261	CG 4367	1524A/B
Bombacaceae				
Ceiba	1	219	CG 3651	187A/B
Matisia cordata Bonpl	3	220	CG 3714	102A/B
Matisia cf *longiflora* Gleason	13	217-227	CG 4087	-
Matisia cf *bracteolosa* Ducke	2	227	CG 4247	1198A/B
Matisia sp2	19	199-261	CG 3608	644A/B
Ochroma pyramidale (Cav. ex Lam.) U.	-	100	-	-
Pachira acuatica Aubl.	1	227	CG 4161	-
Quararibea	1	261	CG 4395	1547A/B
Quararibea	1	238	CG 4454	1646B
Quararibea	2	223	CG 4515	1695B
Indet	1		CG	1690A/B
Boraginaceae				
Cordia	1	199	CG 3621	42A
Cordia	1	227	CG 4163	898A/B
Indet	1	228	CG 4482	1628A/B
Burseraceae				
Crepidospermum rhoifolium Bent (T& Pl)	1	199	CG 4075	665A/B
Crepidospermum	-	238	CG 4457	1636A/B
Protium ecuadorense Benoist	2	199-200	CG 3839	370A/B
Protium cf *fimbriatum* Swart	1	220	CG 3916	570A/B
Protium glabrescens Swart	1	220	CG 3818	399A/B
Protium polybotrium (Turcz.) Engl	1	217	CG 3731	212A/B
Protium cf *robustum (*Swart.) DM Porter	1	227	CG 4053	595B
Protium trifoliolatum Engl.	1	261	CG 4418	1497A/B
Tetragastris panamensis (Engl.) Kuntz	1	238	CG 4481	1583A/B
Trattinikia		261	CG 4368	1513A/B
Protium	5	219-227	CG 4157	751B
Protium	2	238-261	CG 4386	1533A/B
Protium	1	223	CG 4531	-
Protium	1	227	CG 4040	-
Protium	1	227	CG 4159	743A/B
Protium	-	219	CG 4356	1459A
Protium	-	227	CG 4157	887A/B
Protium	-	238	CG 4439	1665A/B
Indet	-	227	CG 4036	619A
Indet	-	227	CG 4184	835A/B

Protium				1704A/B
Capparaceae				
Capparis	1	261	CG 4405	1558A/B
Caricaceae				
Jacaratia cf *digitata* (Poepp & Endl.) Solm	5	219-227	CG 4553	625A/B
Cecropiaceae				
Cecropia tomentosa	4	217-227	CG 3718	293A/B
Cecropia sciadophylla Mart.	4	219-261	CG 4345	1422A/B
Cecropia ficifolia	3	219-227	CG 3721	158A/B
Cecropia	3	220-227	CG 4276	-
Cecropia	1	227	CG 4301	-
Cecropia	1		CG 3885A	-
Cecropia	-	227	CG 4121	690A/B
Coussapoa cf *villosa* Poepp & Endl.	2	200	CG 3833	369A/B
Pourouma bicolor Mart.	2	199	CG 3600	50A/B
Pourouma ferruginea cf	1	219	CG 3681	200B
Pourouma guianensis Aubl.	?	?	CG 3710	-
Pourouma napoensis C. Berg.	4	223-238	CG 3781	243A/B
Pourouma cf *ovata*	1	223	CG 4526	-
Pourouma cf *villosa*	?	?	CG 4474	-
Pourouma sp1	2	199-227	CG 3609	886A/B
Pourouma sp?	3	199-261	CG 3599	-
Pourouma	3	219-227	CG 4377	-
Pourouma	-	227	CG 4271	1291A/02
Celastraceae				
Maytenus	1	210	CG 3867	447A/B
Maytenus	1	238	CG 4444	1642A/B
Maytenus	1	227	CG 4265	1122B
Chrysobalanaceae				
Couepia	1	217	CG 3732	258A/B
Couepia	2	261	CG 4378	1523A/B
