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Ecophysiological Leaf Traits of Cerrado Woody Plants

by

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Abstract

The Cerrado is a biodiversity hotspot undergoing land conversion with need of broad-extent quantification of species and associated ecosystem function. The effects of species on ecosystems can be tested when functional traits are related to ecosystem properties. The patterns of ecophysiologically-linked leaf traits were characterized with the goals of understanding functional diversity of the above ground biomass for ecosystem characterization and discrimination of this status using remote sensing spectroscopy data. Functional groups of plant life form had more consistently different trait status than taxonomy based groups. Specific leaf area and leaf water content were the most significant traits distinguishing functional groups. Spectral indices from a handheld spectrometer were insufficient to capture the variation of these key traits. Future studies integrating remote sensing to understand the effects of Cerrado functional diversity on ecosystem properties would benefit from incorporating life form functional groups, specific leaf area and leaf water content.

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Abbreviations & Definitions

Cerrado *sensu stricto* -open-to-closed treed patches of archetypal Cerrado physiognomy
Cerrado *sensu lato* -inclusive of all physiognomies in Cerrado biome of Brazil
CWM -Community-weighted mean, an estimate of trait diversity
FD -Functional diversity
EP -Ecosystem property
FDvg -Functional divergence
Ephen -Concentration of polyphenol estimate using the Dualex instrument
molCar -molar concentration of carotenoid pigments
molCHLab -molar concentration of chlorophyll A & B pigments
DryWgt -Dry weight of leaves (g)
LeafArea -Area of leaf (cm^2)
%Water -Percentage leaf water content
LeafThick –Estimated thickness of leaf (mm)
CHL = Total Chlorophylls A + B (mol)
Car = Carotenoids (mol)
%H2O = Percentage Leaf Water Conent
SLA = Specific Leaf Area ($m^2\ kg^{-1}$)

Chapter 1 : Introduction

1.1 Biodiversity is all living things

Green plants appear in a remarkable diversity of forms, innovations and specializations whilst all nurtured by the same basic resources. This diversity drives primary production in terrestrial ecosystems and thus is inextricably linked to all levels of food webs. Biodiversity is the variety of species forms, characteristics and genes in totality as well as their patterns of dispersion across the planet. The importance of biodiversity exists at many levels. In recent years, we have begun to regard biodiversity as an essential component in the stability and value of natural systems (Hooper et al. 2005). Biodiversity is also crucial to ecosystem resilience against environmental change and disturbances, such as climate change and fire frequency (Chapin et al. 2000).

One of the strongest patterns visible in nature is increasing biodiversity towards the equator (Willig et al. 2003). But biodiversity is being rapidly depleted. Global extinction rates are magnitudes higher than background and still increasing (Pimm and Raven 2000). We are in the sixth mass extinction event and species replacement takes many generations. Therefore, extinction we cause as humans and their detrimental effects are very long term, if not permanent. Overall habitat loss is the strongest proximal cause of biodiversity loss (Fahrig, 2003). Understanding the causes and patterns of regional distributions of biodiversity is essential to its preservation and appreciation for future generations.

Biodiversity is especially threatened in the tropics. Future land conversion will threaten biodiversity, but the projected rates are complex and still under debate (Brook et al. 2006; Wright and Muller-Landau 2006). Systems for prioritizing biodiversity conservation efforts differ, but the overlap of these are primarily in tropical, developing nations (Brooks 2006).

1.2 The Brazilian Cerrado

Brazil possesses high plant diversity unique to its region (Klink and Machado 2005b) Conservation International has identified two biomes in Brazil, the Cerrado and the Caatinga tropical dry forests, in their list of global "hot spots" of biodiversity & endemism that are at risk to land area loss or degradation (Myers et al, 2000). Of all the 25 hotspots, which contain 44% of all plant species limited geographically, the Cerrado is the 3rd largest in land area and possesses the 9th highest endemic plant diversity (Myers et al, 2000). It is also the largest of all tropical savannahs (Fearnside, 2002) and most diverse (Klink et al, 1993; Myers et al, 2000).

The Cerrado biome is a seasonally dry, tropical treed savannah unique to Brazil, accounting for 20% of the national land area (Felfili et al. 2004) Ratter 1997, 2006, Figure 2), over 60% of the total area has already been disturbed (Myers et al. 2000b; Oliveira and Marquis 2002), with only 2% currently under conservation protection (Furley 1999; Scariot et al. 2005). Cerrado vegetations are characterized by aluminum rich soils, adapted to disturbance by fire, have alternated with tropical forests boundaries with increasing dryness in recent evolutionary history. The high diversity of the Cerrado is due to its environmental heterogeneity, broad extent and proximity to many other tropical biomes (Silva et al. 2006). The Cerrado biome is subject to ongoing habitat loss and fragmentation (Oliveira and Marquis 2002; Klink and Machado 2005b; Silva et al. 2006; Durigan et al. 2007) which decrease ecosystem function and persistence (Westoby and Wright 2006) and has a detrimental effect on market-valued services ecosystems provide. Habitat loss more clearly and negatively increases biodiversity loss relative to fragmentation (Fahrig 2003).

The name Cerrado is from the Portuguese word “closed” and applies to the characteristic vegetation subtype, or to the entire ecosystem and its contained mosaic of physiognomies. Cerrado *sensu lato* refers to all the vegetation subtypes and the region as a whole, whereas Cerrado *sensu stricto* is the archetypical physiognomy: an understory of shrubs and grass, covered by patchy to moderate canopy closure of contorted trees & lianas up to 14m in height (Oliveira-Filho and Ratter 2002). The gradient of vegetation closure varies (Figure 1) from a completely closed canopy with restricted understory (Cerradão) to grassland with shrubs (*campo sujo*) or without (*campo limpo*).

The richness of endemics is a strength of the Cerrado, as well as being why it is a concern. Plant biodiversity is a potential source of bioprospecting, and the Cerrado already suggests it is an untapped resource in this regard. There is an active culture of Brazilians making economic use of herbal traditions of endemic Cerrado species (deGois Auino and de Oliveira, 2006). The Brazilian berries Guaraná (*Paullinia cupana*) and Açai (*Euterpe oleracea*) are ubiquitous within the country and becoming popular abroad. Within Brazil there is an abundance of traditional medicinal species in need of further development (Rodrigues and Carlini 2005). The gain of genetic diversity from outcrossing crops to native varieties adapted to xeric conditions can increase crop vigor and tolerance (for example *Manihot* sp. as referenced in (Klink and Machado 2005b), and the ongoing economic value of herbal medicines worldwide (Rates 2001) are examples how the Cerrado's high endemicity of plant diversity is a financial asset.

The Cerrado is not greatly valued in its natural state, traditionally regarded as less productive, and is even culturally regarded as an inferior ecosystem, less intrinsically valuable to conserve (Cavalcanti et al. 2002; Oliveira-Filho and Ratter 2002). This disregard has been institutionalized by its prior omission from designation as a national heritage area; a status other vegetated areas of Brazil have, which legislates required area for conservation (Ratter et al. 2006b). This ecosystem is one of the most diverse in the world but faces pressures on many levels.

1.3 Degradation and deforestation of the Brazilian Cerrado.

The Cerrado biome is subject to ongoing habitat loss and fragmentation (Oliveira and Marquis 2002; Silva et al. 2006; Durigan et al. 2007). Deforestation rates within the Cerrado are estimated to be higher than those in the Amazon (Cavalcanti and Joly 2002; Ratter et al. 2006b). Cerrados are under threat from development for agricultural intensification (Fearnside, 2002), which affects land values such that conservation is an economic disadvantage (Lourival et al. 2008). The high rate of deforestation is primarily due to agriculture such as ranching and cropping (Myers et al. 2000b; Klink and Machado 2005b; Ratter et al. 2006b). Areas of high diversity in the Cerrado frequently overlap with areas of high agricultural value (Rangel et al. 2007), reinforcing the threat of land use change.

The major challenge for the future of the Cerrado is balancing the socioeconomic benefits of continuing land use changes, including agricultural development, and the necessity of conservation (Scariot et al. 2005). Development of soybean cultivars adapted to Cerrado climate and soil conditions arrived at the same time as a government-subsidized development that increased the conversion rates to agriculture, all to feed an export market with incommensurate growth to local employment (Fearnside 2002). Conservation is hindered when local populations are under economic pressure and gains by exploitation outweigh the perceived costs of land use.

1.4 Biodiversity assessment and loss in the Cerrado

The rates at which biodiversity is being degraded within the Cerrado ecosystem as a result of habitat loss is not well known. The effects of habitat loss and fragmentation on biodiversity loss and ecosystem function in the Cerrado need more detailed investigation (Jepson 2005). Current estimates of biodiversity loss are based upon habitat loss predictions (Myers et al, 2000), and this is in dire need of validation (Jepson, 2005). The rates of secondary regeneration is high (Jepson 2005), which is attributed to fire adaptation. However, regeneration in dry forests is not equivalent in the presence of fire relative to its absence (Vieira and Scariot 2006) and the total effects upon biodiversity between these disturbance regimes is unknown in the Cerrado. Without explicitly understanding the distributions of biodiversity within the Cerrado, estimation and adequate preservation is ineffectual.

Biodiversity assessment in the Cerrado has been largely focused on vertebrate distributions (Diniz-Filho et al. 2008; F. Diniz-Filho et al. 2008). To date, ground based surveys of Cerrado vegetation diversity are limited but demonstrate high beta diversity (Felfili and Da Silva Jr 1993; Ribeiro and Tabarelli 2002; Bridgewater et al. 2004; Felfili et al. 2004; Ratter et al. 2006b). For example, Da Silva and Bates (2002) used bird distributions to demonstrate the variability of endemics across the Cerrado and the lack of overlap with existing conservation areas. These studies point to a key issue of biodiversity conservation in the Cerrado is to describe patterns of endemism and diversity to identify areas of focus.

There is a lack of research in detailed investigation of vegetation biodiversity distributions across this biome. In taxonomically diverse, yet structurally graduated, vegetation such as the Cerrado *sensu lato*, it is possible to approach biodiversity assessment through stratification into the various physiognomic subtypes, and investigate the relationships within. The accuracy of plant richness distribution models can be increased by the use of functional groups (Steinmann et al. 2009). To assess the loss of biodiversity in secondary systems, a benchmark of natural vegetation biodiversity patterns with observable predictors is necessary. Methods that allow extensive quantification and description of undisturbed Cerrado biodiversity patterns within vegetation types will help to develop prediction and quantification across the landscape. Using hyperspectral data, discrimination of functional groups is possible in tropical dry environments when accounting for environmental gradients (Alvarez-Ahorve et al. 2008) which vary spectral response as a result of ecophysiologically linked traits (Castro-Esau et al. 2006).

The Cerrado is a large threatened ecosystem that is valuable economically, but also a key region in the progress of global biodiversity conservation. The sensitivity to endemic plant loss makes it a priority, but the extent, grain and alpha/beta diversities of vegetation distributions in this region are not well described. Remote sensing and GIS modelling provides a rapid and relatively cheap way to assess large areas.

1.5 Remote sensing of plant diversity and Cerrado vegetation

The study of biodiversity is arguably as old as biology itself. The latitudinal gradient of biodiversity is a well-established global pattern (Willig et al. 2003; Mittelbach et al. 2007) and regional prediction using remote sensing methods is possible (Gaston 2000). Biodiversity mapping & modelling using remote sensing data is a field rapidly improving (Gillespie et al. 2008) but species detection is largely scale dependent (Nagendra 2001). At forest canopy level, species identification has been achieved with some success using high-resolution hyperspectral data (Clark et al. 2005b; Foody et al. 2005; Zhang et al. 2006a) and indirect prediction of vegetation diversity using multispectral band combinations (Turner et al. 2003). Vegetation diversity is a subpixel phenomenon at the standard 30m satellite resolution, and the variations in Cerrado physiognomies are an obstacle to their classification (Filippi et al. 2009). To address classification of Cerrado ecosystems at the scale of diversity, we must look at the ecological drivers of spectral diversities and distributions.

Plant species distributions are closely linked with the environmental conditions which they can tolerate because the ecophysiological tolerance of tropical species are narrow (Janzen 1967). This is well demonstrated in the Cerrado ecosystem where vegetation subtypes occur predictably based upon proximity to water bodies or elevation (Da Silva and Bates 2002). Surveys of broad spatial extent and detail of biodiversity patterns in the Cerrado are needed for conservation planning (Jepson 2005). Total richness of a site can only be obtained by exhaustive taxonomic surveys and identifications of unknowns. In speciose tropical regions this requires fieldwork by experts in local species identification. Remote sensing techniques have been investigated as methods for predicting species richness quickly and across large areas where diversity is linked to satellite observable correlates to field data (Foody and Cutler 2006). Spectral vegetation indices such as a normalized difference vegetation index (NDVI; Tucker, 1979), photochemical reflectance index (Gamon et al. 1997; Sims and Gamon 2002) have been used to describe variation within satellite-derived vegetation cover e.g. (Gamon et al. 2005). Variation of spectral indices can moderately predict species richness in known assemblages (Gould 2000). The inclusion of landscape layers, such as topography and physiognomic classifications, increase the accuracy of these models (Smith et al. 2003). Landscape level mapping of biodiversity patterns in this manner requires an understanding of diversity across environmental conditions and the use of predictive modelling to create remotely-sensed surrogates of field data (Ferrier 2002).

The use of remote sensing has been used to classify ecotones, continuous species patches, or as a proxy to biodiversity. A primary application for remote sensing in landscape ecology has been to separate thematic vegetation classes (Kerr and Ostrovsky 2003). Classified vegetation types converge to plant species assemblages that share environmental preferences, known as ecological communities (Kerr and Ostrovsky 2003; Hernandez-Stefanoni and Ponce-Hernandez 2004). The Cerrado exhibits a high diversity of physiognomic forms (Oliveira-Filho and Ratter 2002), which has made multispectral image (Ferreira et al. 2004) and aerial photo (De Castro 2005b) classification of the varying subtypes in the landscape difficult. Within the Cerrado *sensu stricto* difficulties arise in classification due to a gradient of canopy closure (Ferreira and Huete 2004). Classification of the *sensu stricto* gradient is ameliorated when separated from all other classes by preliminary binary classification (Ferreira et al. 2007b) and mixed-class identity classifications (Stuart et al. 2006). Maximum likelihood classifiers have performed inadequately separating graduated physiognomic subtypes in tropical savannas (Stuart et al. 2006) and the varied nature of plant communities is better addressed through fuzzy classifications (Biondi et al. 2004). Despite the overlapping variation, vegetation subtypes are easily distinguishable by field workers (Oliveira-Filho and Ratter 2002). Classification of biodiversity within the Cerrado *sensu stricto* vegetation may be improved by investigating the variation of plant signatures within vegetation subtypes are relate that variation with remotely sensed imagery.

Description of the Cerrado ecosystem & its physiognomies using satellite imagery to date is limited (Ferreira and Huete 2004; Ferreira et al. 2007a; Brannstrom et al. 2008; Filippi et al. 2009) and is thus far limited to four classes of physiognomy (Filippi et al. 2009). The gradients of Cerrado vegetation make these classes a bit abstract and generalize the variation within patches, which may have important consequences on richness or ecosystem function. More detailed physiognomic investigation is possible with airborne imagery, but there is a trade-off between accuracy of prediction and the number of classes (De Castro 2005b).

Individual species variation can be mapped from imagery given sufficient spectral and spatial variation (Nagendra 2001). Although plants have very similar signals, with ample spectral resolution they can be distinguished from one another (Price 1994) based upon species-level differences (Castro-Esau et al. 2006), or functional differences (Sims and Gamon 2003). There is a trade off between spectral and spatial resolution for satellite & aerial data. Satellite data is preferred for large scale applications as it is less expensive, and sometimes freely available for many years prior to present day. With all landscape imagery, there are limitations of what is sensed in a pixel. Light is reflected, absorbed and transmitted, and a pixel is a generalized result of all interactions prior to the sensor. In a complex canopy of leaves, the photons detected by the sensor have travelled a multitude of paths representing all the light interactions in that path. Each pixel on a remotely sensed image is thus a mixture of many things, and is affected by the physical properties interacting with light at the atomic, chemical, cellular, branch and canopy levels. Therefore to gain an understanding of biodiversity, a literal ground-up methodology is ideal, piecing together variations within the species present in a pixel to understand the interplay of spectral and taxonomic differences.

1.6 Leaf spectroscopy and functional ecology

Spectroscopy of leaves can describe photosynthetic pigment content (Gates et al. 1965), polyphenol content (Goulas et al. 2004), which also can be estimated from remotely sensed imagery (Kalacska et al. 2007b). The spectral responses of plants have been linked to functional traits. Functional traits are characteristics that have adaptive affects on individual plants. The most imformative traits are those linked to ecological currencies (e.g. biomass/growth) (McGill et al. 2006; Westoby and Wright 2006). Trade-offs in plant structure (Reich et al. 2003) and leaf ecophysiology (Shipley et al. 2006b) have lead to the global diversity of plant forms that specialize their exploitation of shared resources (Wright et al. 2004; Shipley et al. 2006a). The extent and variability of traits relate to niche-dispersion between species (Cornwell et al. 2006) and, in a distinct region, represent the functional diversity of that system (Diaz and Cabido 2001; Lavorel and Garnier 2002).

Physiognomic and spectrally distinct groups can be ordinated using trait information, a common method in functional ecology (Cornelissen et al. 2003). Functional ecology, using the traits and structure present in a system to describes its properties, has become an alternative paradigm to taxonomic description of communities to understand their diverse interactions. In tropical systems, where the species number prohibits the possibility of investigating all pairwise interactions, it is incredibly valuable to reduce the complexity of a system while retaining an accurate description of its behaviour. Functional ecology offers methods to characterize tropical ecosystem diversity in a manner more practical to assess ecosystem stability and function. Additionally, if plant species spectral responses are controlled more by their functional traits or groupings thereof, then remote sensing is a natural extension of these methods to operate at a landscape scale.

The use of leaf traits that are spectrally linked is a fusion of functional ecology and remote sensing that has not been widely explored. Understanding of plant functional diversity is key to the processes that govern all trophic levels at a site (Westoby and Wright 2006). Thus, a trait-based remote sensing approach offers potential insight to assess ecosystem function & diversity across a landscape.

1.7 Thesis objectives

This thesis attempts to address two questions within a larger framework of research:

1. Are the functional groups described by niche and phenotype distinguishable by ecophysiological traits? Which grouping method separates them best?
2. Are the functional groups described by niche and phenotype distinguishable by spectral response? Which grouping method separates them best?
3. Can the functional diversity of Cerrado regions be estimated using these distinguishable spectral groupings?

The long-term goal of this study is to continue development of the methodology for remote sensing of plant biodiversity. Comparisons of leaf level data will test whether functional groupings drive spectral characteristics. Determining functional group spectral identities are integral to using remote sensing methods to rapidly assess Cerrado vegetation at finer scales than physiognomic subtypes.

1.8 Significance

This study will increase the knowledge in tropical dry ecosystems, in particular the Cerrado which is a hotspot and is understudied. Remote sensing studies in the Cerrado are few and there is no wide scale quantification of biodiversity patterns. Since biodiversity is linked to so many crucial points in a healthy ecosystem, developing methods for biodiversity assessment will aid in focusing conservation efforts. In addition to the specific area of Cerrado plant diversity, general application of our findings could aid the development of remote sensing of vegetation. This study aims to find predictors that allow distinguishing between plant life forms or functional groups. Trends will be applicable not only to tropical dry forest species, but also help to develop the methodology which is trying to find patterns that aid species recognition using remotely sensed data.

Tropical dry ecosystems are under-represented in scientific investigations (Sanchez-Azofeifa et al. 2005) yet make up 47% of the land area in these hotspots (Myers, 2000). Compared to tropical rainforests, tropical dry ecosystems are essentially avoided in their scientific investigation (Sanchez-Azofeifa et al. 2005). Yet these regions are intrinsically important, forming much of the arable land in the tropics. The Cerrado is a large, threatened ecosystem that is valuable and developing but is also a hotspot of diversity.

This study will increase our knowledge of plant biodiversity in the Cerrado. Understanding biodiversity patterns allows focusing of conservation efforts to reduce our impact on its loss. Since biodiversity is linked to ecosystem function (Garnier et al. 2004b; Hooper et al. 2005; Petchey and Gaston 2006b) and valuable ecosystem services (Diaz and Cabido 2001) that are linked to long-term land productivity (Hooper et al. 2005), there are important economic benefits to effective biodiversity conservation. This study will also increase our knowledge of how plant functional groups relate to spectral signatures, continuing to bridge the gap between the strength of remote sensing quantifying large areas, and the ecological theory that describes ecosystem processes and distributions.