Couepia	1	227	CG 4320	1320A/B
Couepia	1	227	CG 4305	1388A/B
Licania cf *elliptica* Standl	-	227	CG 4197	938AA/B
Licania cf *caudate* Prance	-	219	CG 3695	166A
Licania glablanca	1		CG 4341	1418A/B
Licania	1		CG 4524	1727A/B
Licania	1	199	CG 3581	-
Licania	1	217	CG 3769A	277A/B
Licania	2	200	CG 3801	344A/B
Licania	1	210	CG 3861	423A/B
Licania	1	238	CG 4451	-
Licania	1	227	CG 4211	1008A/B
Licania	1	227	CG 4244	1036A/B
Licania	1	227	CG 4269	1104A/B
Licania	1	227	CG 4081	
Parinari cf	1	227	CG 4216	1000A/B
Indet	1	219	CG 3887	-
Indet	2	227	CG 4102	-
Clusiaceae				
Chrysoclamis cf *membranacea* Pl & Tr	1	223	CG 3589	-
Chrysoclamis	1	199	CG 4510	1683A/B
Tovomita cf *amazonica*	2	217	CG 3750	-
Vismia cf *sprucei* Sprage		217	CG 3756?	265A/B
Vismia	2	227-261	CG 4127	812A/B
Indet		219	CG 3712?	105A/B
Combretaceae				
Buchenavia	1	227	CG 4090	632A/B
Dichapetalaceae				
Dichapetalum cf *rugosum*	-	217	CG 3730	222A
Tapura	-	261	CG 4387	1537A
Elaeocarpaceae				
Sloanea	1	199	CG 3628	72A/B
Sloanea	1	261	CG 4404	1571A/B
Sloanea	4	217-219	CG 3762	275A/B
Sloanea	-	217	CG 3780	283A/B
Sloanea	-	200	CG 3825	331A/B

Sloanea	1	238	CG 4499	-
Sloanea	1	217	CG 4097	735A/B
Sloanea	1	227	CG 4203	-
Sloanea	1	199	CG 4499	1603A/B
Euphorbiaceae				
Pausandra trianae (Muell. Arg.) Baill.	7	219-227	CG 3698	1003A/B
Acidoton nicaraguensis			CG 3782	232A/B
Hasseltia floribunda	-	227	CG 4171	1071A/B
Alchornea triplinervia (Sprengel) Muell. Arg	1	199	CG 3624	51A/B
Conceveiba	1	227	CG 4288	1223A/B
Alchornea latifolia Sw	3	227	CG 4171	877A/B
Hyeronima alchorneiodes Allemao	-	227	CG 4084	648A/B
Mabea "comun"	2	217-219	CG 3768	280A/B
Mabea superbrondu	6	220-223	CG 3807	339A/B
Mabea occidentalis Benth.	-	223	CG 4546	1678A/B
Mabea	1	227	CG 4232	1081A/B
Phyllanthus cf *urinaria* L.	1	227	CG 4105`	710A/B
Richeria racemosa	1	227	CG 4240	1068A/B
Alchornea triplinervia	1	261	CG 4433	1509A/B
Acalypha cf	5	227	CG 4218	993A/B
Acalypha cf *cuneata Poepp & Endl.*	1	220	CG 3906	585A/B
Sapium cf *ovobatum* K ex Müll. Arg	1	261	CG 4390	1554A/B
Croton	1	227	CG 4230	1094A/B
Nealchornea cf	1	220	CG 3927	547A/B
Pera cf	1	227	CG 4318	1367A/B
Pera duguet	1	227	CG 4250	1185A/B
Hyeronima	1	227	CG 3601	-
Hyeronima cf	1	227	CG 4496	-
Acalypha cf	5	227	CG 4218	993
Indet	-	-	CG 4404	-
Richeria racemosa	1	217	CG 3774	274A/B
Indet	1	217	CG 3787	-
Indet	1	220	CG 3923	-
Indet	2	238	CG 4475	-
Indet	-	-	758	-
Indet	1	227	CG 4262	-
Fabaceae				
Inga auristellae Harms	-	200	CG 4035	-
Inga	1	199	CG 3583	10A/B
Inga	1	238	CG 4484	1618AA/B
Inga velutina Willd	1	199	CG 3588	16A/B
Inga rusbyi Pittier	-	219	CG 3662	-
Inga brachyrachis/capitata	1	219	CG 3665	-
Inga aff umbratica			CG 4455	1668A/B
Inga	1	219	CG 3667	-
Inga	1	219	CG 3682	186A/B
Inga cordatoalata Ducke	1	219	CG 3653	193A/B
Inga umbratica Poepp	1	219	CG 3655	196A/B
Inga	1	217	CG 3778	-
Inga acreana Harms	2	217	CG 3741	220A/B
Inga	1	217	CG 3740	-
Inga	-	217	CG 3913	-
Inga multijuga o ruiziana	7	217-227	CG 3745	252A/B
Inga cf *microcoma* Harms	-	200	CG 3798	343A/B
Inga sarayacuensis T.D.Penn	2	200	CG 3763	285A/B
Inga	-	210	CG 3873	452A/B
Inga alata	-	210	CG 3856	461A/B
Inga	1	210	CG 3855	-
Inga	1	210	CG 3872	-
Inga tenuistepula Ducke	-	220	CG 4141	-
Inga cf *splendens* Willd.	-	219	CG 4350	1430A/B
Inga	1	219	CG 4338	1437A/B
Inga	-	261	CG 4311	-
Inga	-	261	CG 4523	-
Inga umbellifera (Vahl) Steud ex DC.	2	261	CG 4432	-
Inga cf *stenoptera* Benth.	1	261	CG 4434	1501A/B
Inga spectabilis (vahl) Willd.	2	261-223	CG 4426	1724A/B

Inga capitata Desvaux			CG 4473	1602A/B
Inga	1	261	CG 4394	1539A/B
Inga	2	227-261	CG 4408	1541A/B
Inga cf *umbelliferae* (Vahl) Steud. ex DC.	-	261	CG 4556	1760A/B
Inga velutina Willd.	2	261	CG 4428	1550A/B
Inga	1	261	CG 4403	1556A/B
Inga	1	238	CG 4473	1602A/B
Inga	-	238	CG 4513	-
Inga	1	223	CG 4540	-
Inga cf *suaveolens* Ducke	9	223-238	CG 4513	1691A/B
Inga spectabilis Vahl. Willd	1	227	CG 4111	703A/B
Inga aff setulifera T.D. Penn			CG 4523	1763A/B
Inga	1	227	CG 4099	716A/B
Inga	1	227	CG 4215	1001A/B
Inga punctata	5	227	CG 4213	1005A/B
Inga tessmannii Harms	1	227	CG 4289	1221A/B
Inga			CG 3789	250A/B
Inga	1	227	CG 4285	1235A/B
Inga marginata			CG 4374	1481A/B
Inga aff *heterophylla* Willd	1	227	CG 4272	1282A/B
Inga			CG 3794	296A/B
Abarema jupunba	1	210	CG 3871	492A/B
Lecointea peruviana	1	217	CG 3769	272A/B
Bauhinia brachycalyx	1	227-238	CG 4452	1669A/B
Dalbergia frutescens (Vell.) Britton			CG 3822	381A/B
Macrolobium angustifolium (Benth.) Cowman			CG 3636	78A/B
Macrolobium gracile Spruce & benth			CG 3709	128A/B
Macrolobium archeri R.S.Cown			CG 3744	251A/B
Macrolobium colombianum aff			CG 3686	132A/B
Zygia *heteroneura* Barneby & Crimes	6	227	CG 4086	645A/B
Hymenae oblongifolia	3	227	CG 4088	643A/B
Zygia aff *latifolia* (L.) Fawcett & Rendle	1	227	CG 4476	1602A/B
Zygia schultzeana	1	277	CG 3589	1555A