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1.10 Figures

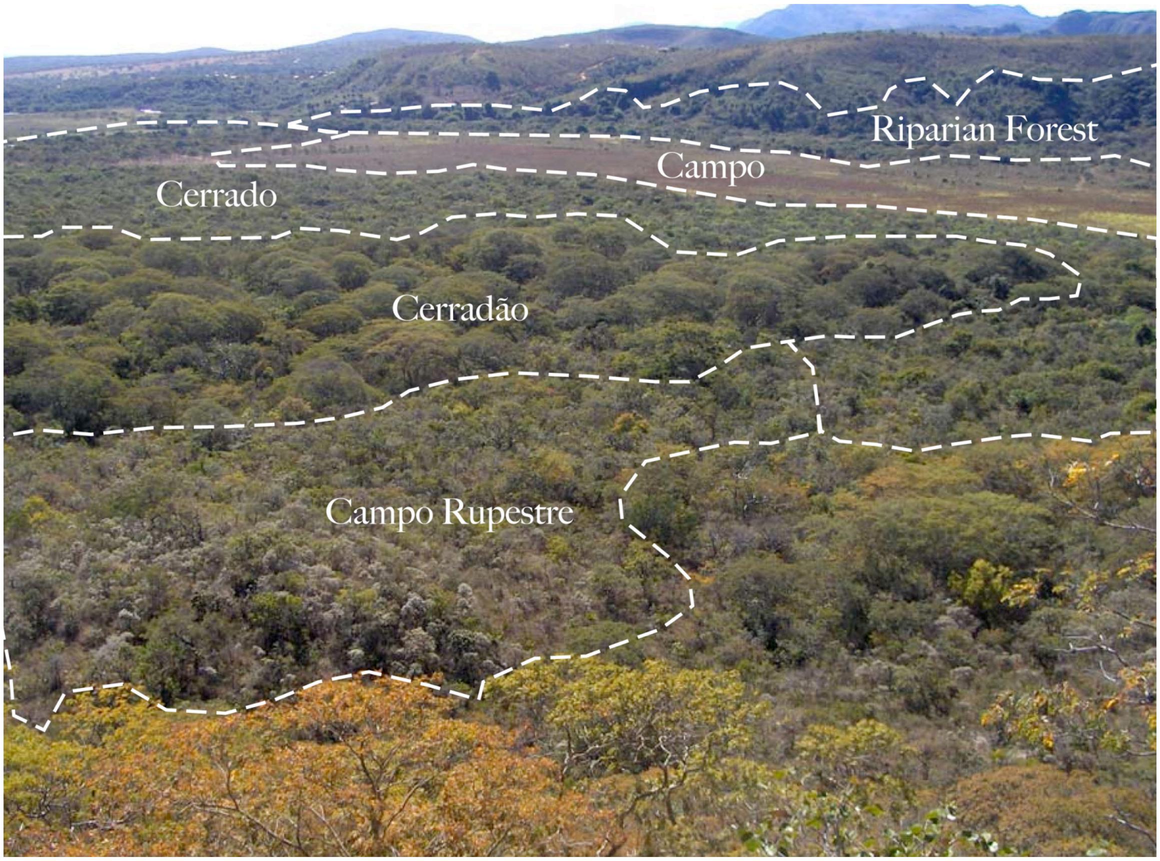

Figure 1.1: Physiognomic types of the Cerrado *sensu lato* ecosystem in the study area of Serra do Cipò, NP. The entire visible landscape together is Cerrado *sensu lato*. The vegetation subtypes are texturally distinguishable and outlined. Campo rupestre is on the rocky hill in the foreground. The canopy trees beyond that are Cerradão, followed by the shorter sparse canopy of Cerrado *sensu stricto* and a quick transition into the grassland Campos beyond that.

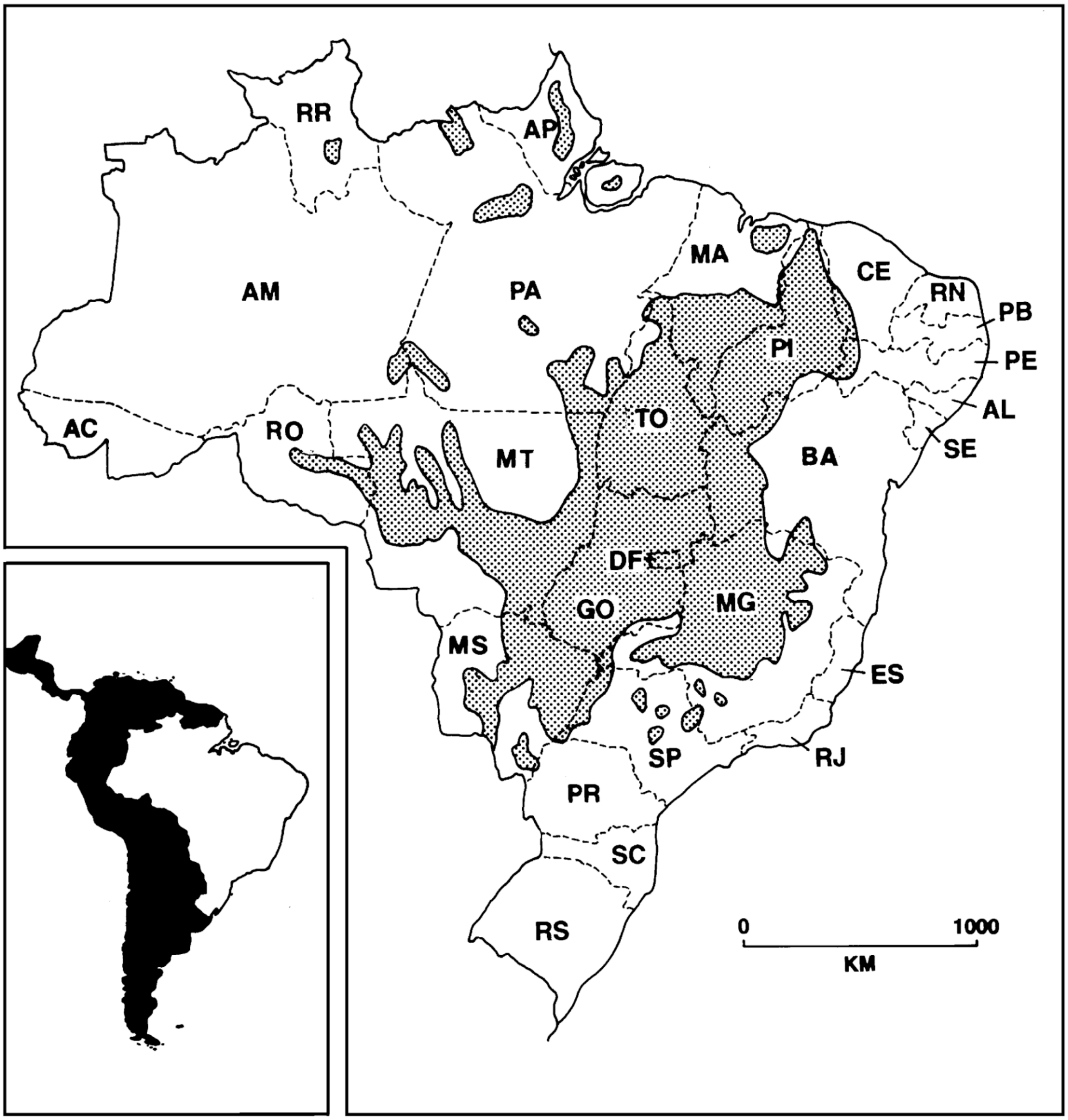

Figure 1.2 Distribution of Cerrado ecosystems, from Ratter 1997.

Chapter 2: Leaf functional trait variation and hyperspectral reflectance of woody Cerrado Species.

2.1 Introduction

Conservation and management of tropical biodiversity is dependent on the availability of the appropriate data (e.g. species distribution maps) or tools (e.g. predictive models) to provide contextual information on the distribution of key species for the prioritization of conservation effort (Groves et al. 2002). The development of these planning tools is ideally utilizing data from ecological field surveys, which are then linked to remote sensing surrogates (Ferrier 2002) or to other geographic information via Geographic Information Systems (GIS) (Foody 2008). The integration of field surveys and their extrapolation to species distribution maps with remote sensing application allows the consideration of linkages between ground observations and a given pixel reflectance in the satellite imagery. Pixel reflectance is a combination of all light interactions among the different components of the ecosystem (e.g. canopies, tree gaps, understory, etc.). Thus, we hypothesize that the development of methods aiding remote sensing discrimination of plant species reflectance and their interrelation with biodiversity will aid in conservation efforts.

A description of biodiversity patterns in the Cerrado biome are needed for conservation planning (Jepson 2005). The Cerrado is the largest (Fearnside 2002) and most diverse tropical savannah (Myers et al. 2000b; Klink and Machado 2005b) which has been identified as a global biodiversity hotspot at risk (Myers et al. 2000b). Not only is it diverse, but the Cerrado spans 20% of Brazil (Ratter et al. 1997; Felfili et al. 2004; Ratter et al. 2006b), with over 60% of the total area already disturbed (Myers et al. 2000b; Oliveira and Marquis 2002). Only 2% of this large area is under conservation protection (Furley 1999; Scariot et al. 2005). The Cerrado biome is undergoing continued habitat loss and fragmentation (Oliveira and Marquis 2002; Klink and Machado 2005b; Silva et al. 2006; Durigan et al. 2007). Specific pressures are: agricultural intensification (Fearnside 2002; Rangel et al. 2007)), socioeconomic challenges in land valuation trade-offs between conservation and development (Scariot et al. 2005; Lourival et al. 2008), cultural devaluation of the intrinsic state of the biome (Cavalcanti et al. 2002; Oliveira-Filho and Ratter 2002) and legislative challenges for conservation requirements lower than other biome in the country (Ratter et al. 2006a). Deforestation rates within the Cerrado are estimated to be higher than those in the Amazon (Cavalcanti and Joly 2002; Ratter et al. 2006a).

In the context of the Cerrado biome, landscape reflectance is primarily driven by soil exposure, vegetation density and vegetation structure (Filippi et al. 2009). Variation and gradation in the physiognomic structures within the Cerrado are an obstacle to their classification (Filippi et al. 2009). Species overlap between physiogonomies is a way of describing the patterns inherent to the Cerrado vegetation subtypes. Currently, ground based surveys of vegetation biodiversity are limited to patchy descriptions of sites, but demonstrate high beta diversity (Felfili and Da Silva Jr 1993; Ribeiro and Tabarelli 2002; Bridgewater et al. 2004; Felfili et al. 2004; Ratter et al. 2006b). Detailed descriptions of biodiversity patterns at broad extent are an important step in conserving this biome at risk (Jepson 2005).

Since vegetation is the largest biomass component of an ecosystem and forms a substantial portion of the reflectance, the first step towards estimating plant diversity in Cerrado communities of Brazil using remote sensing is to relate plant diversity with spectrally distinguishable groups. Remotely sensed information can be used to study richness through direct species detection or proxies to environmental parameters (Turner et al. 2003). Species discrimination requires high spatial or spectral resolution, and sometimes both (Cochrane 2000). The spectral signatures of plants are largely similar in the 400 – 2500 nm range (Allen, 1968), with their primary defining features controlled by photosynthetic pigments (Tucker and Garrat 1977), water absorption features (Tucker 1980) and the relationship between a red absorption feature and a NIR plateau (Tucker 1979). With unlimited spectral resolution species discrimination may not be possible in all cases, as some species share sufficient similarity in spectral responses to make separating by absorption features alone improbable (Price 1994).

The measurement of lights interaction with the internal structure of the leaf, pigments, water and cellular matrix is known as spectroscopy. Spectroscopy was used to detect plant pigments for photosynthesis research (Willstätter and Stoll 1913; Mackinney 1941; Gates et al. 1965) long before optics went into space for satellite remote sensing to exist. Leaf level spectroscopy data and statistical techniques can now reliably discriminate plant species

(Cochrane 2000; Castro-Esau et al. 2004; Clark et al. 2005b; Castro-Esau et al. 2006; Vaiphasa 2006; Zhang et al. 2006b; Kalacska et al. 2007a; Asner and Martin 2008c; Rivard 2008).

No leaf level spectroscopy study has yet been published in the primary literature for the Brazilian Cerrado and there is a lack of literature on the spectral properties of tropical trees and canopies in general. An investigation of the relationship of chemical and spectral traits in a Australian rainforest (Asner et al. 2009) parallels the context and environmental conditions of this study. In the neighbouring Caatinga tropical dry forest ecosystem phenologic leaf changes were described (Roberts et al. 1998). The changes described at that time are consistent with recent phenology studies of the Cerrado using satellite imagery (Ferreira et al. 2003). Furthermore, emerging work aimed to provide information on species differences as function of life form in tropical forests have concluded that significant differences can be observed among lianas and trees for dry forests but not rainforests (Castro-Esau et al. 2004; Castro-Esau et al. 2006; Kalacska et al. 2007a; Arturo Sanchez-Azofeifa et al. 2009).

Although significant work has been done into the spectral and leaf trait separation of different life forms (Gamon and Surfus 1999; Sims and Gamon 2003; Castro 2006; Kalacska et al. 2007a; Alvarez-Ahorve et al. 2008; Arturo Sanchez-Azofeifa et al. 2009), the integration of these two elements in relation to a central tenet of functional ecology has not been conducted. Functional ecology is defined here as the study of ecosystem properties which result from the combined diversity of traits that a given set of species possesses. Functional ecology is an alternative method to define a community in a different manner than taxonomically, and offers the possibility for mechanistic predictions of species interactions rather than pair-wise species comparisons. Traits used in functional ecology studies are best when linked to primary growth requirements (Cornelissen et al. 2003), and roughly correspond to the physiognomic, or structural diversity of plant communities and the diversity of niches occupied (McGill et al. 2006; Ackerly and Cornwell 2007; Cornwell and Ackerly 2009). Traits linked to resource gain and use are directly related to a plant species' niche, and therefore if remote sensing can be used to investigate niches and functional traits it could be extended to understand community composition and function at larger scales than possible with field surveys. The texture and content of differing physiognomies are primary factors in distinguishing Cerrado vegetation classes (Filippi et al. 2009), hence the relative contribution of life forms to the satellite imagery should not pass unnoticed.

Supplementary to spectral characteristics, there is a complex series of trade-offs in leaf physiology (Wright et al. 2004). All of these traits are important to a plant's life history strategy and many, such as pigment concentration, leaf water content, are spectrally detectable. The similarities in trait allocations is consistent within some tropical plant life forms (Santiago and Wright 2007). The variability and interaction of leaf metabolic economics with spectral reflectance shows great promise for remote sensing studies of vegetation dynamics and diversity (Asner and Martin 2008a; Asner and Martin 2008c) but the generality and meaning of trait variabilities for species spectral discrimination remains to be understood.

Functional trait groupings contrasted to distinguishable structural growth forms, offer spectrally detectable and ecologically meaningful information that has potential for biodiversity mapping use. For example, using climatic maps, a digital elevation model and vegetation classifications patterns of functional group diversity showed increased accuracy of tree richness prediction (Steinmann et al. 2009). This study did not make use of additional remote sensing information or diversity estimates from satellite imagery. Studies that make use of functional groups and remotely sensed imagery are rare (a review of related topics can be found in (Alvarez-Ahorve et al. 2008). The lack of such fusion in the literature presents the opportunity for this study to test if functional groups determined from classifying leaf traits and reflectance is beneficial for plant biodiversity mapping. To aid in this process, leaf level hyperspectral plant reflectance and associated ecophysiological data were investigated in a Cerrado region of Minas Gerais, Brazil. The importance of this study is to contribute to the ongoing research of species discrimination using hyperspectral data as well as to advance our knowledge of the relationships between spectral reflectance and plant functional measures, specifically in the Cerrado ecosystem and tropical dry environments.

2.1.2 Objectives

Within this outlined context, this study has two specific objectives: 1) to evaluate leaf level ecophysiological traits to establish a classification of functional groups for the woody species sampled from the Cerrado *sensu stricto* of Serra do Cipó National Park, in south-eastern Brazil, to determine the primary factors that affect leaf separation in the classification model; and 2) Relate these traits to remote sensing data using hyperspectral leaf spectroscopy.

2.2 Methods

2.2.1 Site Description

This study was conducted within the Cerrado vegetation of Serra do Cipó National Park in Minas Gerais, Brazil (19.36°W,43.60°S; Figure 2.2.1). The Cerrado *sensu lato* is a broad term encompassing the biome's many vegetation physiognomies, whereas the Cerrado *sensu stricto* is a term specific to the treed savannah physiognomy. The Cerrado *sensu stricto* is a tropical dry ecosystem under the Holdridge classification system (Holdridge 1967) characterized by a gradient of vegetation density; ranging from shrubby savannah to tropical dry forest. It is a very speciose ecosystem, with upwards of 1500 woody plant species (Ratter et al. 2003) and estimates of 10 000 vascular plant species (Diaz, 1992; Ratter, 1997). This ecosystem contains primarily dry-deciduous plants, with leaf greening taking place at the end of the winter months, August-October (Ratana et al. 2005). The primary distribution of woody Cerrado *sensu stricto* vegetation in the Serra do Cipó National park is within a concave topographic gradient along the river Cipó (Figure 2.2.2). The conservation status of the Park has prevented disturbances from cattle grazing for more than 30 years, and fire (which is a common agricultural practice in the region) for more than 10 years (Dubois-Collet, personal communication). The region was chosen to be representative of a natural condition of the Cerrado landscape.

2.2.2 Sample Collection

All plants were sampled during two dry seasons, June-July of 2007 and June-August of 2008. Dry season satellite imagery provides better classification separation of tropical dry forest regions (Portillo et al. 2010) and Cerrado (Liesenberg et al. 2007). Plants were sampled at pseudorandom points stratified by vegetation type (n=21), limited to Cerrado *sensu stricto*, Cerradão, and Campo Rupestre (Figure 1). Although random points were generated in a GIS for polygons of different physiognomies, the aims of this study to characterize Cerrado vegetation prevented some of the randomized points from being sampled. Limited accessibility, small patch size and lack of *sensu stricto* species overlap prevented a truly random site selection. Cerrado *sensu stricto* sites were preferentially selected (n=12) relative to other physiognomies.

Individuals of woody plants were collected from within 30 meter diameter patch of contiguous physiognomy (Figure 2.2.4).

Prior knowledge of the phytosociologies of the area was unknown, therefore plant individuals were selected for sampling based upon those most abundantly and most frequently encountered species across the landscape. Cornelissen et al (2003) posits that sampling all plant species in an area that comprise 80% of the total community biomass are sufficient for assessing that community's functional diversity. Our study restricted itself to assessing the community most relevant to remote sensing in Cerrado; woody plants and their aboveground components. Plants that were more abundant across all sites and/or comprised substantial percentages of the canopy were preferentially sampled. In this manner, trees, large shrubs and sprawling lianas were sampled first at sites, comprising the majority of sampling effort and relative aboveground biomass, and less sampling effort was expended on species that comprised less of the canopy cover and therefore pixel composition. Initial sampling followed the above methods to get the most dominant species. Once the most dominant species for all sites had all been collected, additional sampling effort was aimed to increase the collection overlap of species existing at multiple sites. Logistics and time constraints made equal measures in all tests for every individual prohibitive. Completeness across all tests was prioritized for the most prevalent species.

Grasses, although an abundant portion of the Cerrado vegetation (Batalha and Martins 2002; Furley 2006; Gardner 2006), were not sampled because they are almost completely senescent or dormant during the dry season (Filgueiras et al. 2002). The separation of tree and grasslands are already strongly established in existing classifications of Cerrado regions (De Castro 2005a; Ratana et al. 2005; Silva et al. 2006; Ferreira et al. 2007b). For each plant species, we collected a herbarium sample of branches, leaves, inflorescences (whenever possible), and digital photos were collected for species identification. Expert identification was performed by personnel at the at the Universidade Federal de Minas Gerais (UFMG, Belo Horizonte, Minas Gerais, Brazil).

Between 10 and 30 sunlit, healthy leaves were taken from each individual and put into bags to prevent desiccation, which affects spectral response (Foley et al. 2006). Spectroscopy and leaf traits studies in the neighbouring Caatinga ecosystem found that the magnitude of effects between leaf age and epiphyll colonization, were greater than interspecies differences

(Roberts et al. 1998). To control for possible physiological differences of variation in the leaf environment and history, only healthy leaves were collected. If a leaf was substantially damaged, consumed by herbivores or subject to galls or disease, it was not selected for measurement. Shade leaves were excluded on the basis that it alters the light capture environment of pigments (Lee and Kaufman 1986)Lee et al. 1990; Lee and Graham 1986) and are not representative of canopy reflectance (Terashima and Hikosaka 1995). The ability to retain leaf freshness also limited the transportation distance to maintain confidence in sample quality. Samples that had visible tissue degradation from transportation prior to measurement were recollected from closer sites to decrease time of decay. To control for spectral variance outside of a healthy state, leaves that showed any indication of senescence, herbivory or parasitism were not sampled for any test.

Following collection, leaves were assessed spectrally in the VNIR following the protocols of Castro-Esau et al (2006). In addition to those protocols, an IR normalized estimate of UV reflectance was measured to predict polyphenol content on each leaf. Leaves were also subjected to different physical and chemical measures for photosynthetic pigment concentrations, specific leaf area (SLA) and water content. Spectral samples were available for all leaves that underwent other leaf trait analyses. Some trait analyses were destructive and prevented simultaneous measurement of all traits (e.g. pigment coring preventing water content).

2.2.3 Spectral Measures

2.2.3.1 UNISPEC Reflectance

Leaf spectra were measured using a portable spectrometer (UNISPEC SC, Analytical Spectral Devices, Innsmouth, MA, U.S.A.) using a leaf clip with a 2mm aperture. All spectra were converted to bidirectional reflectance by dividing the data by the radiance from a barium sulphate standard and the internal halogen light source. The following sections detail methods in their specifics in addition to the outlined protocols of Castro-Esau et al (2006).

Three UNISPEC readings per leaf measured areolar space proximal to the medial axis while avoiding innervations, damaged tissue or areas where the natural leaf coating had been removed. Spectral measures were taken from the tip, in the middle, and at the base of the leaf, and averaged to account for internal variation. On highly serial compound leaves, such as the Fabaceae, readings were done on the small leaf units near the end of the series, the middle, and the base. As a result of PCA investigation and expert experience, instrumentation noise at the extremes of the spectrometer were deleted, using spectral bands only between 450 and 1050nm. A spectral profile for each individual were created by averaging all measures.

2.2.3.2 Polyphenol Estimation

A UV-excitable chlorophyll absorbance index was measured using a Dualex-FL 3.3 (Force-A, 91405 Orsay Cedex, France). UV absorbance is determined using a ration of chlorophyll fluorescence between the red and UV wavelengths. Dualex measures can be used as a linear estimate of the polyphenol contents, photoprotection (Goulas et al. 2004). Dualex readings that are a sum of adaxial and abaxial measures (Equation 1) were used as an index for polyphenol content, as established by Meyer et al (2006). Dualex sums were found highly correlated to polyphenol contents in beech r=0.99 (Goulas et al. 2004) and wheat r=0.81 (Cartelat et al. 2005) leaves.

Equation 1 $$Ephen = (adaxial + abaxial\ \ Dualex\ measurements)/\varepsilon$$

Where **ε** = molar extinction coefficient 20 micro mol^{-1} cm^{2} (20mM^{-1} cm^{-1}) at 375nm. Expressed in equivalents of quercetin (aglycone).

2.2.4 Laboratory Measurements on Leaves

2.2.4.1 Pigment extraction

Photosynthetic pigments were assessed using extraction and subsequent in vivo spectrophotometric absorption analysis following methods described Holden as revised by Wellburn (1994). Leaf sections were cored from healthy tissue closest to the center of each half as possible, avoiding major veins or innervation. Leaf sections were kept airtight at -20°C freezer in the field, then moved for longer-term storage (up to 1 month) in a -70°C freezer prior to extraction. Due to the high sclerophyly of many leaves and to increase solvent emulsion, sections were thoroughly ground then immersed in 10 mL 80% acetone and distilled water. Solutions were kept cold and dark for 24 hours undergoing extraction and then were filtered, centrifuged (5000 RPMs for 8 minutes) and spectroscopically assessed for absorbance using a CIRRUS 80MB SPECTRO-PHOTOMETER (Femto Industria e Comercio de Instrumentos Ltda, São Paulo, Brazil) at 470, 645 & 663nm wavelengths. Measurements were calibrated with a reference absorbance spectra of 80% acetone. Calculations of chlorophyll A, chlorophyll B and carotenoid concentration (mg/g) follow those presented in Holden (1965) as revised and optimized by Wellburn (1994; Table 4) to correct for carotenoid absorbtive effects in chlorophyll feature regions (Equations 2, 3, 4). Pigment concentrations were then converted to molar units (μmol m^{-2}) using the respective pigment molar masses and the consistent circular area from the leaf cores (Equation 5).

Equation 2 $$CHLA = 12.21 \bullet A663 - 2.81 \bullet A646$$

Equation 3 $$CHLB = 20.13 \bullet A646 - 5.03663$$

Equation 4 $$CAR = (1000 \bullet A470 - 3.27 \bullet CHLA - 104 \bullet CHLB) / 198$$

Where $\mathbf{CHL_A}$ = Concentration (μg ml^{-1}) of Chlorophyll A in 80% acetone solution (units), $\mathbf{CHL_B}$ = Concentration (μg ml^{-1}) of Chlorophyll B in 80% acetone solution, **CAR** = concentration of carotenoids in 80% acetone solution standardized for the absorbance of chlorophylls at 470nm. $\mathbf{A_\lambda}$ = the wavelength (nm) of absorbance measurement.

Equation 5 $$micromols = [Pigment] \bullet (Molar\ Mass)\ P/100 \bullet (9 / \pi)$$

Where [Pigment] is the pigment concentrations produced from equations 3-5, and molar mass is specific to the chlorophyll a, b or carotenoid.

Specific leaf area (SLA) was assessed by scanning fresh leaves in a desktop home scanner and calculating the area digitally. Due to the thickness of leaves and irregular shapes, Adobe Photoshop CS3 was found to be more accurate than alternative leaf area computer programs by avoiding area calculations that included shadows caused by leaf thickness. For large leaves, differences due to shadowing effects contributed variation up to 5% of leaf area (data not shown).

Multiple leaves were weighed wet, and then oven-dried at 60°C until there was no change of weight loss from the previous test. The resultant difference measured water content, and the remaining dry weight was used to calculate specific leaf area in tandem with the calculated leaf area mentioned above.

Water content was the difference between wet and dry leaf weights. Leaves were weighed wet when brought back to the lab and then put into drying ovens at 60°C until there was no net change of weight loss. Water content was the difference between wet and dry leaf weights. The resulting weights were then the dry leaf weight.

2.2.5 Statistical Analyses

To assess if averaging at the leaf and individual level could skew statistical comparisons, the normality of leaf and individual samples were plotted. These all appeared fairly normal, except some were linearly skewed to the lower distribution (leaf thickness, dry mass). Transformation of data should not be performed without adequate justification (Wilson 2007). Analysis of variance is quite robust to moderate skewness (Tan 1982) and thus we did not transform those data. Instead, the resultant skewed distributions were highlighted in the discussion. ANOVAs were used to test the variance between groups, using each trait against each grouping paradigm. One-way ANOVAs of each ecophysiological trait were tested against the grouping paradigms separately. The growth form and plant family were the two grouping paradigms that were used as factors for the one-way ANOVAs. Two-way ANOVAs were to assess the relative contribution of each grouping paradigm compared to the other on traits, and a multivariate ANOVA was performed on the samples complete across all trait measures to test the relative importance of all factors for discrimination. The correlation between the traits was also investigated, to see if the traits were related to one another. Relation of traits at this level would imply an ecological linkage in Cerrado plants.

2.2.5.2 Spectral Variation

Spectral variation within leaf samples was described using simple linear regression of the trait values and their associated spectral indices and the use of spectranomic indices.

2.2.5.3 Spectranomics indices

Trait variation was compared between groupings of a priori distinctions of category (life form or family) using an index technique known as spectranomics, developed by Asner et al (2008). This index is calculated by the mean of all groups, and the index value of each group is the distance of the group value from the mean value of all groups, over the standard deviations of all groups (Equation 6). The score of a trait's spectranomic index can be interpreted as the distance of that grouping's mean from the global mean. This was calculated for both hypothetical categories, family (Figure 2.3.5) and life form (Figure 2.3.6; Table 2.3.2) for all traits measured.

Equation 6 ***|(group – average of all groups)| ÷ standard deviation of all groups***

2.3 Results

2.3.1 Sampling Summary

A total of 336 plant individuals were sampled from 21 sites (Figure 2.3.1c). Plants of the 5 *Cerradão* sites and 4 *Campo rupestre* sites contained some families that also existed in the Cerrado sites, and greater than two-thirds of the species in secondary ecotypes were encountered in Cerrado sites as well. The *Mata Ciliar* (Riparian Forest) was also sampled at two sites, which possessed fewer species co-occurring in the Cerrado *sensu stricto*. The inclusion of shade leaves necessitated exclusion of these sites from analyses. More than 6500 leaves were sampled in this study (Table 2.3.1)

2.3.2 Taxonomic samples

Of the life form groups, lianas were less speciose than shrubs or trees. The numbers of individuals sampled of each group were also accordingly relative to their site biomass (30 lianas, 98 shrubs, 105 tree individuals). Individuals were from 38 taxonomic families (Figure 2.3.2). Families that were present at many sites also had higher richness overall those families that occurred at only a few sites; richness trends approximated abundance of encounters. The Melastomataceae and Leguminoseae were the most speciose families and had the highest combined canopy cover / biomass within the study area. The observed patterns of family richness and occurrence are consistent with those noted by Ratter *et al* (2004). Felfili and da Silva Jr (1993) found Leguminoseae (19) and Vochysiaceae (8) as the most speciose of large canopy trees between 7 Cerrado sites. Comparatively with their sampling list, the species encountered in this study had the most in common with their list of species common to any Cerrado site (14) and more in common with the Brazilia Distrito Federal region (8) of higher altitude than the less distant Patrocíno-Paracatu site (3) (See Felfili and daSilva Jr 1993, Table 3). Of the 22 species they found at all sites, our study area encountered 10. Malphigiaceae and Asteraceae were also encountered frequently throughout the study area, which was due more to the abundance of certain species than a high diversity (*Banisteriopsis* sp. and *Eremanthyus* sp, respectively). Caryocaraceae was sampled 11 times but represented only a single species, *Caryocar brasilense.*

In six of nine families sampled containing lianas, they were the exclusive life form (Figure 2.3.2). Most families containing shrubs also contained trees. See appendix 1 for sampling counts, life form identities and summary statistics by species.

2.3.3 Data Variation

Of eight leaf traits the deviation in 5 traits are normally distributed at the individual level (Figure 2.3.3). The shape of distributions of variation within leaves of individuals was consistent with those between averages of individuals. The distribution of leaf level trait variation paralleled the shapes of population distributions (Figure 2.3.4). The averaging procedures did not appear to alter the distributions of the data. The three traits deviating from strict normality (dry weight, leaf area and leaf thickness) were skewed towards lower values. This suggests a relative preference towards smaller-sized leaves in Cerrado woody plants. Dry weight ranged from 0.02-4.96g, leaf area from 2-25cm^2 and leaf thickness from 0.1 to 1.5mm. The normality of SLA relative to other leaf size measurements supports its use as measure of leaf size. Normally distributed data allows greater statistical flexibility by avoiding transformations or non-parametric statistics. Averaging the data from leaf measures to the individual level effectively removes some detail in the variability, but does not appear to affect normality (Table 2.3.1; Figures 2.3.3 and 2.3.4) although it did reduce the skewness of the majority of traits (Figure 2.3.4). Averaging related data to treat many subsamples as a single statistical unit avoids pseudoreplication and the lack of total statistical independence between samples of the same individual.

The relationship between some leaf traits was strong where previously established (Figure 2.3.3). Leaf level pigment ratios (total chlorophyll to carotenoid) were strongly correlated (r^2=0.76, p<0.0001), as expected (Gitelson et al, 2002 reported r^2=0.87, Sims & Gamon 2002, r^2=0.87). Leaf area and dry weight were also positively correlated (r^2= 0.63, p<0.0001), so intuitively the largest leaves weighed the most. Polyphenol content (Ephen) was positively correlated with leaf thickness (r^2= 0.23, p<0.0001) but negatively correlated with SLA (r^2= 0.33, p<0.0001). Specific leaf area was not significantly related with concentrations of chlorophylls (r^2<0.001, p=0.77) or carotenoids (r^2=0.002, p=0.64). (See Table 2.3.2 for all pairwise linear regressions of trait data). Leaf cores for pigment sampling were of equal area but did not account for differences in density or thickness, thus the mass used in pigment analysis was not identical between species of differing leaf densities.

The distributions of variance in measurements averaged to the individual level were similar in form to their respective histograms of variation at the leaf sample level (Figures Scatter matrix, and Distributions). Dry weight, leaf area and leaf thickness were all negatively skewed towards an abundance smaller sized leaves (Figure 2.3.4; Table 2.3.1). There were fewer species with large leaves in good condition, or present on the trees, as is expected in a dry deciduous forest when large, thin leaves have a high cost of water use.

2.3.4 Spectranomics

No two families were identical in their pattern of spectranomic variation (Figure 2.3.5). Leaf thickness had the highest variability, with an average index value of 6.2. Dry weight was the next most variable trait among groups with an average index value of 2.8. The variability in spectronomics might be a result of the skew/normality within the original distributions; a few high values increase the mean of a grouping and place it further from the mean of all groupings. Interestingly, leaf area also was non-normally distributed but did not have high spectronomic index values like the other two non-normally distributed traits just mentioned. This suggests that leaf area deviation was more moderated within family groupings than between. The remaining trait index averages were less than 1 standard deviation from the global mean; total Chlorophylls and EPhen being the least variable means between groups with an average index value of 0.74. Separation of spectranomic index into individual traits provides better ability to compare the variation of index values between families (Figures 2.3.5B&C).

Spectranomic figures with many groupings allow a cursory visual assessment of relative differences of group means within a population. Spectranomic comparisons of life forms appear more dramatically different (Figure 2.3.6). Lianas had higher index values for all traits except for total chlorophyll (for which all group means are ~ 0.095 SD from each other). The difference visually suggested in liana variation relative to the other life forms is exaggerated by the spectranomic index. Comparison of spectranomic indices between life forms suggested groups were more different from others in the sum of all index variation (the size of the stacked bar) than the difference of families compared by their stacked bars.

2.3.5 Investigation of Variation for Groupings

Evidence for groupings was detected with significantly different variation in univariate and multivariate analyses. One-way ANOVAs on 8 life traits revealed water content and specific leaf area differed between life forms (Table 2.3.2, Figure 2.3.7). In both these traits, it was the lianas that differed from shrubs and trees (Table 2.3.2). Two-way ANOVAs on traits of life form by family, or life form by site (Table 2.3.2) affected the significance of differences relative to one-way tests.

The inclusion of family as a second factor in two-way ANOVAs increased the significance level of liana differences except for when SLA, leaf thickness and water content were the traits considered. Water content was removed as being attributable to life form differences when family was included, such that family appears to be more important to find distinguishable groupings between water content than life form alone. Trees were significantly different than lianas and shrubs for polyphenol content for both life form and family, but were not significant in a one-way ANOVA. Specific leaf area remained significant with both the two-way ANOVAs (Table 2.3.2) with lianas differing from other life forms.

For those variables whose *p*-values increased as a result of inclusion of families as a factor, a post hoc one-way ANOVA relative to family was performed. Of 38 families, 3 were significantly different from one or more others ($p<0.01$, data not shown). The Nyctaginaceae, Celastraceae and Dilleniaceae had variation that differed from some other families for total chlorophyll (Nyctaginaceae), EPhen (Dilleniaceae) and water content (Celastraceae). These families each averaged a small number of samples collected (their trait data can be found in appendix 1). From the Celestraceae only trees were encountered from a single species, *Plenckia populnea* (Figure 2.3.8). A typically large canopy tree, this species occurred throughout the landscape, and was sampled in six locations as a tree. It was also encountered as saplings with height less than 2 m but never sampled from at that size. The Dilleniaceae was sampled both as trees and shrubs of the single species *Curatela americana* (Figure 2.3.9) and grew throughout the Cerrado ecotype. The Nyctaginaceae contained only one species *Guapira graciliflora* (Figure 2.3.10) which was sampled at Cerrado *sensu stricto* sites. It was sampled both as a tree and shrub. Interestingly, none of the families that were found to be different contained lianas, even though for all two-way ANOVAs lianas were still separable.

Inclusion of site as a factor decreased the *p*-values for all traits, although EPhen was highly significant different between sites (*p*<0.0001) and SLA was significant for life form (*p*=0.004) and site (*p*=0.014). The consideration of site as a factor improved p-values better than using vegetation type (data not shown). Polyphenol content was the only variable made significant by the 2-way ANOVAs that was not already significantly different in the univariate tests. The difference of polyphenol content between sites may be a result of varying sun exposure due to aspect between the sampling areas.

In order to standardize for the effects of leaf structure, a multi-variate ANOVA using individuals with samples for all leaf traits was attempted for life form, (Figure 2.3.11). Sufficient degrees of freedom were not available to perform this analysis for every sampling site or family.

2.3.6 Spectral response with respect to leaf traits

Indices which we expected to have a relationship with the significant groupings found were not strongly related (Figure 2.3.12a). Water band index was not appreciably correlated to the water differences (r^2 =0.03) observed between individuals. In addition, the patterns observed in water content vs. water band index did not show a tendency to clump by life form (Figure 2.3.13). These were not significantly different when tested with an ANOVA (p=0.93, F=0.08).

Specific leaf area was able to be tested using the hyperspectral data as much of the data detected for leaf structure is in longer wavelength ranges (Gates 1965) beyond the sensor capabilities of the UNISPEC instrument.

To validate the usage of hyperspectral leaf data, we compared the pigment trait data to common indices used to detect chlorophyll concentrations (Figure 2.3.13b&c). A modified NDVI (mND705) developed by Sims & Gamon (2002) performed much better in correlation with the observed chlorophyll extractions than three other indices designed for hyperspectral chlorophyll detection (Simple Ratio 704/774, Gitelson-Merzylak A 750/700, and Gitelson-Merzylak B 750/550 (Gitelson & Merzylak, 1994). Although all indices were meant to approximate the detection of chlorophyll using centers of LANDSAT bands used to calculate NDVI, the mND705 was developed specifically for the UNISPEC instrument (Sims & Gamon 2002). When the relationship of mND705 was compared between life forms, no significant difference was found (Figure 2.3.13b).

Investigation of the spectral variation of plants was plotted against wavelength, using averaged reflectance from individual averages (Figure 2.3.14). Variation in the average of spectra was not different between spectra averaged to the family level. The differences between the standard deviation of the spectra averaged to family level showed more differences, suggesting that the hyperspectral variation present might prove to separate family groupings more so than functional traits or indices.

2.4 Discussion

2.4.1 Validity of grouping concepts

A larger proportion of species were separable from others using the life form paradigm for grouping woody plant species. The results of the two-way ANOVAs reveal there is a relative rank in establishing factors driving differences. Life form is a primary structuring factor in between trait data, followed by taxonomic family, and weakly by site effects. This suggests that niche partitioning is happening, evolutionary history has an effect and that site effects are mediated by these stronger controls.

Between the functional groups, it was found that lianas differed with respect to two functional traits. Relative to the taxonomic family grouping paradigm, this separated more species. This supports the use of life forms for investigating plant variability, specifically that lianas are distinct in some ways from the rest of woody plants. As lianas are likely to rise in the face of global warming and increased CO_2 (Sánchez-Azofeifa et al. 2005) this is an important conclusion to reinforce. Using taxonomic families as groupings produced more significant distinctions in the ANOVA between the functional traits, but the number of species found to be distinct in this manner relative to the main groupings were fewer. This offers potential for these to be indicator families more easily detected with trait measurements and the associated spectral characters. The amelioration of results when combining life form and families in two-way ANOVAs suggests that both life form and family are useful paradigms, and should be used in tandem, rather than assessed independently. In the field the use of dichotomous keys to establish generalization of taxonomy would allow identification approaching genus or species level without requiring extensive knowledge of all woody plants in the region.

In addressing the presence of groupings within the woody plants, differences between groups were found both at the life form level and the family level. The differences between life forms were ameliorated when family was also factored. This suggests that both are meaningful concepts for describing functional differences between plant species. Life form and family variations were more significant than differences between sites. This suggests that environmental variation within a local area is less important in determining trait balance than the functional biology of niches.

The results of the two-way ANOVAs reveal there is a relative rank in establishing factors driving differences between groupings. Life form is a primary structuring factor in distinguishing trait data, followed by taxonomic family in the next level of significance, and weakly by site effects. In terms of relative importance of factors contributing to spectral reflectance, our argument is that the functional traits of plants are more closely linked to their use of niche. Species traits have evolved to exist in adaptive states for resource acquisition and use (Ackerly, 2009; Violle et al. 2007; Reich et al. 2003), especially in determining community assemblages (Kraft et al. 2007). Since this is a natural area, we can only assume evolution has made them effective at what they do in the landscape. The levels of significance were higher than the strength of groupings when plants were separated by family. The family grouping definitions is closely linked to the concept of evolutionary history. A plant family is different from others because of the morphological and molecular inheritance diverging. However, convergent evolution shows that species from different lineages can make use of the same functional niche in the environment. Since plants are in competition for the same resources, niche convergence is very prevalent (Reich et al. 1997). So, although we found significant separation by the family level of grouping, these were more due to certain families being quite different from others. The least significant grouping we saw was that of site vegetation physiognomy. This study reveals that the trait response for different vegetation types is fairly consistent within this ecosystem. This suggests that niche partitioning is happening; evolutionary history has an effect and that possible site effects are mediated by these stronger controls within the Cerrado *sensu lato*. Complimentary to our findings, vegetation physiognomy classification has already been achieved at satellite levels (Ratana et al. 2005; Felippi et al. 2009; Ferreira et al. 2007), and supports vegetation classes alone will not be adequate to connect ecophysiological traits to spectral response. Since there is a huge amount of spectral data to tie to relatively few ecophysiological variables, it might be more prudent to optimize sampling methodologies that track cumulative variation in traits (Walker et al. 2008), or even target life form groups in model building (Steinmann et al. 2009). Ground-based life form surveys to find relative abundance could also be compared to high spectral-resolution imagery where individuals of each species can be compared to the leaf level data, using the amassed spectral library from this study.

2.4.2 Importance of Functional Traits

Between life forms and families, it was clear that water content and specific leaf area were the most important traits to separate variation. Shrubs and trees were not separable as predicted by defining as distinct functional groups, presumably this is due to the overlap of species being both trees and shrubs from the definitions supplied by Cornelissen (2003). Our methodology assumed no specialized botanical knowledge, which is expected to be the default conditions when approaching a high diverse ecosystem; most individuals are non-specialists at local identification if not taxonomists. This is related to the degree which we can allow resources to be allocated to do rapid assessment of conservation surveys over a large scale; validation.