Zygia?	1		CG 4505	1732A/B
Indet	1	219	CG 4338	1437A/B
Brownea macrophylla Hort ex Mast	3	277	CG 4189	937A/B
Calliandra trinervia	1	277	CG 4293	1204A/B
Marmaroxillon			CG 4410	1532A/B
Indet	1	277	CG 4100	734A/B
Dalbergia	1	277	CG 4188	831A/B
Dussia	1	277	CG 4479	1592A/B
Zygia	2	261	CG 4374	1481A/B
Browneopsis ucayalina Huber	78	223-238	CG 4328	1450A/B
Macrolobium	5	217	CG 3728	940A/B
Swartzia multujuga				
Brownwea grandiceps			CG 3622	32A/B
Flacourtiaceae				
Casearia arborea (Rich.)Urb.	1	277	CG 4296	
Casearia	7	277	CG 4257	
Casearia cf *javitensis* Kunth		277	CG	432A/B
Casearia nigricans Sleumer		277	CG 4257	813A/B
Casearia			CG 4414	1511A/B
Carpotroche cf	1	199	CG 3642	69A/B
Lozania	1	227	CG 4060	593A/B
Ryania cf *speciosa* Vahl		277	CG 4166	866A/B
Tetratylacium macrophyllum Poepp		217-277	CG 3754	301A/B
Casearia cf *prunifolia* Kunth*(Ryania en list)*		277	CG 4096	738A/B
Casearia		277	CG 4450	843A/B
Hasseltia floribunda Sw		277	CG 4115	701A/B
Casearia			CG 4257	1148A/B
Neosprucea cf		277	CG 4535	1714A/B
Lacistema cf		277	CG 4132	803A/B
Casearia		261	CG 4431	1505A/B
Casearia		238	CG 4450	1660A/B
Casearia		277	CG 4221	980A/B
Hippocrateaceae				
Salacia cf spectabilis Ac. Smith			CG 4226	921A/B

Salacia			CG 4077	661A/B
Humiriaceae				
Vantanea			CG 3770	277A/B
Ventanea		219	CG 4343	1412A/B
Lauraceae				
Cinnamomun triplinervia		277	CG 4174	873A/B
Endlicheria		277	CG 4168	881A/B
Edlicheria	3	238	CG 4463	1587A/B
Nectandra	1	199	CG	8
Nectandra	1	261	CG 4421	1530A/B
Nectandra	2	261	CG 4398	1564A/B
Nectandra	1	238-277	CG 4449	1657A/B
Ocotea?	1	199	CG 3585	6
Ocotea?	2	199	CG 3617	38
Ocotea?	1	199-217	CG 3602	57A/B
Ocotea	1	261	CG 4420	1488A/B
Ocotea	2	219	CG 4101	730A/B
Persea	1	227	CG 4180	854A/B
Mezilaurus	1	222-219	CG 3712	105A/B
Rhodostemonodaphne	3	217	CG 3790	297A/B
Indet	1		CG 3817	307A/B
Indet.	1	199-227	CG 3611	24A/B
Indet	2	199	CG 3634	76A/B
Indet	3	222-227	CG 3717	107A/B
Indet	1	199-200	CG 3671	177A/B
Indet	3	222	CG 3652	194A/B
Indet	2	217-277	CG 3775	233A/B
Indet	1	217-238	CG 3776	234A/B
Indet	1	217	CG 3760	267A/B
Indet	2	217	CG 3770	297A/B
Indet	1	200	CG 3799	377A/B
Indet	1	200	CG 3869	413A/B
Indet	2	200	CG 3875	432A/B
Indet	3	200-261	CG 3874	442A/B
Indet	1	200-222	CG 3859	489A/B
Indet	1	220	CG 3920	500A/B
Indet	1	261	CG 4393	1542A/B
Indet	1	223	CG 4527	1686A/B
Indet	3	223	CG 4514	1715A/B
Indet	1	223-277	CG 4528	1723A/B