2.4.3 Photosynthetic pigments

The pigment concentrations found in Cerrado woody plants were consistent with other studies of tropical trees (Castro-Esau et al, 2006). However, those measured did not a have level of correlation as high as expected with the spectral indices specifically designed for their detection. Leaves with larger areas often tended to be thicker, and the standardization of pigment sampling was by a constant area, not total leaf volume. Dry weight and leaf area also showed the same high degree of positive correlation with leaf thickness, which also supports the hypothesis of increasing volume for pigment sampling in larger leaves. Leaf thickness however was negatively correlated to pigment concentrations, which does not substantiate this idea (see Figure 2.3.3 and Figure 2.4.1). The potential of leaf mass sampled affecting other variables (such as pigment) could be addressed by SLA. Positive SLA changes represent an increase in the mass to area ratio in the leaf, and pigment concentrations are positively correlated (Figure 2.3.3). However, dry weight and leaf area were negatively correlated to SLA. This suggests that the density of pigments is decreasing with thicker leaves but increasing with leaves of higher density.

The leaf thickness was positively correlated with polyphenol concentration estimation. No literature was found to suggest that there were effects from leaf structural in the UV spectral region assessed by the Dualex instrument. However, the Dualex also standardizes its UV measurements against the chlorophyll absorption by the use of reflectance in the red spectra. The correlation of leaf thickness to polyphenol concentration is strongly positive, suggesting a leaf structural effect or increasing polyphenol mass with larger leaves. The negative correlation of EPhen to pigment concentration suggests less photoprotection is present in the presence of more pigments, or that the pigment reflectance is controlling the estimates. In order to determine the interrelations and controls of all traits it would be advantageous to use multivariate regression methods other than blocked designs (such as the ANOVAs used in this study). The physiological balance of leaf traits has converged to a set of patterns (Wright et al. 2004; Wright et al. 2005) and trade-offs (Shipley et al. 2006).

2.4.4 Polyphenol estimates

The polyphenol content was assessed using a NIR-corrected UV reflectance of the Dualex instrument. The total abundance of polyphenols is a result of many ecological functions, such as the protection from ultraviolet light, infection and depredation (Levin 1971; Matsuki 1996). However, the NIR region is sensitive to leaf structural changes (Gates, 1965; Wooley, 1971; Boyer et al, 1988; Curran, 1992;), the thickness of the leaf tissue may affect estimation of the polyphenol content due to either structural effects or concentration differences. Therefore, the observed increase of EPhen with leaf thickness suggests that greater leaf structure relates to an increase of polyphenol estimation within a given leaf area. The inverse relationship of SLA to EPhen also supports this. Specific leaf area is a measure of leaf area to mass, such that a lower SLA value corresponds to a denser leaf. Meyer et al. (2006) used above Ephen(area) / Leaf Mass Area to find a standardized SLA estimate of Ephen(mass) which was less strongly correlated to LMA (previously was 78%). Polyphenols are more concentrated in leaves with longer lifespans (Coley et al, 1985).

2.4.5 Fuzzy boundary between Shrubs and Trees

The methodology adopted for this study distinguished shrubs and trees on the basis of plant height instead of relying on plurality of stem growth. A growth pattern observed in the trees of Cerrado *sensu stricto* is the preferential root network development of saplings when they are small in size (Felfili et al, 1997). This is the size in our study that was counted as shrubs. As a result of this methodology, all plant species with multiple stems were considered shrubs, but plant individuals that were less than 2 m were also considered shrubs even if other individuals of this species in the landscape were classified as trees. This is a natural ambiguity of non-specialists interpreting the methodology described by Cornellissen et al (2003) that will require revision for future studies in this context. Without prior taxonomic knowledge, the decision to describe a plant as a shrub or tree must rely on a structural or functional trait. This assumes there is some functional difference in the niches of trees and shrubs in the Cerrado. It is also possible that, in the lack of understory that we see in the Cerrado *sensu stricto* ecotype, there is decreased functional difference between trees and shrubs because of the reduction of shade competition. Below ground nutrient competition is a trade-off between root resource acquisition, and size of plant to be supported. In this way, small plants are able to co-exist with large trees with broader spatial access to soil resources.

Plant size may have had other effects upon our study. In leaf metrics, a size-scaling effect has been observed. Niklas et al. (2007) found that leaf size (both in terms of dry mass and leaf area) had scaling effects with respect to leaf density, nitrogen, dry weight etc. They analyzed samples from 1943 species, and found that shrubs, trees and lianas differed quite a bit in both traits and trait relationships. Dry mass increases faster than leaf area; leaf area is tied to light acquisition. Growth rate scales isometrically with total leaf dry mass even between very different species (West et al, 1997 science; Enquist & Niklas 2002 science).

2.4.6 Family level differences

The relative proportions of families encountered was consistent with that noted by Cerrado researchers (Ratter *et al.* 2004; Felfili and da Silva Jr 1993), so we assume our collections were adequate to cover the phylogenetic diversity present in the study area. The families were not a grouping paradigm that showed patterns of statistical separation across traits. Because these families did not differ from all others in the study in their respective traits; there is not a consistent way to separate family groupings. Still, the families mentioned above have unique signatures with respect to a single trait and these traits could be used as indicators of their presence in canopy spectra targeting traits. The fact that they also contain a single species suggests there may be unique trait signatures with respect to the species level. However, the degrees of freedom required for a species level comparison are not feasible with data averaged at the individual level.

2.4.7 Spectranomics

The variability in spectronomics might be a result of the skew/normality within the original distributions; a few high values increase the mean of a grouping and place it further from the mean of all groupings. Interestingly, leaf area also was not normally distributed but did not have high spectronomic index values, like the other two non-normally distributed traits just mentioned. This suggests that leaf area deviation was more moderated within family groupings than between. However, inspecting the indices by family for traits (Figures 2.3.5B&C) did not prove consistent with the families found to be different in one-way ANOVAs. For example, the Celastraceae was different with respect to water content, but the spectranomic index value for this trait is neither the largest, nor seems much different from the Caesalpinoideae. The Nyctafinaceae was found to be different in terms of pigment concentration, and the index value for this trait out ranks other families quite noticeably. The differences suggested in liana variation relative to the other life forms are exaggerated by this index. Visually interpreting the graph (Figure 2.3.6) implies that the lianas are consistently three times larger in variation from the other two groups. However, the degree of variation within each groups is discarded by the spectranomic index, and the means of the life forms for each functional trait are enver this distant from each other. This is an artefact of how the spectranomic index is calculated. From a mean of 3 groups, it is not unlikely that one group is further from the global mean than others. This may be an inherent sensitivity to the application of spectranomics in that the number of groups used to calculate an index act in a similar way to how degrees of freedom work. With a smaller number of groups, the index values have pronounced differences rather than a more continuous distribution possible with a large number of groups. The use of spectranomic indices to judge variation of a group relative to the population is not a complete measure of variation because it compares only the means of the groupings included. To establish statistical relationships of trait data among groups, the distribution of variation within groups must be considered. In our study those three families which were found to be significantly different in one trait also possessed the largest index value for that respective trait. And similar visual comparisons of a group with a spectranomic trait index value mulitple times higher in the life form groupings was not consistent with the traits being significantly different. So our results suggest the spectranomics index is potentially useful for the visual comparison of many groups, it could be misleading if used for a small number of groupings in the creation of the overall mean and standard deviation used for the calculation of index itself.

2.4.8 Trait relationships in other studies

Lianas were found to have higher water content and SLA than trees in both a tropical dry forest and tropical wet forests in Panama (Sanchez-Azofeifa et al, 2009). This is consistent with the results presented here. Their study did however find separation between trees and lianas in terms of pigment concentrations in dry forest regions which was not mirrored in this study. Instead the pigment concentrations we observed more closely approximated the overlapping distributions Sanchez-Azofeifa et al (2009) observed in the tropical wet forest (Figure 2.4.1). They used dimethyl sulfoxide (DMSO) extraction with slightly different wavelengths (447, 646, 664nm). The wavelengths for both our study and theirs are those optimized for pigment estimation using the respective solvents, but 80% acetone has been shown to be potentially less optimal solution for photosynthetic pigment extraction relative to 100% acetone or DMSO due to the effect of acetone concentration in the presence of water markedly affecting the absorption rate of chlorophylls A & B (Wellburn, 1994). Tait et al (2003) found that the equations used to calculate pigment concentrations affected the significance of comparison between solvents used in extraction. They compared the equations of Barnes (1992) to those of Wellburn (1994) and found significant differences between solvents with the former, but not the latter. The methods of Barnes (1992) were those DMSO methods upon which Richardson (2002) were based, and used Arnon's (1949) equations which we shown by Wellburn (1994) to be less than optimal. Wellburn (1994) additionally showed that his revisions of Arnon's equations (1949) were robust to changing resolution between spectrometers. The variability of our pigment reflectance data relative to that of the Panama observations of Sanchez-Azofeifa et al (2009) makes it questionable whether the differences we see are due to extraction solvent or other potential sources of error such as sample degradation in the field resulting from variable time before reaching ideal laboratory storage. Photosyhetic pigment extractions are depedent upon the lack of degradation of the pigments by chlorophyllase and other enzymes which digest the pigments (MacKinney, 1940). These enzymes require the presence of water, thus freezing or immediate solvent immulsion to remove water from the system is necessary. In field conditions, laboratory methods may be less feasible, as DMSO extractions require heating. Acetone availability limited our study, as in Brazil it is a controlled substance.

Other studies have supported the difference of functional trait as a result of growth form. Santiago and Wright (2007) tested the consistency of leaf traits to three growth forms (Trees, Lianas and Understory vegetation) in a lowland Panama wet tropical forest. The occurrences of trees and lianas in that study had overlapped distributions, and they only the understory plants functional group was distinct in statistical comparisons. This is quite possibly a shade effect. Evans and Poorter (2001) state that the leaf nitrogen balance for photosynthetic use is differently adapted in shade leaves. Luttge et al (2007) suggested that adaptation to daily light variation in the rupestrian fields separated the light response curves of taller, continually sun-exposed plants relative to undersory plants which were more likely to be shaded at some point during the day. The distinction of the riparian forest trait variation from the rest of the sample we observed also suggests that shade still plays an important role in determining trait variation in functional groups. The overlapping Cerrado species in the riparian forest did not prevent that ecotype from differing significantly as a whole. While the shade affects were not quantified, the preference for plants in sun was still followed in these areas. An unidentified but ubiquitous liana species of *Banisteriopsis* (Malphigiaceae) was sampled in all riparian areas as well as 7 occurrences within the three other ecotypes. The individuals of this species sampled in the riparian area were emergent lianas and all leaves were full sun. This suggests that either the species overlap and sun-leaves were not of sufficient sampling ratio within the riparian forest to cause overlap with the other ecotypes, or that there is a site effect that effect trait balance regardless of grouping used.

2.4.9 UNISPEC for Species Discrimination

The UNISPEC instrument did not seem to perform well for species discrimination based upon correlation of individual features to the functional traits within the leaves. There was a low correspondence for the pigment traits observed. Those factors that were seen to be significantly different in our study, have spectral features beyond the detection of the unispec sensor. Existing water band indices created for the UNISPEC (Sims and Gamon, 2003) did not perform well for this selection of species, despite a large sample size. Sanchez-Azofeifa et al (2009) found instrumentation noise and second order effects preventing the reliability of the UNISPEC sensor at the water band of 970 and above.

The Unispec is a useful instrument for measuring a certain range of variables, but may require more sophisticated techniques of spectral analysis in order to make full use of the data. The data can be compared with that of other spectroradiometers, but consideration of the differences inherent to each tool and their calibration must be accounted for (Castro-Esau et al, 2006a).

Functional groups have been separated using the hyperspectral reflectance of the UNISPEC system (Castro-Esau et al, 2006b) demonstrating the potential for species discrimination. Broader range hyperspectral sensors have also been able to discriminate species and functional groups (Kalacska et al, 2007). These studies have made extensive use of the hyperspectral data in many wavelengths through analyses such as wavelet decomposition, principal components. Their connection to functional traits was not explored, but the foundation of comparing between functional groups was discovered.

Reflected light wavelengths observed may have limited the ability to relate functional traits in leaves to spectra. Asner & Martin (2009) found that SLA, Water Content and all pigments had a high correspondence between predicted and actual (r^2>0.7 for all) using wavelengths from 400nm to 2500nm. This study shows correspondence between indices and traits but not at that strength of relationship. In 2009, Asner et al. used partial least squares regression (PLS) to explore the trait-hyperspectral reflectance relationships. Substantial weightings for all traits occurred at wavelengths greater than 1000nm, the range at which the Unispec sensor ends.

This suggests two things. The leaf reflectance considered as a whole provides greater information to predict functional traits. The range of the UNISPEC sensor does not capture the wavelengths that describe the structural arrangement within leaves that contribute significantly to leaf reflectance. The UNISPECis more suited to the analysis of plant signals which occur within its spectral range; chlorophyll a and b, carotenoids, and anthocyanins (Blackburn 2007; Figure

1). The weightings of the PLS used by Asner et al (2009; Figure 6) are quite high in the visible regions and red-edge for the three primary pigments (Chlorophylls a and b, and Carotenoids).

To approach this, it would be conceivable to use multiple spectrometers to validate or standardize measures. This would require consideration of the differences in between spectrometer readings (see Castro et al, 2004). Or, adjust the traits by the SLA observed in a leaf. The chemical components present in the leaf will be affected by the total internal mass-area of this leaf. Using models which account for the variation in SLA could reveal greater differences in the other traits, once the auto-correlated variation caused by leaf mass was accounted for.

2.4.10 Study Limitations

2.4.10.1 Ecotype, site and location factors

Not all the ecotypes within the study area responded identically. The multivariate ANOVAs did not reveal any additional significant differences among ecotype or life form. This is contrary to expected with an increased amount of interrelated information, but the test may have been weakened due to the decreased available sample set (N=71) that required complete sampling across variables.

The *Mata Ciliar* or riparian gallery forest, was found to be distinct for functional traits compared to other ecotypes in the Cerrado *sensu lato*. These gallery forests contain a mostly disimilar biodiversity, with fewer species overlapping, a characteristically distinct physiognomy with decreased deciduousness due to the higher water availability (Schiavini, 1992). Based upon this degree of overlap of species and physiognomy, we expected the Campo Rupestre physiognomy to be separable as well. Roughly 2/3 of Cerrado vascular plants grow exclusively within the campo rupestres (Alves et al, 2007), 1626 species found specifically in the Serra do Cipó range (Giulietti et al. 1987) which this study area was a part of. The physiognomy is also structurally distinct, consisting of smaller shrubs, cryptophytes, hemicryptophytes and different soil conditions including exposed granite. A potential reason for the lack of habitat separation by MANOVA was the degree of overlapping number of woody species of the canopy in Cerrado *sensu stricto* also being in the Campo Rupestre. The species sampled in Campo Rupestre was chosen for those existing in *sensu stricto* as well, to test the effects of different habitat and elevation on spectral response, and this study should not be taken as a complete spectral survey of the plants of the Campo Rupestre. This distinction might make our species measurements in *campo rupestres* more similar to what is called *Cerrado rupestre.* An additional Cerrado *sensu lato* ecotype has been defined as *Cerrado rupestre* when the herbaceous layer is dominated by *campo rupestre* species and the canopy by Cerrado trees (Alves & Kolbek, 2009), however these authors determined by a review of floristic surveys that these were not florositically distinct from *campo rupestres* and that the previously established term should still apply to these ecotypes in formal descriptions even if the differentiation could find use in a descriptive sense.

2.4.10.2 Time of Study and Phenological Effects

The dry season shows indications for being the best time to tell apart cerrado physiognomies (Ratana et al. 2005; Ferreira et al, 2003) and wet season months are more likely to saturate vegetation response (Ferreira and Huete 2004). The phenological effects upon species discrimination in Cerrado has not been explored. During the dry season most deciduous species lose their leaves, and the availability of leaf samples of some individuals was limited as a result of visible leaf senescence. The degree of senescence may be a cause of variability seen in this study. In the dry season the phenology of plants differ, the timing in between leaf dropping, flushes and flowering events is staggered between species. No assessment of phenology compared between functional groups and families has been done in the Cerrado.

The extent to which senescence obscured variation between groups was also not quantified. To address this, an additional study evaluating the senescent effects on the species would be necessary to compare wet and dry season data. Alternatively, a time series of many more individuals less intensely sampled over the early months of the dry season may more accurately reveal the role that senescence and phenology have on species discrimination within this environment.

2.4.10.3 Statistical Concerns

Averaging multiple scans from the handheld spectrometer to the level of individual plant was been used in this study to reduce instrumentation noise. The UNISPEC instrument was configured to take four scans of a small amount of milliseconds each (10-100) and integrate reflectance from all scans. Taking the averages of averages may not be necessary to capture an accurate representation of leaf reflectance, and potential useful statistical variation may be have been lost. However, more complex regression models utilizing nested design (Srivastava, 1978) would be necessary to consider samples within leaves in order to control for the lack of independence in related levels; scans, leaves, etc.

The level of sampling should be considered at the design phase of experiments. If the research question is in regards to individual, as this study intended, then aggregating data at the level of individuals is appropriate. Some of the variation within the samples may be meaningful if there is a balance of trait relationships at the leaf level, and this could still be incorporated into the individual level if a model were customized to account for nested variation. For studies at the leaf level, such as those concerned with leaf energy balances or physiological experiments, it would be ideal to use all samples and link each leaf reflectance measure to the trait samples from the same leaf, while accounting for the lack of complete statistical independence.

2.5 Literature Cited

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2.6 Tables

		Traits							
		Ephen	*molCar*	*molCHLab*	*DryWeight*	*LeafArea (mm^2)*	*SLA*	*% Water Content*	*LeafThick (mm)*
Averages at Level of Individual Plant	Skewness	0.097	0.293	0.471	2.295	1.348	1.402	0.165	2.440
	Kurtosis	0.660	-0.329	0.185	7.043	2.040	3.497	4.451	9.235
	Count	336	173	173	231	141	258	99	178
Averages at Level of Leaf	Skewness	1.807	1.366	0.454	2.203	2.221	1.438	-0.481	4.143
	Kurtosis	5.491	6.062	0.190	6.612	7.180	3.440	2.301	39.196
	Count	2601	950	952	1235	2957	2742	975	340

Table 2.3.1: Comparison of distributions between leaf and individual level for all ecophysiological leaf traits.

	Liana		Shrub		Tree	
	Average	Standard Deviation	Average	Standard Deviation	Average	Standard Deviation
Chlorophyll A + B	387.1	104.4	351.3	126.6	387.6	147.4
Carotenoids	96.33	35.35	97.81	41.75	99.14	50.39
Ephen	0.149**	0.04	0.169	0.057	0.174	0.059
SLA	9.031*,**	4.901	6.101	3.456	6.744	3.816
LT mm	0.2335	0.0564	0.3927	0.2428	0.3601	0.2333
LeafArea	39.539	29.786	42.231	39.884	50.89	49.18
% Water Content	65.02*	14.6	55.29	17.19	51.19	16.75
DryWgt	0.4598	0.3408	0.7547	0.8899	0.8479	0.7164

Table 2.3.2: Summary of leaf trait variation by by life form. Values significantly differing (<0.01) from other life forms with a one-way ANOVA are denoted by *, values significantly different (<0.01) by two-way ANOVA due to site variation are denoted by **.