Indet	1	223	CG 4561	1738A/B
Indet	1	277	CG 4164	888A/B
Indet	1	277	CG 4198	949A/B
Indet	1	277	CG 4207	1026A/B
Indet	3	277	CG 4236	1067A/B
Indet	1	200-277	CG 4228	1095A/B
Indet	1	277	CG 4227	1098A/B
Indet	1	277	CG 4268	1107A/B
Indet	1	277	CG 4260	1142A/B
Indet		277	CG 4290	1218A/B
Indet	2		cf	1266
Indet	1	277	CG 4273	1276A/B
Indet	1	277	CG 4279	1278A/B
Indet	1	277	CG 4085	647A/B
Indet	1	277	CG 4125	819A/B
Indet	1	277	CG 4185	840A/B
Indet		277	CG 4280	1240A/B
Indet				1706A/B
Lecythidaceae				
Eschweilera andina	8	222-277	CG 3702	154A/B
Eschweilera cf *rufifolia O tessma* S.A. Mori	2	223-261	CG 4416	1577A/B
Eschweilera	1	199	CG 3590	7A/B
Eschweilera	4	261	CG 4370	1477A/B
Eschweilera	1	238	CG 4469	1594A/B
Grias neuberthii J.F. Macbr	2	222	CG 3700	115A/B
Gustavia longifolia Poepp ex berg	8	220-277	CG 3632	68A/B
Lecythis	1	200	CG 3865	478A/B

Lecythis	2	223-238	CG 4462	1581A/B
Indet	2	277	CG 4154	?
Malpighiaceae				
Byrsonima cf	1	238	CG 4472	4A/B
Melastomataceae				
Blakea	2	223-261	CG 4567	1747A/B
Miconia	1	217	CG 3784	?
Miconia	1	261	CG 4425	1492A/B
Miconia	5	223-261	CG 4506	1701A/B
Miconia	1	277	CG 4044	610?
Miconia	1	277	CG 4150	765A/B
Indet	1	217	CG 3771	279?
Indet	1	200	CG 3803	318A/B
Indet	1	200	CG 3826	403A/B
Indet	1	200	CG 3868	494A/B
Indet	1	223	CG 4539	1725?
Indet	1	277	CG 4104	712A/B
Mouriri	1	223	CG 4533	1716A/B
Mouriri	1	277	CG 4267	1111?
Indet				1707A/B
Meliaceae				
Cedrela cf	1	261	CG 4417	1476A/B
Guarea cf goma Pulle	1	219	CG 4357	1448A/B
Guarea pterorachis Harms	7	200-220	CG 3736	242A/B
Guarea purusana cf	5	277	CG 4063	589A/B
Trichillia septentrionalis			CG 3650	195A/B
Guarea	1	222	CG 3715	122?
Guarea	1	217	CG 3772	236?
Guarea "gomma"	6	220-277	CG 3928	527A/B
Guarea	5	220-238	CG 3912	542A/B
Cabralea cangeriana	1	261	CG 4435	1508A/B
Guarea silvatica	2	261-277	CG 4415	1517A/B
Guarea guentheriana	12	220-277	CG 4466	1579A/B
Guarea	3	238-220	CG 4448	1650A/B
Trichilia	1	223	CG 4545	1687A/B
Guarea	7	277	CG 4176	847A/B
Guarea	1	277	CG 4217	992A/B
Guarea	1	277	CG 4306	1392?
Trichilia	16	222-277	CG 3684	150?
Trichilia	7	238-261	CG 4368	1479A/B
Indet	2	277	CG 4210	1009?
Indet	1	277	CG 4316	1325A/B
Menispermaceae				
Abuta cf	1	219	CG 4363	1464
Monimiaceae				
Mollinedia	1	277	CG 4147	774A/B
Siparuna	1	277	CG 4258	1147A/B
Siparuna	1	277	CG 4324	1317A/B
Moraceae				
Brosimum	2	200	CG 3832	357A/B
Brosimum	1	277	CG 4275	1269A/B
Castilla cf	3	217-261	CG 3751	246?
Castilla	4	238-277	CG 4478	1627?
Clarisia	4	199-277	CG 3603	54A/B
Clarisia	2	261-277	CG 4382	1572A/B
Ficus	2	222	CG 3720	97
Ficus	1	238	CG 4497	1624A/B
Ficus	2	223	CG 4518	1731A/B
Ficus	1	277	CG 4287	1229A/B
Ficus	1	277	CG 4283	1258?
Ficus	2	199	CG 3703	93?
Helicostylis	2	277	CG 4095	737A/B
Maquira	1	261	CG 4411	1535A/B
Naucleopsis	1	277	CG 4195	924A/B
Naucleopsis cf	2	222-217	CG 3737	214A/B
Naucleopsis			CG 3841	383A/B
Perebea	6	220-222	CG 3673	180?

Poulcenia armata	1	219	CG 4344	1424A/B
Pseudolmedia	1	238	CG 4438	1670A/B
Sorocea	2	199	CG 3689	143A/B
Sorocea	56	200-222	CG 3800	337A/B
Batocarpus "ramaroja"	1	220	CG 3884	516A/B
Sorocea	2	219	CG 4349	1432A/B
Sorocea	1	277	CG 4291	1215A/B
Sorocea?	3	217	CG 3691	112?
Indet	2	199-238	CG 3626	18?
Indet	2	222-217	CG 3725	125A/B
Indet	1	217	CG 3669	147A/B
Indet	1	222	CG 3677	189?
Indet	2	222	CG 3739	244A/B
Indet	1	217-22	CG 3758	261A/B
Indet	1	200	CG 3863	486A/B
Indet	5	200-277	CG 3911	582?
Indet	9	238	CG 4487	1597?
Indet	2	277	CG 4069	675A/B
Indet	1	277	CG 4325	1306A/B
Myristicaceae				
Otoba parvifolia cf			CG 4456	1647A/B
Compsoneura			CG 4128	816A/B
Compsoneura			CG 4446	1640A/B
Virola duckei A.C. Smith			CG 4340	1411A/B
Virola mollis (AC. DC) Warb			CG 3619	44?
Virola multinervia			CG 4234	1072A/B
Virola obovata			CG 3866	417?
Virola flexuosa			CG 4536	1712A/B
Virola dixonii			CG 3791	205A/B
Virola			CG 4461	1634?
Virola			CG 4091	634A/B
Virola			CG 4264	1128A/B
Virola			CG 4091	634A/B
Virola			CG 3845	367A/B
Virola			CG 3680	174A/B
Virola pavoni			CG	1009A/B
Iryanthera ulei			CG	718?
Iryanthera			CG 4308	1384A/B
Otoba			CG 4559	1749?
Iryanthera			CG 3917	550A/B
Otoba glycicarpa			CG 3685	135A/B
Otoba				1702A/B
Myrsinaceae				
Ardisia			CG 3795	303A/B
Ardisia "semiovada"			CG 4455	1641A/B
Cybianthus			CG 4130	808A/B
Stylogyne			CG 4335	1436A/B
Myrtaceae				
Eugenia			CG 3645	43A/B
Eugenia			CG 3899	502A/B
Eugenia			CG 4052	598?
Eugenia			CG 4183	836A/B
Eugenia aff stipitata			CG 4292	1213A/B
Eugenia			CG 4358	1475A/B
Eugenia feijoi			CG 4360	1460A/B
Calophyllum			CG 4134	796A/B
Plinia			CG 4229	1024A/B
Plinia			CG 3910	538A/B
Indet			CG 3706	98?
Indet			CG 3761	288?
Indet			CG 3804	341A/B
Indet			CG 3838	396A/B
Indet			CG 4360	1460A/B
Eugenia			CG 4422	1504A/B
Indet			CG 4483	1584A/B
Indet			CG 4465	1588A
Indet			CG 4555	1762A/B

Indet	CG 4549	1767?