Linear r^2	*molCar*	*molCHLab*	*DryWeight*	*LeafArea (mm^2)*	*SLA*	*% Water Content*	*LeafThick (mm)*
Ephen	0.0066	0.0024	* 0.0155	0.0165	*** 0.3287	0.0061	*** 0.2319
molCar	1	*** 0.6162	0.0012	0.0052	0.0016	0.0008	0.0036
molCHLab		1	0.0000	0.0018	0.0006	0.0049	0.0000
DryWeight			1	*** 0.6280	*** 0.6051	0.0082	** 0.1014
LeafArea (mm^2)				1	0.0096	* 0.0684	0.0020
SLA					1	0.0014	0.0018
% WaterContent						1	** 0.0966
LeafThick (mm)							1

Table 2.3.3 Simple linear regression showing global trends between all ecophysiological leaf traits without any groupings. *** significant at the $p<10^{-5}$ level, ** significant at $p<0.01$ * significant at $p<0.05$

2.7 Figures

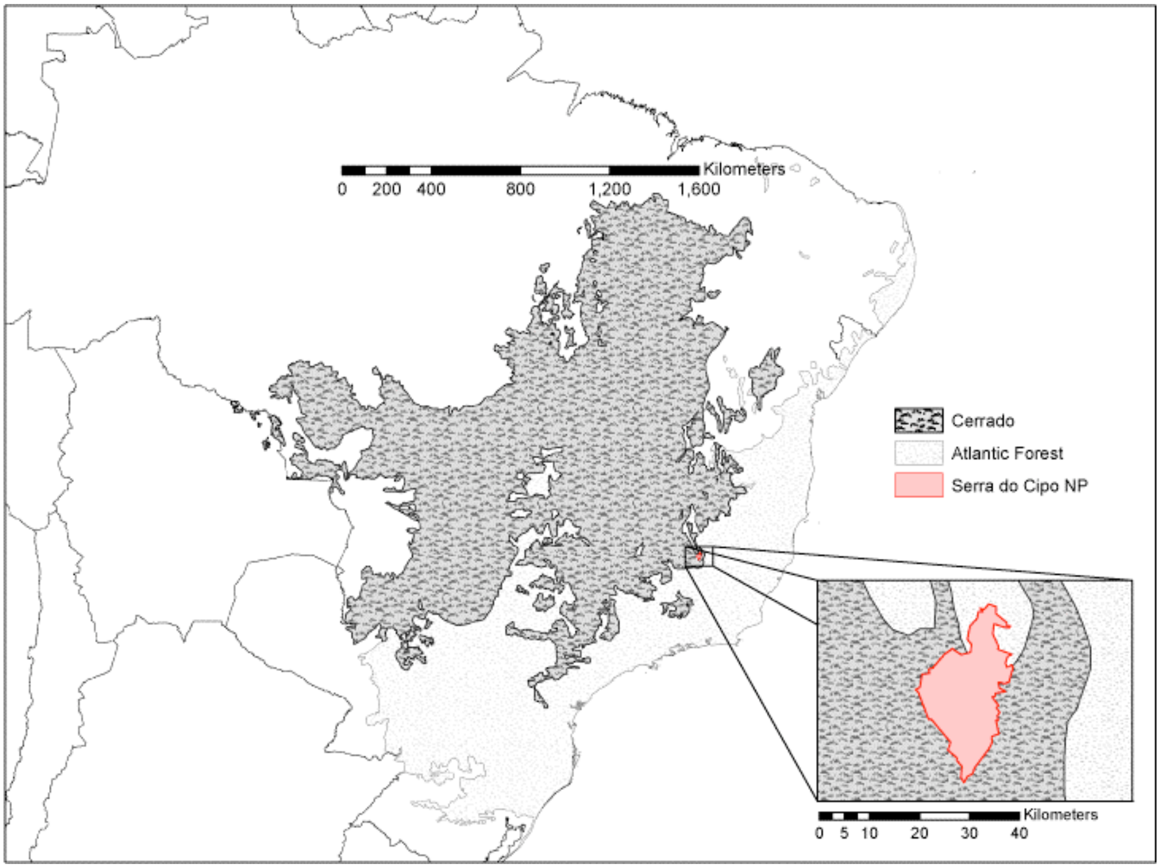

Figure 2.2.1: Cerrado biome distribution, a biodiversity hotspot, in Brasil and the National Park, Serra do Cipò, Minas Gerais in which the study area is contained. the context of Brazil and Minas Gerais.

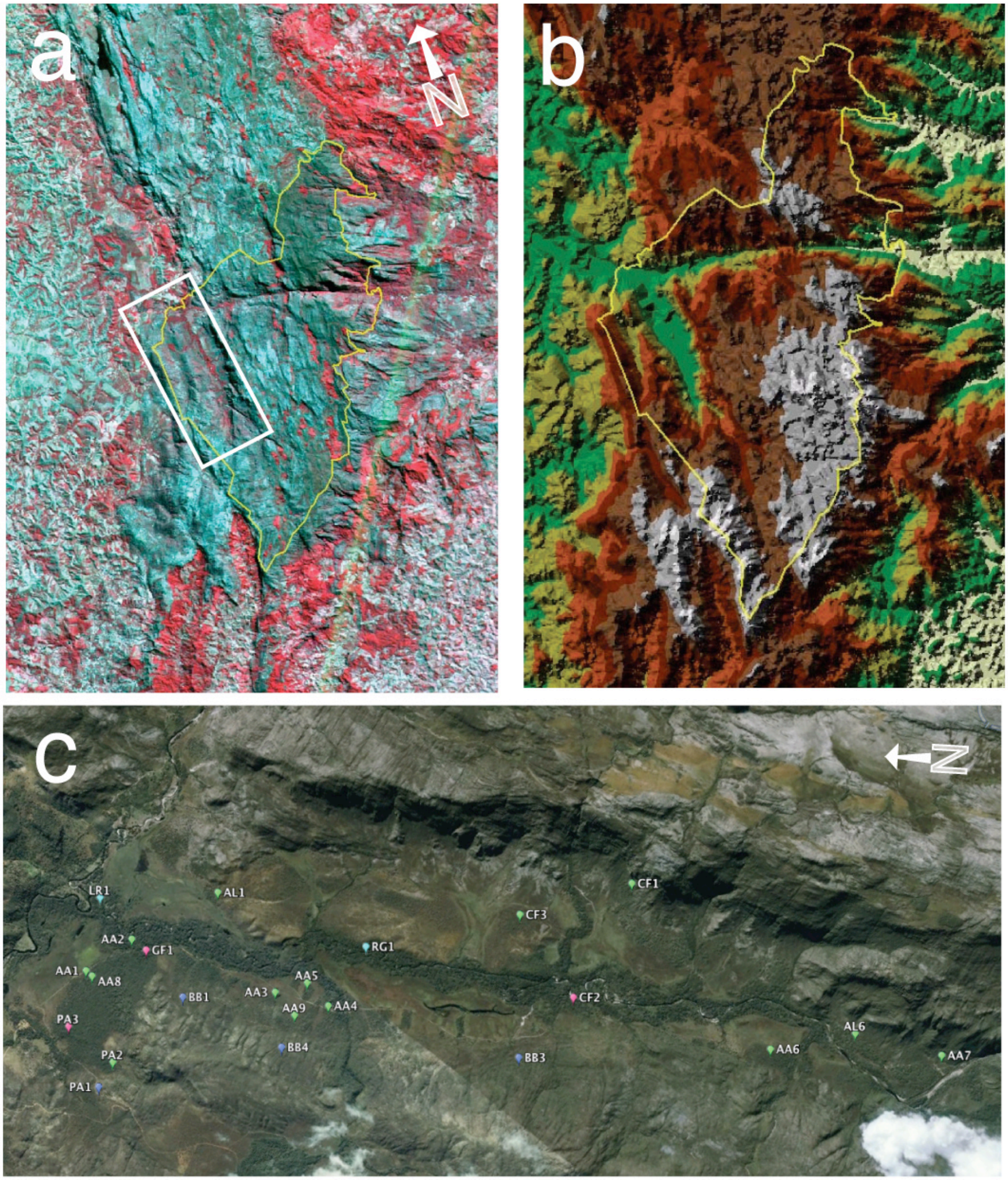

Figure 2.2.2 Imagery of the study site. a) Landsat TM false colour 30m (bands 1,3,7). Park outline is in yellow, study area in white. The NP is adjacent to the Espinhaço mountain range. Red areas are vegetated, to the NE primarily Campo Rupestre,to the W Cerrado and Agriculture. b) DEM of the park and study area. c) Google Earth (2003) imagery of the study area with site locations

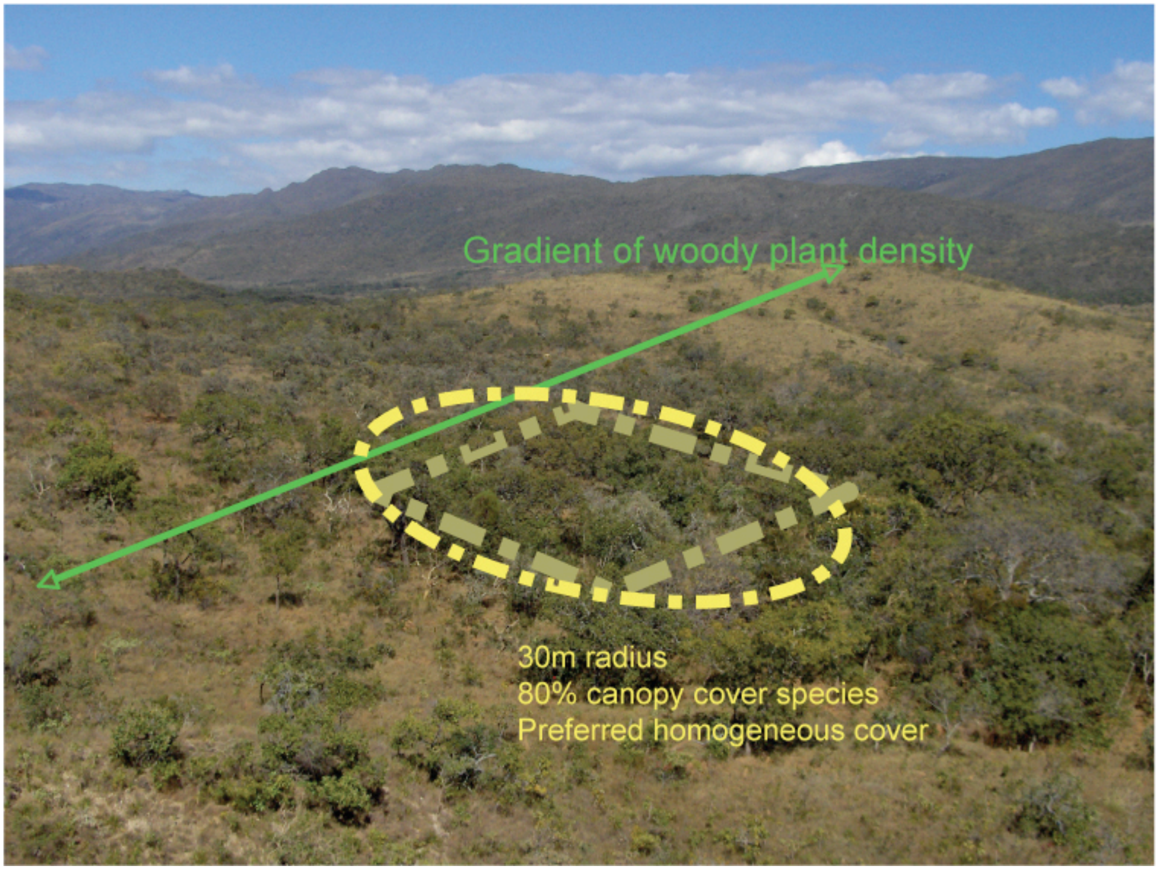

Figure 2.2.4: Sampling point schematic. Each sampling site was a 30m radius (yellow) from a central point of homogeneous Cerrado *sensu stricto* forest coverage. This area was chosen to roughly correspond to the size of satellite imagery pixels.

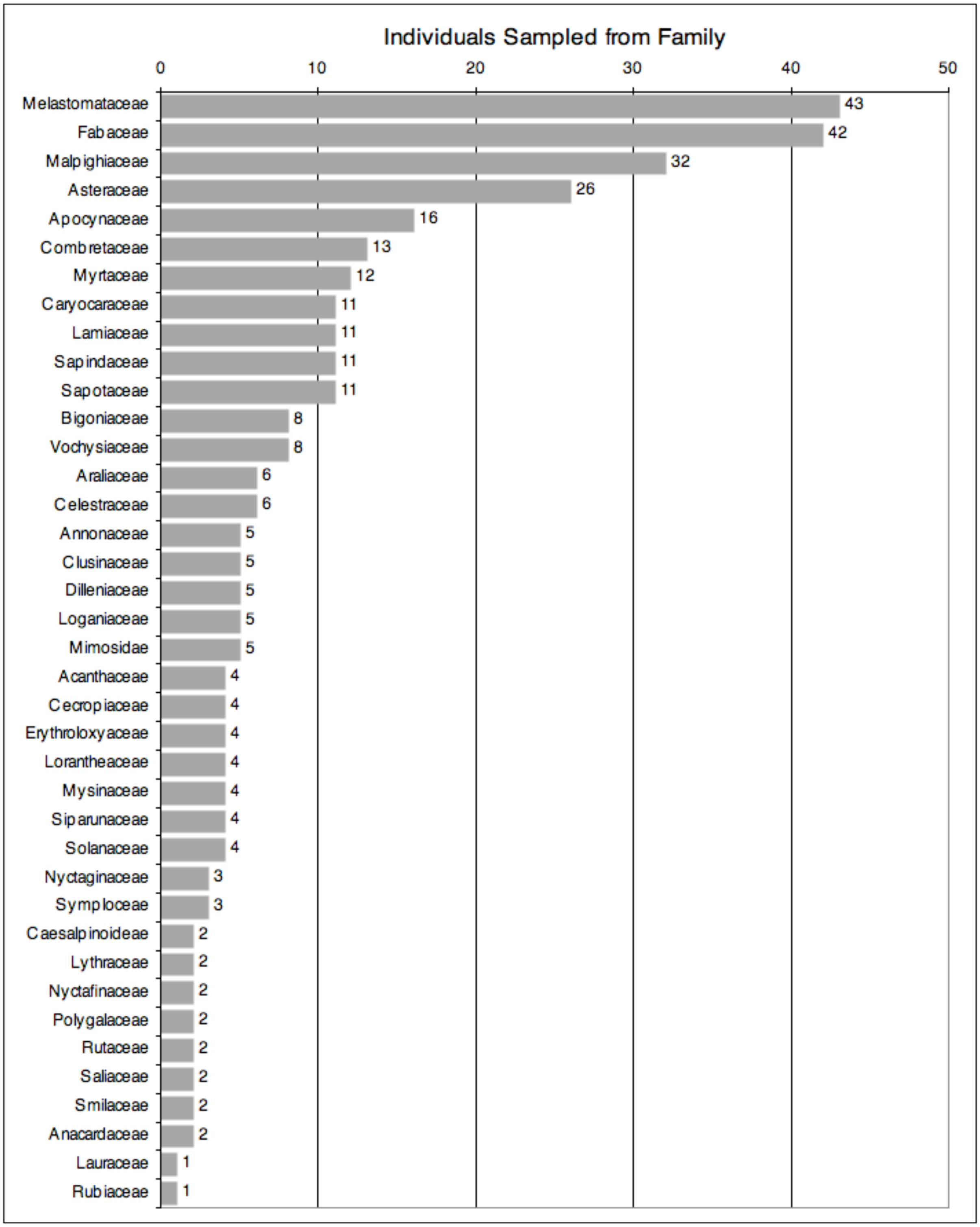

Figure 2.3.2 Sampling counts of the taxonomic families comprising the majority of canopy biomass of woody plants in the Cerrado sensu lato study area.

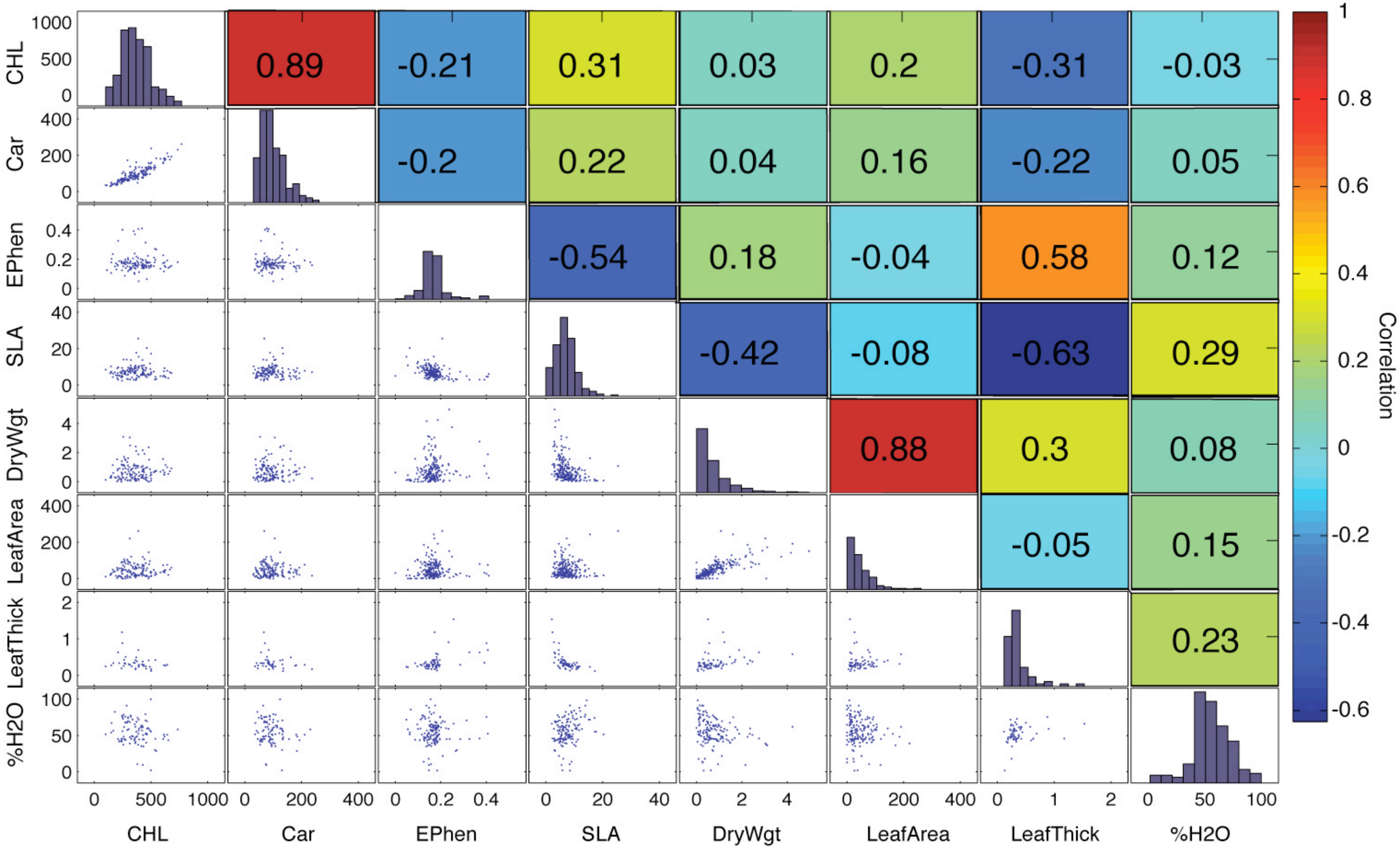

Figure 2.3.3: Leaf trait distributions and relationships independent of grouping schema. CHL = Total Chlorophylls A + B (mol), Car = Carotenoids (mol), EPhen = Polyphenol content, SLA = Specific Leaf Area (m2 kg-1), LeafArea = Leaf surface area (cm2), LeafThick = Leaf thickness (mm), %H2O = Percentage Leaf Water Conent

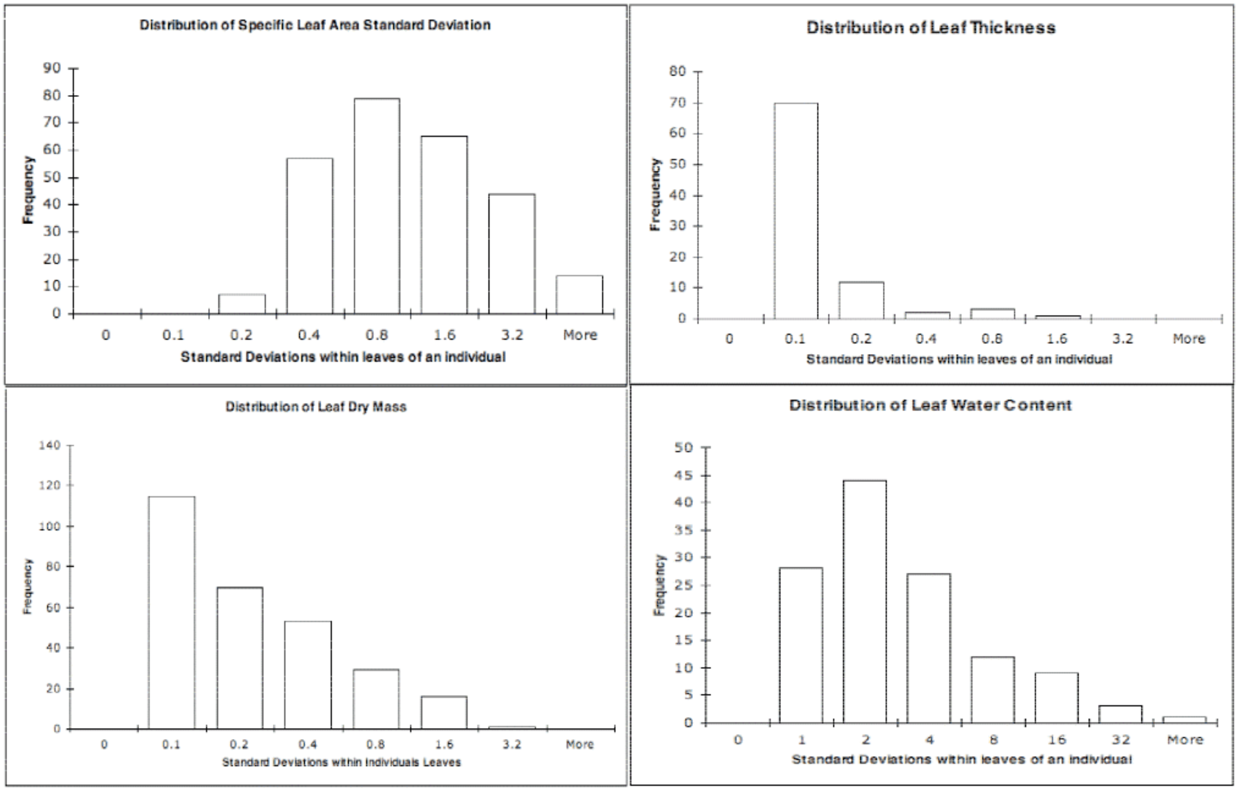

Figure 2.3.4 Histogram distribution of trait variation within leaves of individuals (A) and comparison of skewness between leaf and individual level. The histograms illustrate the distribution sum of standard deviations within samples from an individual. Leaf thickness and total dry weight were non-normal between leaves and the individual average level. Leaf water content and SLA were normally distributed between the leaves, and between the individuals (Figure 2.3.3)