Indet	CG 4551	1768?
Indet	CG 4037	618A/B
Indet	CG 4119	691A/B
Indet	CG 4152	762A/B
Indet	CG	86A/B
Indet	CG 4175	861A/B
Indet	CG 3901	575A/B
Indet	CG 4352	1454A/B
Indet	CG 4392	1543A/B
Plinia	CG 4512	1680A/B
Indet	CG 4542	1693A/B
Indet	CG 4520	1722A/B
Nyctaginaceae		
Neea "supercrasa"	CG 3877	485A/B
Neea	CG 4488	1672A/B
Neea "altomina"	CG 4502	1728A/B
Neea "popular"	CG 4117	695A/B
Ochnaceae		
Ouratea "flaquita"	CG 4467	1622A/B
Olacaceae		
Heisteria	CG 4315	1333A/B
Heisteria	CG 4266	1109A/B
Heisteria	CG 3769	269A/B
Indet	CG 4076	658?
Indet	CG 4544	1692?
Piperaceae		
Piper	CG	1459A/B
Polygonaceae		
Triplaris Americana	CG 3815	1429A/B
Coccoloba fallax	CG 4110	704A/B
Coccoloba densifrons	CG 3919	543A
Indet	CG 4133	800?
Proteaceae		
Roupala montana	CG	59A/B
Rhamnaceae		
Colubrina arborescens (Mill.) Sarq.		1607
Rubiaceae		
Borojoa	CG 4193	925A/B
Duroia hirsuta cf	CG 4353	1449A/B
Faramea glandulosa Poepp	CG 4565	1748A/B
Psychotria	CG 4445	1644A/B
Pentagonia spathicalyx	CG 3713	104A/B
Pentagonia	CG 4329	1439A/B
Posoqueria latifolia	CG 4108	688A/B
Posoqueria?	CG 4169	880A/B
Posoqueria?	CG 3816	321A/B
Cousarea brevicaulis Krause	CG 3812	335A/B
Cousarea cephaloides Taylor	CG 4277	1262A/B
Randia	CG 3659	208A/B
Randia	CG 4253	1178A/B
Simira cordifolia	CG 4107	700A/B
Simira wurdackii Steyerm.	CG 4492	1643A/B
Wittmackanthus stanleyanus cf	CG 4071	671A/B
Psychotria stenostachya	CG 3616	788A/B
Randia armata (Sw.) DC.	CG 4355	1458A/B
Indet	CG 3584	12?
Indet	CG 3593	19?
Cousarea	CG 3711	94A/B
Simira	CG 3663	209A/B
Alseis	CG 3729	228A/B
Cousarea cf	CG 3813	317A/B
Indet	CG 3876	483A/B
Ladenbergia	CG 3925	526?
Indet	CG 4492	1643A/B
Indet	CG 4534	1711A/B
Cousarea macrophylla aff	CG 4530	1719A/B

Indet	CG 4558	1742?
Indet	CG 4522	1750A/B
Indet	CG 4554	1765?
Alibertia	CG 4223	983A/B
Indet	CG 4322	1321A/B
Indet	CG 4298	1403A/B
Sabiaceae		
Discophora guianensis	CG 4079	657A/B
Sapindaceae		
Allophylus	CG 4347	1425A/B
Allophylus	CG 4409	1544A/B
Allophylus	CG 4146	770A/B
Talisia	CG 4330	1446A/B
Indet	CG 4326	1305?