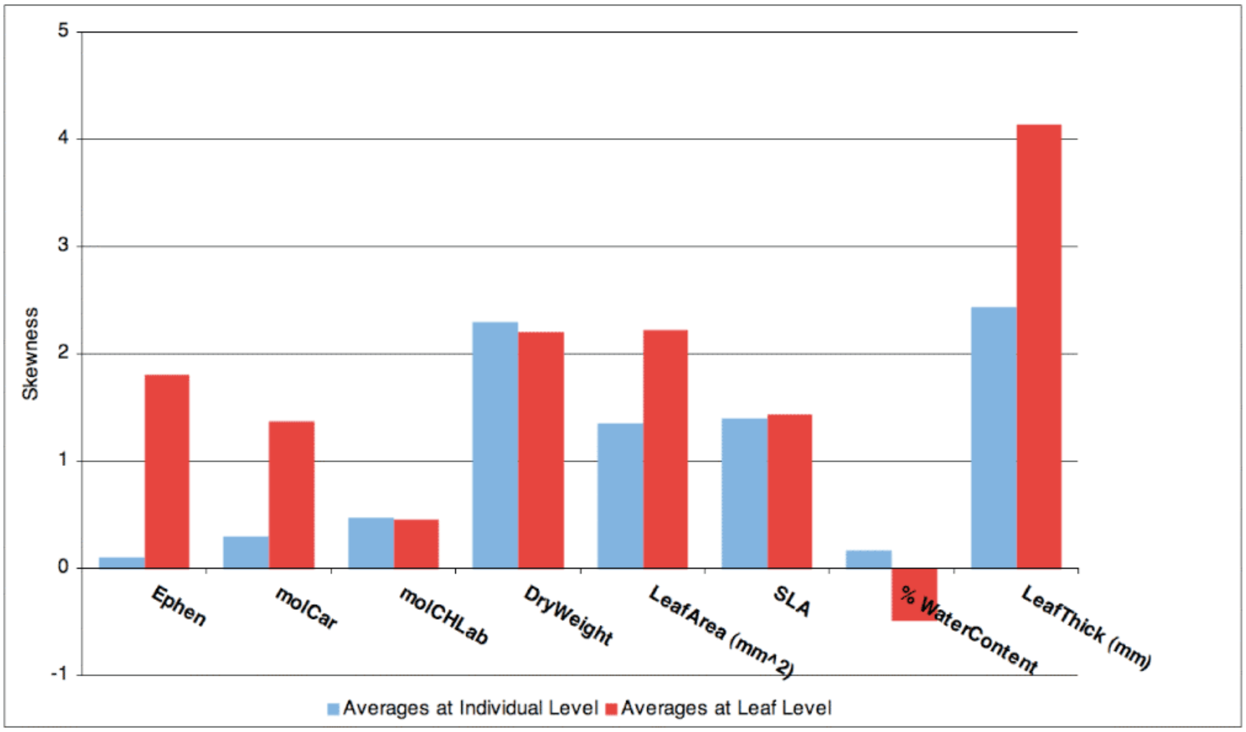

Figure 2.3.4B Comparison of skewness between distributions of samples averaged at leaf level and individual plant level. Higher positive skewness corresponds to a longer tail elongating the distribution when having few high values relative to the bulk around the mean. Averaging the samples to the individual plant level moderated the effect of skewness for five of eight traits.

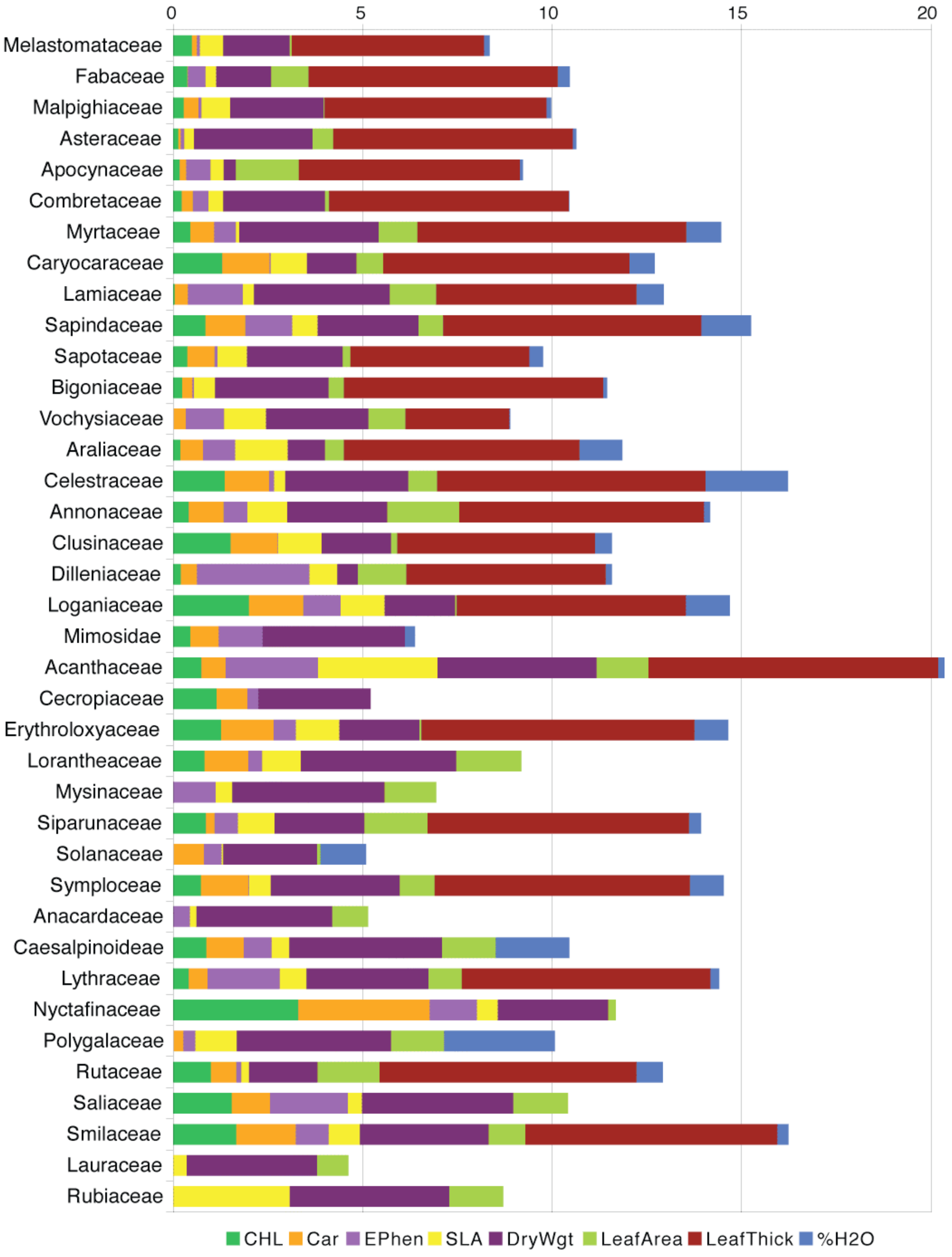

Figure 2.3.5: Spectranomic trait variation by family in descending order of sampling frequency. Index value for each trait is calculated by the distance of that group's trait from the average of all groups traits over the standard deviation of all group traits.

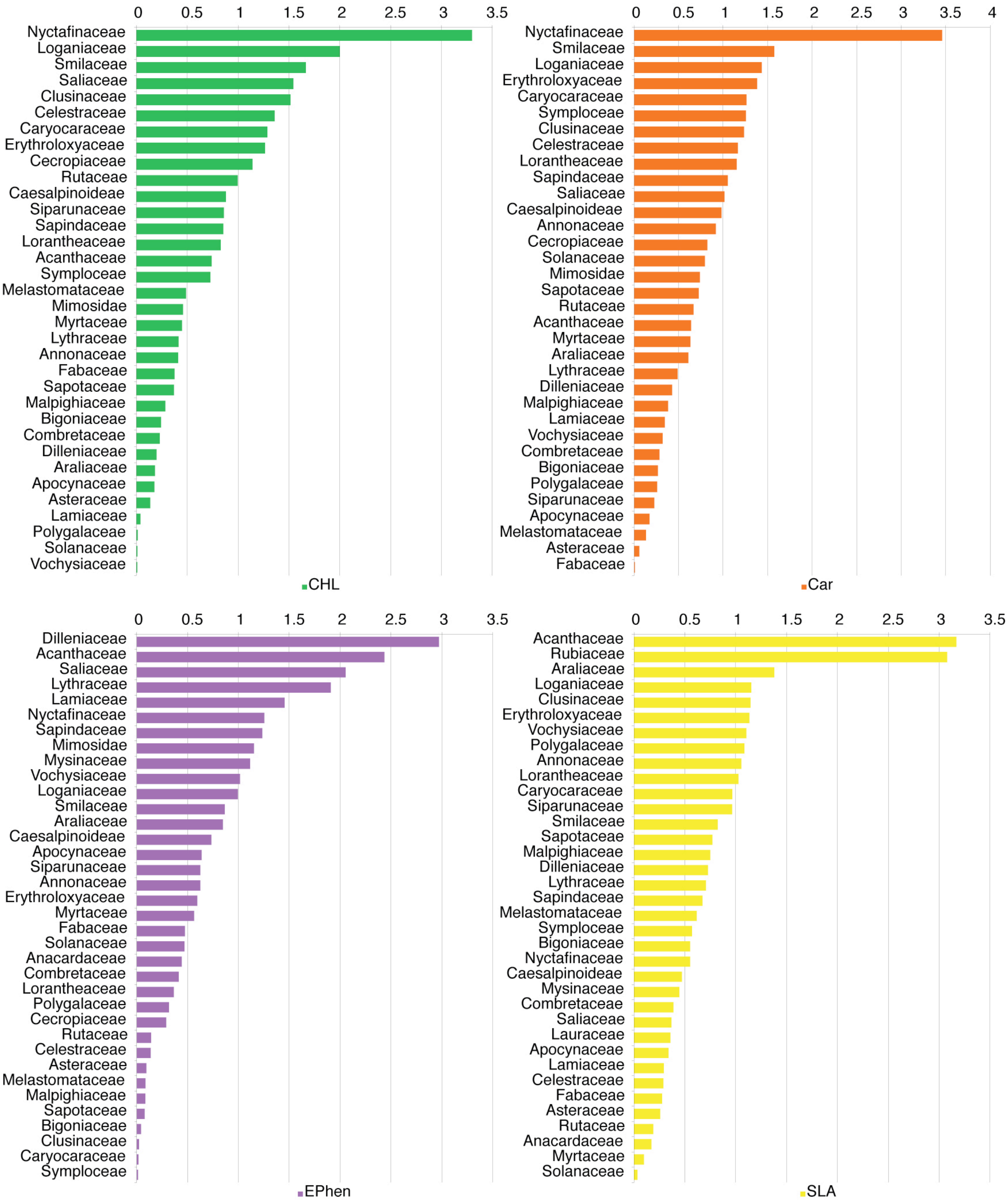

Figure 2.3.5B: Spectranomic trait variation by family in descending order of index value for the following traits: Chlorophyll concentration, Carotenoid concentration, Polyphenol concentration and Specific Leaf Area.

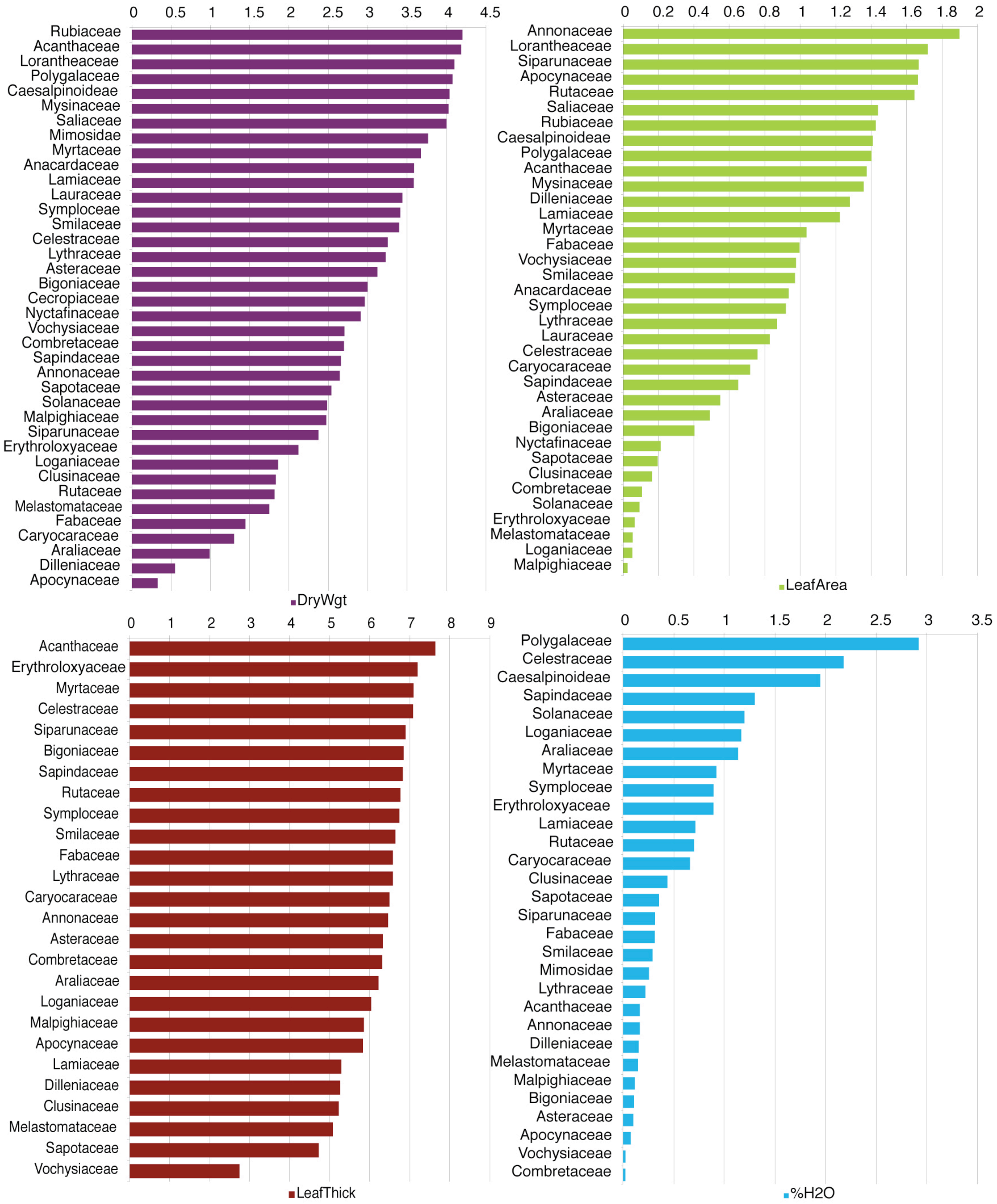

Figure 2.3.5C: Spectranomic trait variation by family in descending order of index value for the following traits: Leaf dry weight, Leaf area, Leaf thickness and Leaf water content.

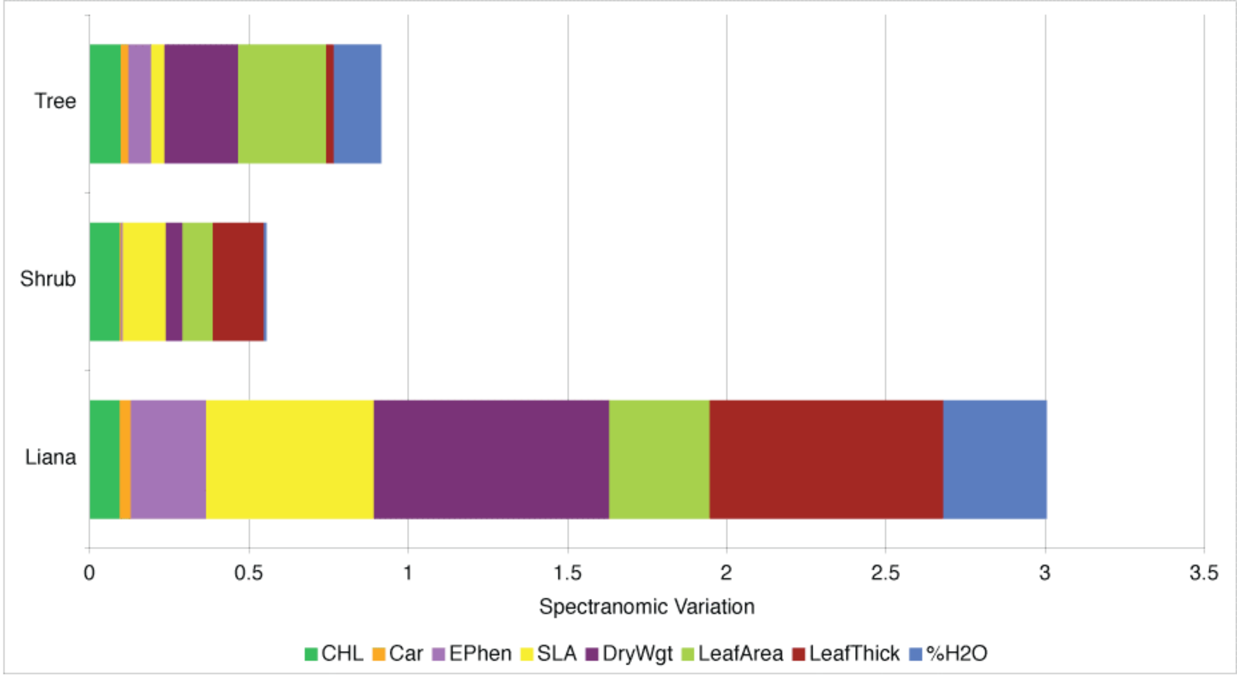

Figure 2.3.6: Spectranomic trait variation as grouped by life forms. Index value for each trait is calculated by the distance of that group's trait from the average of all groups traits over the standard deviation of all group traits. By having only three groups used to calculate this index, the apparent variation of traits is exaggerated. The larger distance from the mean of all groups seen here in the lianas for most traits is not indicative of a significant difference (Table 2.3.2, Figure 2.3.7)

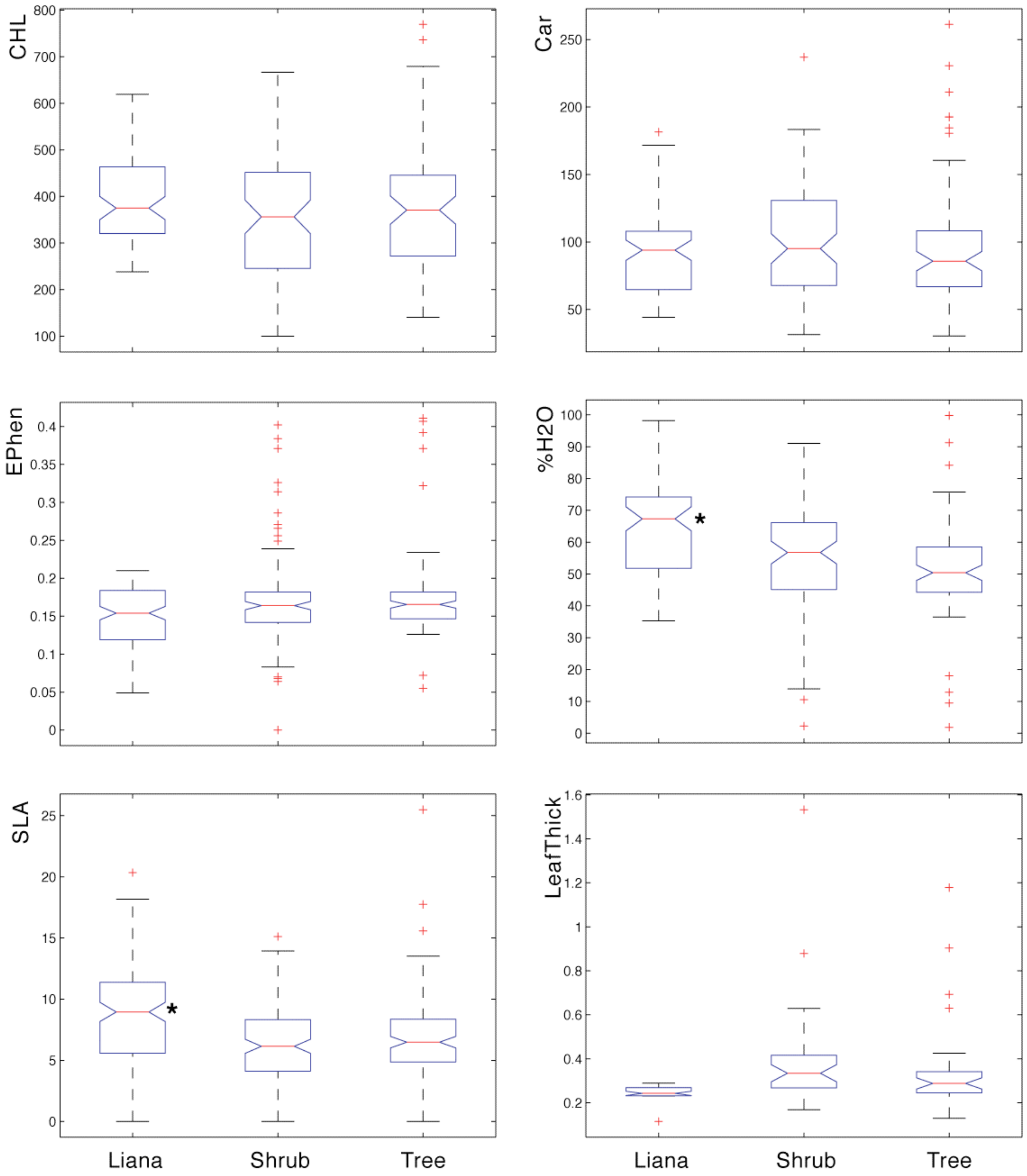

Figure 2.3.7: Comparison of leaf trait distributions between vegetation life forms. Means that significantly differ ($p<0.01$) under one-way ANOVAs are denoted with an asterisk. CHL = Total Chlorophylls A + B (mol), Car = Carotenoids (mol), EPhen = Polyphenol content, %H2O = Percentage Leaf Water Conent, SLA = Specific Leaf Area (m2 kg-1), LeafThick = Leaf thickness (mm)

Figure 2.3.8: Plenckia populnea was the only species present from the Celestraceae family. Although it occurred both as a canopy tree (left) and shrub (right) it was only measured from large individuals. The leaves of this species are thin and pliable.