Sapotaceae		
Chromolucuma cf	CG 3705	134A/B
Chrysophyllum	CG 4508	1684A/B
Sarcaulus	CG 4205	915A/B
Micropholis venulosum	CG 3828A	374A/B
Micropholis “molihoniana”	CG 3757	1614A/B
Pouteria bilocularis	CG 4034	623A/B
Pouteria	CG 3765	80A/B
Pouteria	CG 3620	48A/B
Pouteria	CG 3704	88A/B
Pouteria	CG 3708	100A/B
Pouteria	CG 3724	108A/B
Pouteria	CG 3690	118A/B
Pouteria	CG 3701	124A/B
Chrysophyllum venezuelanense (Pierre)Penn	CG 3693	157A/B
Pouteria vernicosa T.D. Penn	CG	215A/B
Pouteria quianensis Aubl.	CG 4224	986A/B
Pouteria	CG 3657	188A/B
Pouteria multiflora (A.DC) Eyme	CG 3746	238A/B
Pouteria platiphylla cf	CG	1068?
Pouteria	CG 3654	183A/B
Pouteria	CG 3860	443A/B
Pouteria	CG 4489	1655?
Pouteria	CG 4504	1733A/B
Micropholis		1619A/B
Simaroubaceae		
Picramnia	CG 4373	1522A/B
Simaba “smed”	CG 4156	752A/B
Simaruba	CG 4196	939A/B
Solanaceae		
Cestrum	CG 4300	1398A/B
Solanum	CG 4192	957A/B
Staphyleaceae		
Turpinia occidentalis	CG 4051	599A/B
Tapura	CG 4162	894A/B
Sterculiaceae		
Herrania	CG 4179	856A/B
Theobroma subincanum cf	CG 3914	551A/B
Theobroma speciosum cf	CG 4443	1651A/B
Styracaceae		
Styrax argenteus	CG 3648	60A/B
Theophrastaceae		
Clavija	CG 3905	565A/B
Tiliaceae		
Apeiba membranacea	CG 4047	606A/B
Apeiba aspera	CG 4041	612A/B
Apeiba	CG 3900	524A/B
Mollia gracilis	CG 4209	1014A/B
Ulmaceae		
Celtis schippii Standl.	CG	512A/B
Celtis	CG 4491	1617A/B
Trema micrantha	CG	121A/B
Urticaceae		

Urera	CG 4098	714?
Urera cf	CG 4256	1156
Violaceae		
Gloesospermum ecuadorensis	CG 3892	506A/B
Leonia crassa	CG 4136	791A/B
Leonia	CG	1438A/B
Rinorea apiculata Hekking	CG 4045	607A/B
Rinorea lindeniana (Tul.) Kuntze	CG 4282	1252A/B
Rinorea viridifolia Rusby	CG	1435A/B
Vochysiaceae		
Qualea paraensis	CG 3842	348A/B
Vochysia	CG 4511	1689A/B
Collected PLOT 1-9 and problems PITMAN		
Indet		**H**1708
Indet		1710A/B
Annonaceae-*Guatteria*		1713A/B
Indet		1726A/B
Indet		1735A/B
Indet		1743A/B
Fabaceae		1752B
Fabaceae		26A/B
Indet		161A/B
Moraceae		00A/B
Indet		218A/B
Lauraceae		231A/B
Indet		255A/B
Meliaceae?		262A/B
Fabaceae?		531A/B
Fabaceae/*Inga*		325A/B
Indet		332A/B
Annonaceae		372A/B
Indet		000A/B
Sterculiaceae-*Theobroma*		429A/B
Indet		531A/B
Rubiaceae?		541A/B
Annonaceae cf		564A/B
Theaceae?		1413A/B
Indet		1423A/B
Indet		1468A/B
Indet		1607A/B
Indet		1632A/B
Anacardiaceae/Burseraceae		1667A/B
Euphorbiaceae- *Mabea*		273A/B
Fabaceae?		1759A/B
Indet		273A/B
Indet		8A/B
INdet		1769A/B
Indet		1551A/B
Indet		1755A/B
Indet		298A/B
Indet		438A/B
Indet		1736A/B
Indet		450A/B
Indet		90A/B
Indet		528A/B
Indet		H86A/B
Indet		**PPP**1083
Indet		1273A/B
Indet		1295A/B
Indet		1301A/B
Indet		1329A/B
Indet		1336A/B
Indet		1369A/B
Indet		882A/B