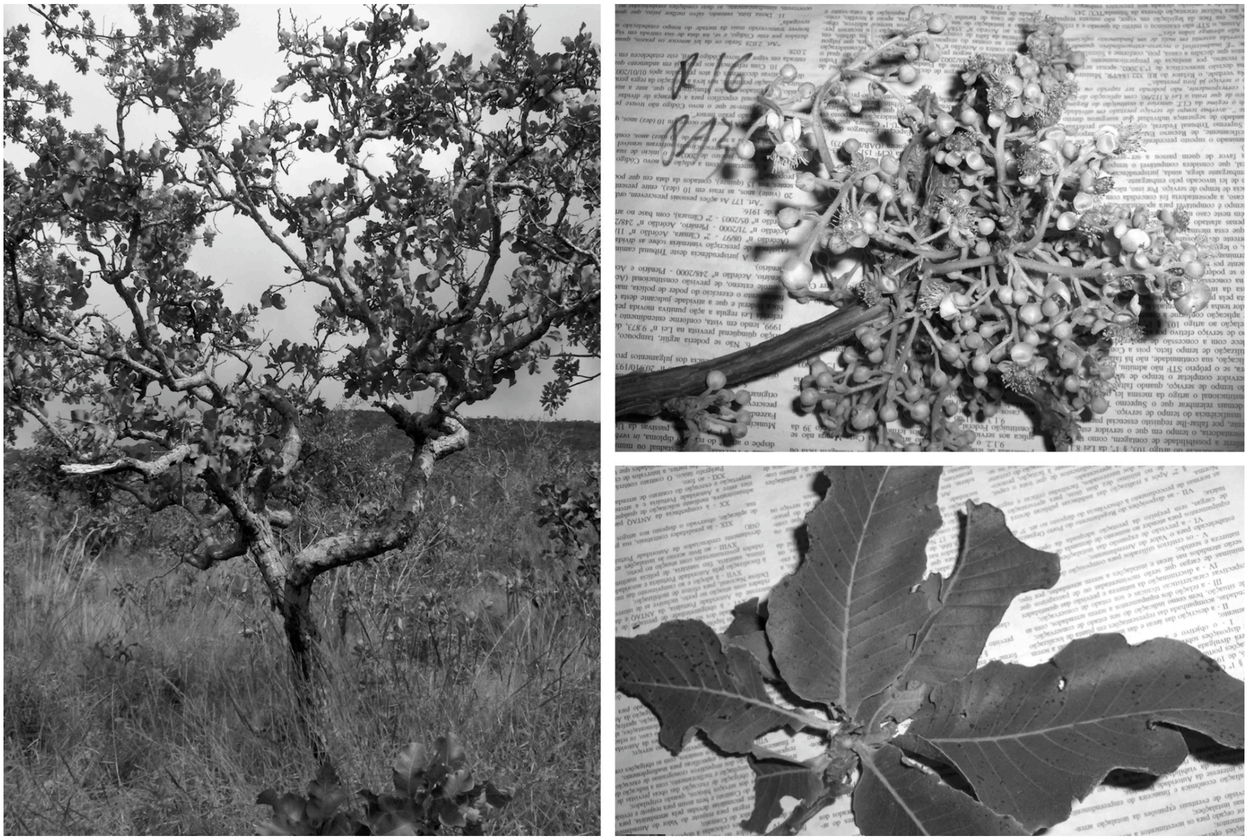

Figure 2.3.9: Curatella americana of the Dilleniaceae possesses thick sclerophyllous leaves with a sandpaper texture surface, the typical turning branch growth pattern of many Cerrado trees, and bloomed in early August.

Figure 2.3.10: Guapira cf. graciliflora of the Nyctafinaceae was sampled in four locations as shrub and tree, its leaves are thick with a velvety texture.

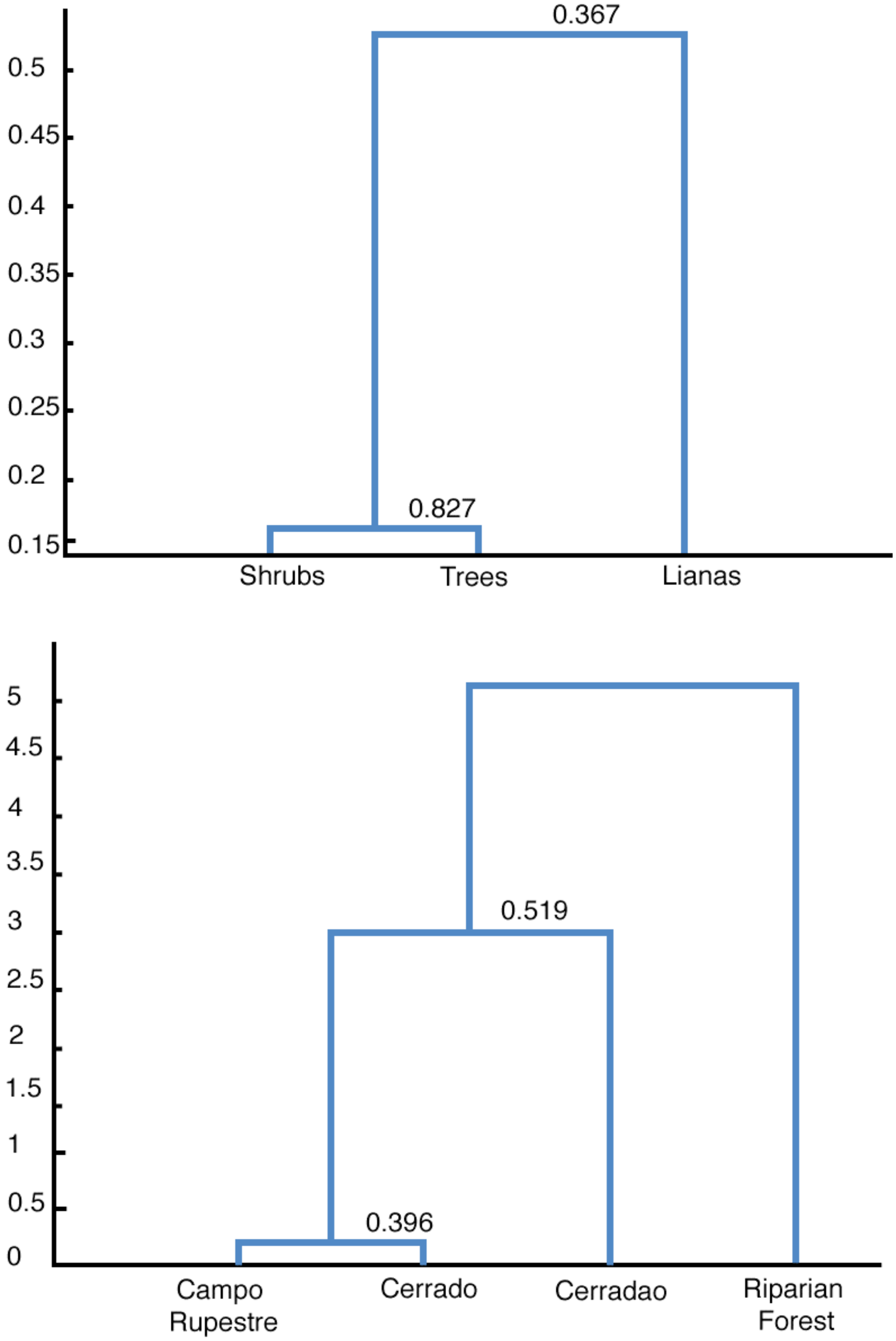

Figure 2.3.11: Decission trees illustrating the results of multivariate ANOVAs including all individuals with complete trait data. Only 71 individuals were sampled for all traits and included in this analysis. Neither life form nor site were significantly different to others, p-values shown on their respective branches.

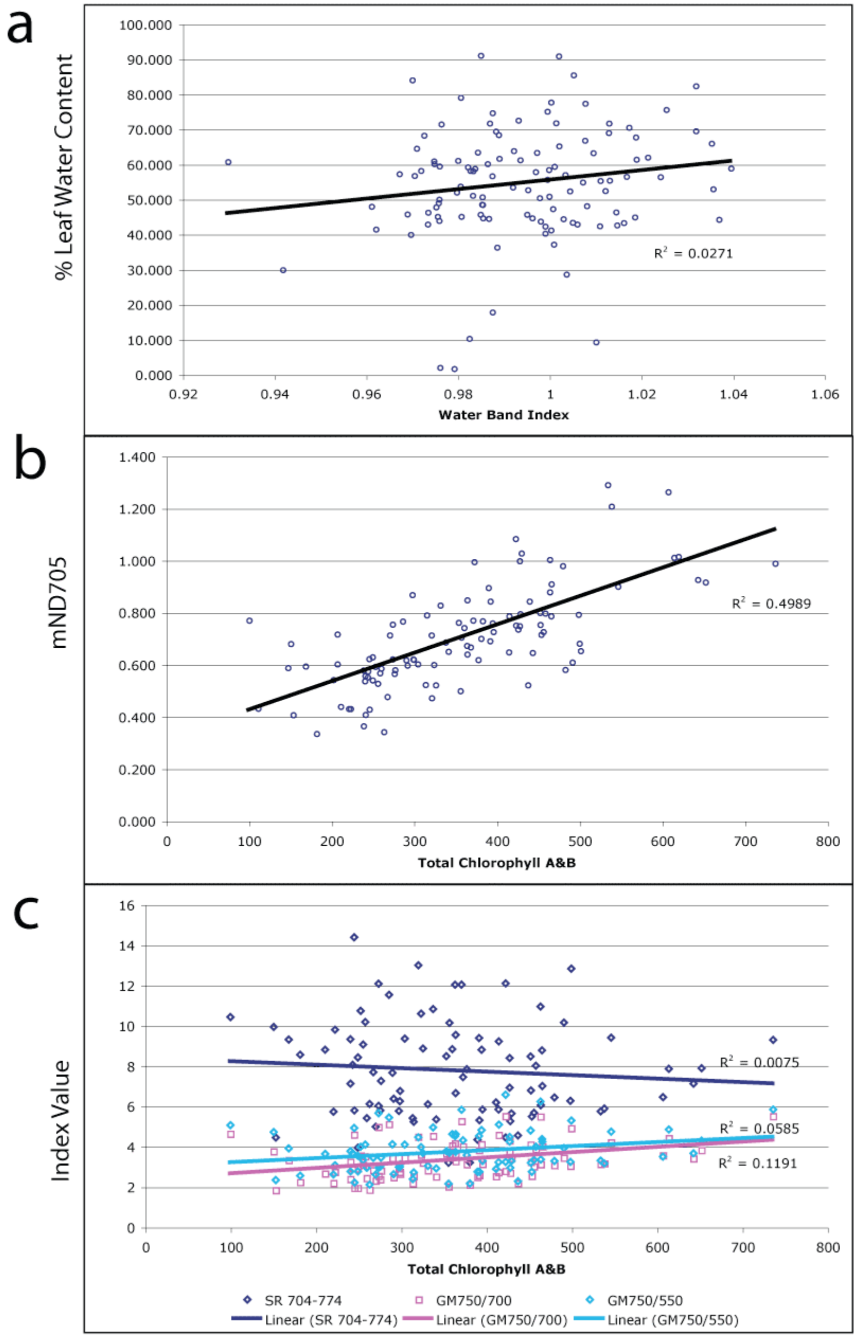

Figure 2.3.12 Ecophysiological traits regressed against related spectral indices. a) Water Band index (900-970/900nm) vs measured water content showed less connection than expected. b) mND705 Normalized Difference index relative showed a strong correspondence. c) Other chlorophyll indices were not as strong a correlatio

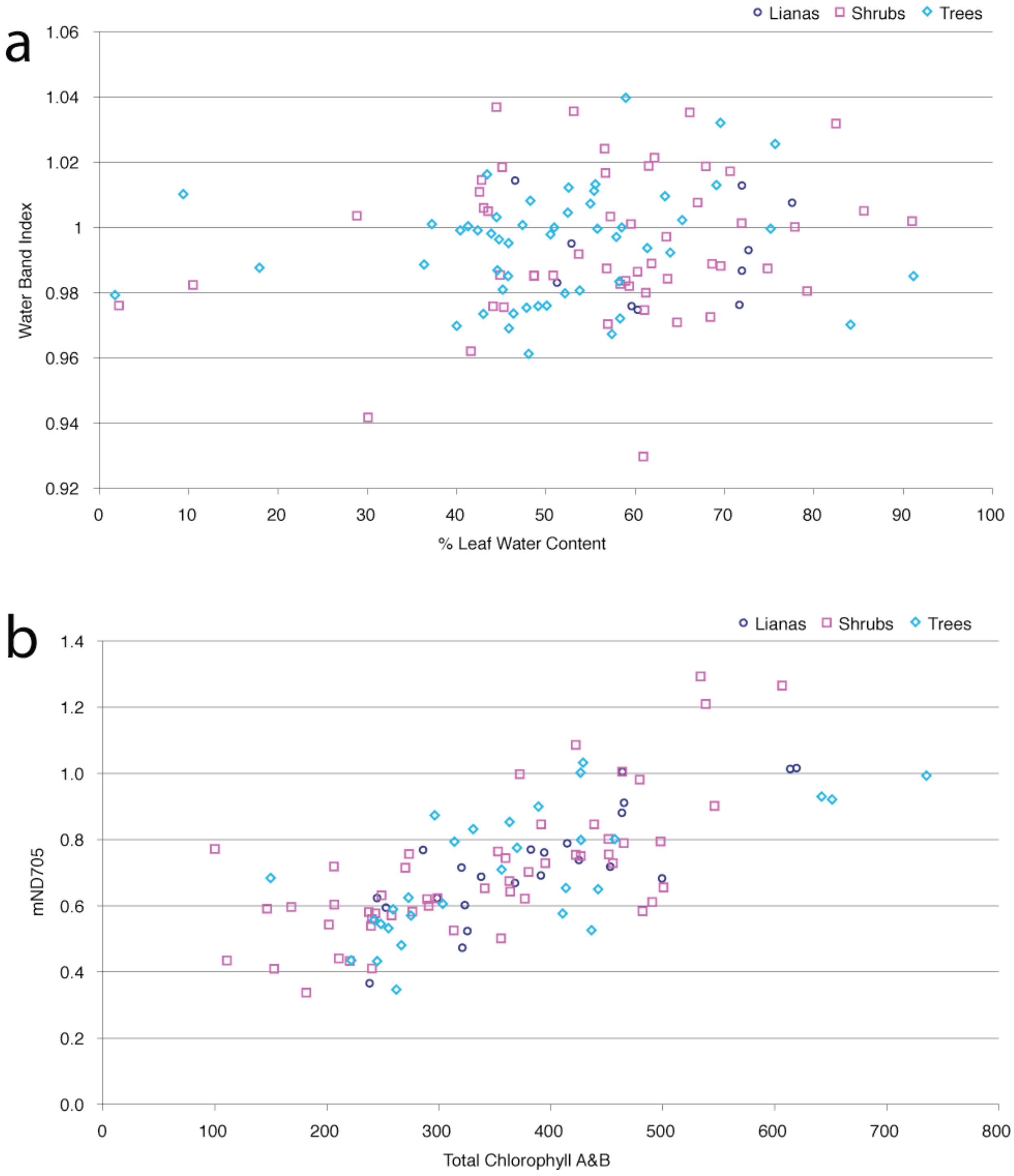

Figure 2.3.13 Leaf functional traits by life form compared to related spectral indices. Neither graph shown here represents a significantly different variation between groups, test by one-way ANOVAs. a) Water Band index (900-970/900nm) relative to leaf water content p=0.93, F=0.08 b) Normalized Difference index relative to total chlorophyll, p=0/84, F=0.18

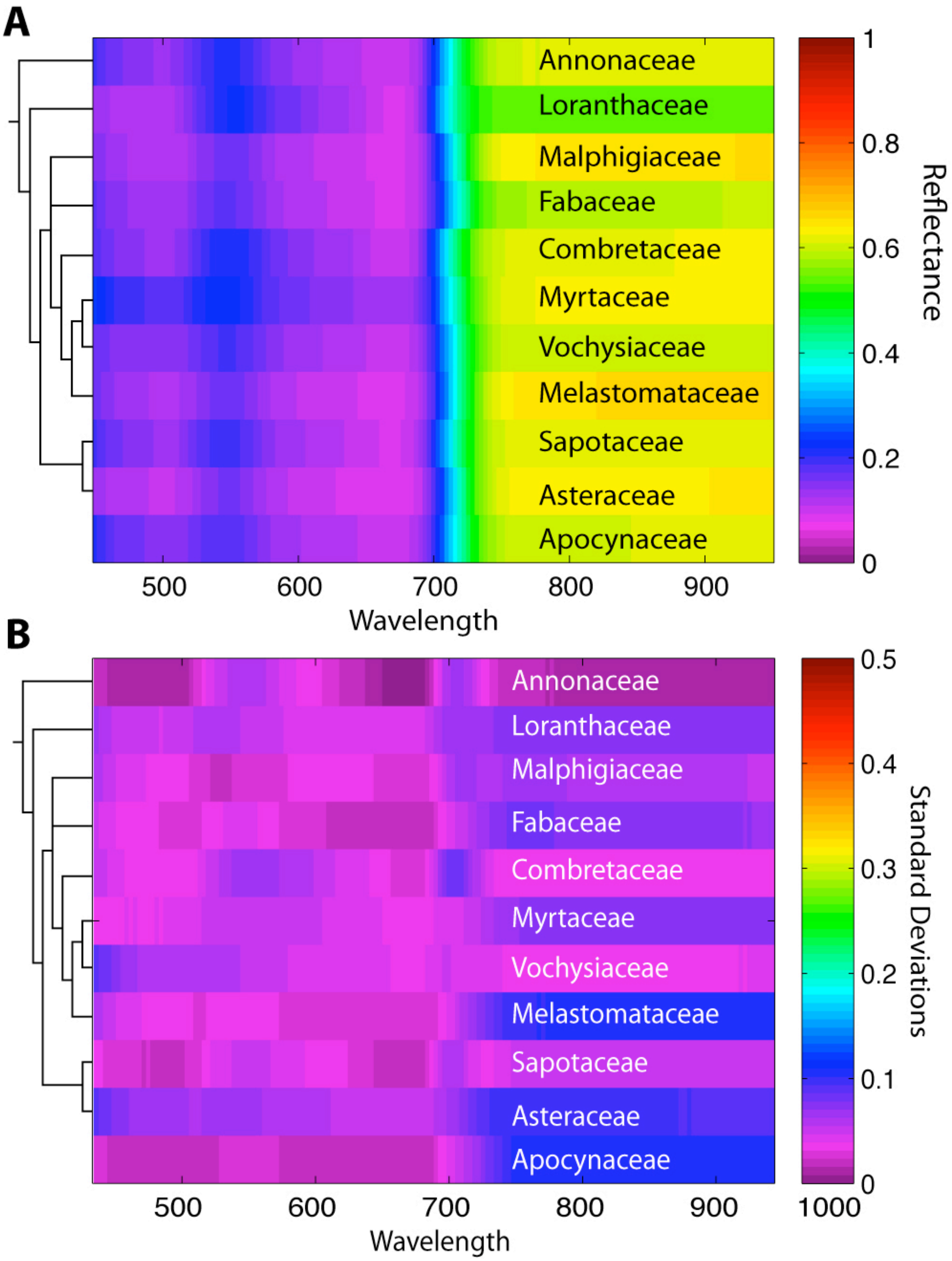

Figure 2.3.14 Spectral variation of the most abundant families in the study area across the wavelength of measurement. The trees at left represent the evolutionary trees of the families present (Angiosperm Phylogeny Group, 2008). Graph A = variation of average reflectance, Graph B = standard deviation across individuals within a family.

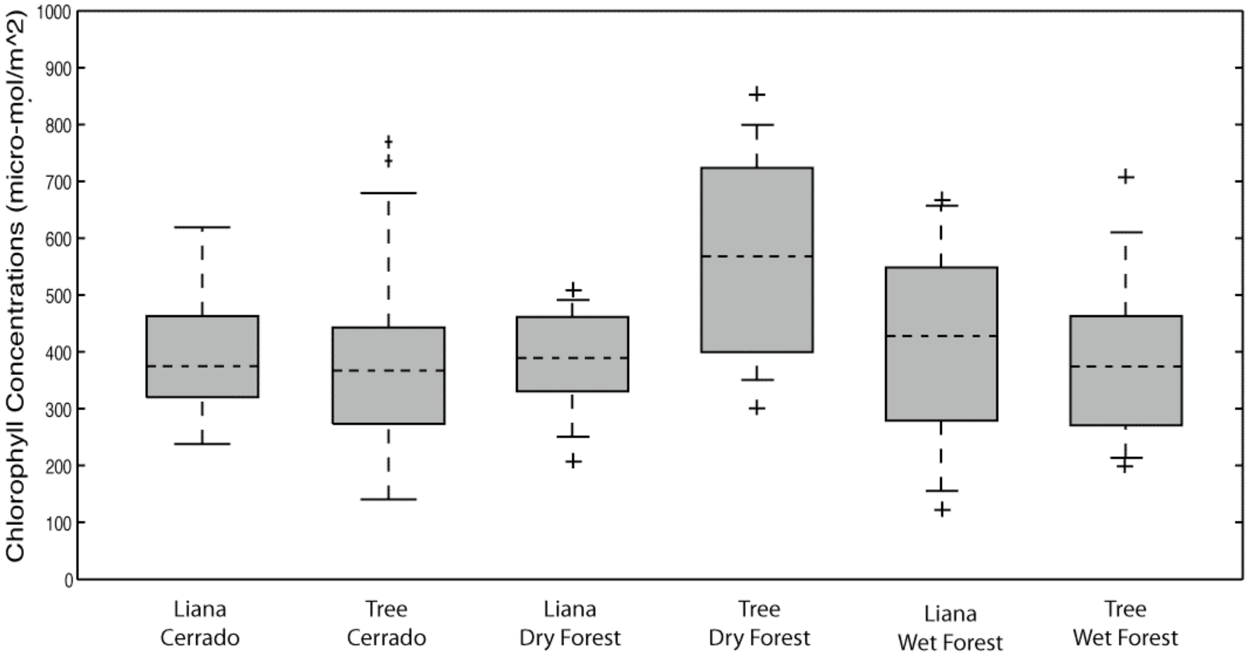

Figure 2.4.1 Comparison of Chlorophyll concentration variation within this study and life form data of a tropical forests of Panama from Sanchez et al (2009).

Chapter 3: Conclusions

3.1 Motivations for study

The aim of this study was to understand what concept of plant species grouping separates leaf traits better as a piece of the puzzle to describe plant diversity through remote sensing. Previous remote sensing of plant studies suggested morphological groups drove leaf reflectance (Sims and Gamon 2002; Castro-Esau et al. 2004; Kalacska et al. 2007a), though there was much progress in the more taxonomically focused practice of species discrimination (Price 1994; Clark et al. 2005). The location of this study, the Cerrado, has high endemism (Myers et al. 2000) a threatened biodiversity due to land use change (Klink and Machado 2005), and is considered a hotspot for future conservation work. Thus, this study fits within long term goals of developing a framework for biodiversity research at a landscape scale using remote sensing for describing the functional diversity of woody plant traits.

The objectives of this thesis were to answer the following questions, as quoted from chapter one:

1. *Are the functional groups described by niche and phenotype distinguishable by hyperspectral and ecophysiological traits?*
2. *Are the functional groups described by niche and phenotype distinguishable by spectral response? Which grouping method separates them best?*
3. *Can the functional diversity of Cerrado regions be estimated using these distinguishable spectral groupings?*

3.2 Significance & Implications

Objective 1

We found that functional groups to be a more significant grouping paradigm than taxonomy for the woody plants of the Cerrado. The functional group separation was stronger patterns of family separation for ecophysiological leaf traits. Thus we have fulfilled objective 1.

The implications of this result offers focus for future insight into the remote sensing of plant communities. Although much research has shown that certain species can be detected with remote sensing (Cochrane 2000; Schmidt and Skidmore 2003; Clark et al. 2005; Zhang et al. 2006) there is no consensus for which method performs best or consistently across species. Thus, the degree to which remote sensing of plant occurrences can be predictive or related to processes that affect them are limited until models relating the driver of plant spectra are formalized. To the author's knowledge, there have been no reviews or conceptual models proposed describing the patterns of species properties that make them spectrally distinct; nor has the discussion of - why some species are differentiable and others are not - been addressed to the same degree as if the target species in each study can be identified. Along with others (Asner and Martin 2008b; Asner and Martin 2008a) this study is a step towards creating models with such generality. (For previous studies evidencing the link of separable optical properties to functional groupings or traits, see sections 1 & 2.1)

The two strongest functional traits driving plant differentiation found in Cerrado vegetation were Specific Leaf Area (SLA) and Water Content. SLA is related to leaf water use efficiency (Hoffmann et al. 2005) and leaf water content to nutrient use efficiency (Bucci et al. 2006). Specific leaf area was found to have slight or varying effects relative to other whole-plant traits across the globe (Wright et al. 2004; Wright et al. 2007). SLA has been successfully used to distinguish forest and savanna species of the same genus within the Cerrado (Hoffmann et al. 2005). SLA has a strong linkage to water physiology in plants which is of particular importance to a xeric community such as the Cerrado (Furley 2006). SLA therefore appears to be a primary axis of variation between functional groups of the Cerrado, and is independent of other life history trade-offs within vegetation.

Thus, the affirmation of the importance of functional groups over taxonomic identification is a significant finding for future remote sensing of vegetation, and the traits we found as indicative of these groups (SLA and water content) are good candidates for spectral description. The ecological linkage to water balance and life history strategies encourages these traits as starting points for modelization.

Objective 2

The variation among ecophysiological traits and their relationships to associated spectral indices was not consistent or strong across traits. Leaf water content was weakly correlated to WBI. Indices related to total chlorophyll varied in the strength and direction of their relationship, with the strongest positive relationship being with mND750, an index previously designed for the UNISPEC index. For none of the indices did we find the ability to separate by functional groups or families. Thus, we were not able to fulfill objective 2 using indices.

Hyperspectral methods of spectral analysis are recommended to further explore the relationships between traits and observed spectra of plants. Two methods for investigation of vegetation using remote sensing are feature detection of signals relevant to plant ecology (such as biomass, NDVI, etc) or class discrimination using whole spectrum comparisons. Both of these types of approaches have advantages for understanding of plant spectra, but produce results useful for different tasks. Feature detection methods concentrate on band combinations that maximize the predictive variance of those specific wavelength related to a feature of interest, while standardizing to reduce the variation of wavelengths not caused by that feature. Spectral indices accomplish this feature quantification through arithmetic combinations of band values (Ceccato et al. 2002; Gobron et al, 1999), whereas wavelets accomplish this through a moving window analysis of the spectral structure (Blackburn 2007). In contrast, methods using whole spectrum for discrimination have taken the precedent from Price (1994), finding that even very similar spectra such as vegetation can be compared to each other with significant distinctions. This line of thought has lead to research such as Castro-Esau et al, (2004) and Clark et al. (2005) which produced motivations for this study. Shape comparisons (Price 1994), Spectral Angle Mapper, non-parametric classification methods; all fall under this same category of using inclusive hyperspectral information to determine the relative variation within similar spectral responses in order to discriminate among vegetation structural groups (eg.lianas vs. trees) or species. Unlike indices or feature detection, these types of remote sensing analysis are not focused on a specific region to test a specific variable but have class outcomes. The understanding of features is useful for understanding trait variation and discrimination approaches for finding detectable classes.

Analogous concepts between these remote sensing approaches and the methods of functional ecology offer ways to integrate the two fields. Like feature detection, functional ecology describes the status of ecophysiological variables, but ties the community status into mechanistic predictions of ecological processes. Whole spectrum patterns may best be used to discriminate functional groups that we have seen are constrained in some traits, but vary in others. The practical link between remote sensing and functional ecology is that imaging spectroscopy can be used to detect biophysical variables of vegetation which can be used to predict ecosystem function and properties (Ustin et al. 2004). For example, understanding canopy biochemistry allows estimation of key physiological traits changing under land changes such as biological invasion, succession and fire (Kokaly et al. 2009). This is a key area of research if functional traits are to be incorporated into a remote sensing research program.

Fortunately, the spectral library that this study has created describing the optical properties and related ecophysiological traits in leaves of Cerrado woody plants. As this data set comprises of 170 species, with more than 15 000 individual spectral measurements, it is a promising source for further remote sensing analysis and comparison to other Cerrado sites.

Objective 3

In this study, spectral response was not significantly connected to functional trait status, nor were other methods assayed. As a result, had functional diversity been calculated for the suite of plant individuals at a sampling site, there would be no spectral derivation of functional diversity understood the correspondence. Thus, this objective was not fulfilled, but the remainder of the chapter will be spent discussing what directions might resolve it.

Research needed to predict and monitor the distribution and dynamics of tropical vegetation communities are studies that bridge the gap between theoretical descriptions of a community and knowledge of species at a scale that remote sensing can provide (Alvarez-Ahorve et al. 2008). Community ecology describes community composition using functional ecology (McGill et al. 2006) and their effects on ecological processes (Suding et al. 2008). At a community level, functional diversity has a strong positive correlation to ecosystem function (Diaz and Cabido 2001; Hooper et al. 2005).

3.2 Future Insights

Linking Functional Ecology & Remote Sensing

The long-term goal of research context in which this study originated was to use remote sensing to assess biodiversity for large extent mapping of Cerrado plant communities to aid in its conservation. Preserving biodiversity is a major, ongoing worldwide goal (Butchart et al, 2010; Myers et al. 2000). We posit that remote sensing of plant traits and communities is integrally useful to functional ecology for quantifying biodiversity and the ecosystem functions provided.

Understanding processes that arises from patterns is a primary goal of ecology (Turner 1989), and thus general models of integrating plant properties and their spectral characteristics is a keystone issue in the future of integration of remote sensing technology into study of vegetation communities at the landscape scale. More specifically, descriptions of species location and biophysical variables are very important to biodiversity conservation (Ferrier 2002) and the effects of climate change on biogeography (Whittaker et al. 2005).

To extend our research to the remote sensing of biodiversity will require integration of: 1) discrimination of functional groups or trait status and 2) scaling from the leaf level to canopy level. Functional diversity is a possible avenue of scaling, since our study suggests structural groups are easier separated than individual species. The relationship of functional diversity of a region and it’s biodiversity has already been described as a strong positive correlation (McGill et al. 2006).

Diaz et al (2007) have provided a framework (Figure 3.2.1) to test the linkages between functional diversity and ecosystem properties. As an exercise to further research of remote sensing and functional traits in the context of Cerrado plant communities and biodiversity, we will describe possible studies for their steps as it pertains to our long-term goal. We are concerned about the loss of biodiversity in the Cerrado habitat, so the ecosystem property (EP) we will focus on is species richness.

Species richness is strongly correlated to ecosystem function (Diaz et al. 2007; Diaz and Cabido 2001; Petchey and Gaston 2006) but the relationship is complex. Taxonomic diversity and functional diversity have varying positive relationships with each other depending upon the rarity and importance of traits to ecosystem function (Naeem and Wright, 2003). The key traits for understanding ecosystem function are those which are reponse or effect traits; those which produce an ecosystem property, or are adaptative to that property (Naeem and Wright, 2003; Lavorel and Garnier 2002). These relationships between species and functional diversity and ecosystem function have not been tested in the Cerrado. There is a real need for diversity-function relationships to be tested at landscape scales (Srivastava and Vellend 2005). In the context of land use change, the change of species richness is mediated by trait selected filters of functional diversity (Mayfield et al, 2010). SLA, leaf dry matter content and leaf nitrogen are traits demonstrated to predict ecosystem properites such as decomposition rates and primary productivity in the context of land use change (Garnier et al. 2004). With some extension, our data is a starting point to ask how the Cerrado community composition and ecosystem function is changing.

Each stage in the Diaz et al (2007) framework provides step-wise additive variation to the prediction of the EP. As a result of this study, each sampling area has a known richness of the woody plants composing ~80% of the aboveground biomass.

Stage 1: Evaluate abiotic factors on the EP (richness).

Significant abiotic predictors of plant community richness are topography-based (Dobrowski et al. 2006), soil type based (Jensen, 1986), and water-based. Many of these questions can be addressed with existing data. Coarse-grained Cerrado vegetation classifications are already available (Ratana et al. 2005) and so are soil maps and coarse topography for prototyping at a regional scale. The national park of Serra do Cipo (Minas Gerais, Brazil) has been studied in depth over the years and detailed Geographic Iinformation Systems, Digital Elevation Models and validated vegetation maps already exist.

Stage 2: Test community weighted means (CWM) of the leaf traits we have relative to richness.

CWM is a measure of functional diversity that averages trait importance as a function of its biomass. Individual traits could also be used for testing their CWM as a predictor of richness. For example, the CWM of pigment or water content is likely to correspond to leaf biomass and be detectable at an imagery level as "greenness" which is well-linked to biomass and through NDVI.

Diaz et al (2007) state that the community mean is largely controlled by the relative abundance of the functional groups present; "the relative proportion of different growth forms (i.e. tussock grasses) can be used as CWM". Functional groups were found to be separable, thus could be used quickly as a CWM. To extend beyond our known sites, if spectral estimates proportional identities of these functional groups were possible in remotely sensed imagery, then landscape surfaces of CWM could be tested and refined.

Stage 3: Test the effect of trait value distributions (functional divergence) on richness.

Functional divergence is the degree of overlap of trait values within a community. This stage would test whether the breadth of functional traits in a site matters to richness.

Stage 4: Test whether there exist keystone species that reveal more information about the EP than the functional traits they have measured alone.

Our study made use of the largest individuals to capture the functional properties of the community as per Cornellissen et al (2003) and Grime (1998) through the mass-ratio hypothesis, suggests that the community traits are most influenced by those of higher relative abundance/biomass. Species which would act as keystones but not be captured by our current methods could be revealed by expert Cerrado ecologists. This can be potentially addressed through the species discrimination techniques already mentioned to have been successful. Since there are certain large, emergent trees that dominate the canopy (Figure 3.2.2) keystone species of this nature have the potential to be detected with existing methods of signal detection, in addition to offering additional tests of scaling relationships between leaf and canopy level.

In summary, the prediction of plant community functional group proportion and therefore the community weighted mean of a trait linked to species richness is a primary linkage to apply remote sensing techniques to the needs of functional ecology, and address ecosystem properties that provide ecosystem services at a landscape extent. Our study suggests that SLA is a good trait to focus detection efforts due to its apparent role as a proxy for functional groups in determining ecosystem properties.

3.3 Figures

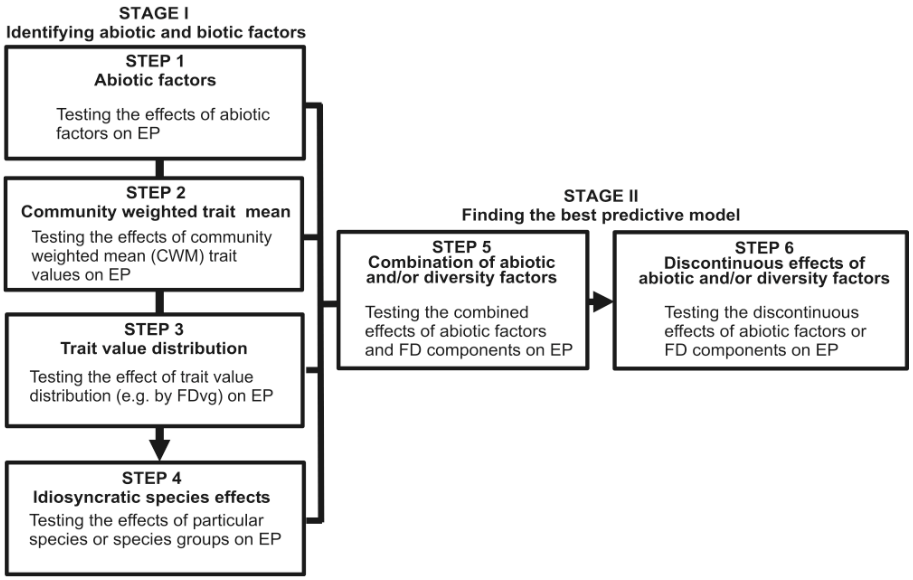

Fig. 1. Diagrammatic representation of the steps proposed to reduce uncertainty in the prediction of EP and ES on the basis of plant FD. In stage I, the models tested at each step (M1–M4) link EP with driving factors of different nature: abiotic factors (AF_i), community-aggregated trait value or CWM of any one functional trait (CWM_i), distribution of values of any one trait present in a community ($FDvg_i$), and local abundance of any one species present in the community ($Ab\ sp_i$). At each step, significant factors are identified and conserved for stage II. In stage II, combined models are built by adding statistically significant factors from steps 1–4 and conserving those that significantly improve the model (following a standard criterion, e.g., the Akaike criterion). The process concludes when further information on FD does not reduce uncertainty in EP prediction any further. Generalized models for each step are as follows: M1, $EP = f(AF_i, AF_j, \ldots, AF_n)$; M2, $EP = f(CWM_i, CWM_j, \ldots, CWM_n)$; M3, $EP = f(FDvg_i, Fdvg_j, \ldots, Fdvg_n)$; M4, $EP = f(Ab\ sp_i, Ab\ sp_j, \ldots, Ab\ sp_n)$; M5, $EP = f(AF_i, CWM_j, FDvg_k, \ldots, Sp\ Ab_n)$; M6, if $CWM_i < T$ then $EP = f1(CWM_i)$; if $CWM_i > T$ then $EP = f2(CWM_i)$; if $CWM_i = T$ then EP cannot be predicted from CWM_i. T = threshold (see stage II, step 6).

Figure 3.2.1: Step-wise modelling approach to determine contribution of functional diversity to ecosystem properties; Figure 1 of from Diaz et al (2007)

Figure 3.2.2: Two large canopy tree individuals (*Copaiba sp.*) roughly the size of a LANDSAT pixel (30x30m) as examples of specific targets to test the relationship of leaf to top-of-atmosphere reflectance

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Appendix 1

On the following five pages, the summary statistics (count, average and standard deviation) for leaf traits are listed for the species sampled in this study. They are displayed in descending order of the most sampled families, the number of individuals corresponding to roughly to biomass and relative abundance using our sampling methods. Please see Figure 2.3.2 for comparison of total numbers of individuals sampled and Figure 2.3.5 for a comparison of the variation between leaf traits of families using spectranomics.

				Dualex		Dry Weight		SLA		Wet Weight	
Family	**Species**	**Life Form**	**Count**	**average**	**standard deviation**	**average**	**standard deviation**	**average**	**standard deviation**	**average**	**standard deviation**
Melastomataceae	*Maieta sp.*	shrub	3	5.98	0.82	0.51	0.05	20.86	6.39	1.40	0.32
Melastomataceae	*Miconia albicans*	shrub	8	3.76	0.66	1.17	0.49	45.28	5.90	1.05	0.31
Melastomataceae	*Miconia stenostachya*	shrub	7	2.99	0.27	0.39	0.15			1.26	0.44
Melastomataceae	*Miconia ibaguensis*	shrub	3	3.65	0.14	0.11	0.03	90.96	9.04	0.64	0.36
Melastomataceae	*Miconia ibaguensis*	tree	1	3.11	0.10	0.88	0.19				
Melastomataceae	*Miconia sp.*	shrub	2							1.02	0.15
Melastomataceae	*Miconia sp. 'broadleaf' (unknown 1)*	shrub	5	4.01	0.66	3.57	1.25			9.03	2.87
Melastomataceae	*Miconia sp. 'light' (unknown 2)*	shrub	4	2.87	0.25	0.32	0.09	95.87	8.51	1.69	0.34
Melastomataceae	*Miconia sp. 'fuzzy' (unknown 3)*	shrub	2	3.22	0.33	0.34	0.11	92.26	42.94	0.73	0.27
Melastomataceae	*Mouriri cf glazioviana*	shrub	1	2.71	0.46	0.69	0.15				
Melastomataceae	*Tibouchina sp.*	shrub	4	3.00	0.22	0.13	0.03	105.16	26.56	0.37	0.08
Melastomataceae	*Unknown*	shrub	1			0.60	0.29				
Fabaceae	*Andira sp*	tree	1			0.11	0.01	121.54	22.08		
Fabaceae	*Andira fraxinifolia*	shrub	3	3.08	0.09	0.36	0.10			1.34	0.17
Fabaceae	*Bauhinia*	tree	6	3.31	0.17	1.38	0.42	123.59	16.87	0.57	0.08
Fabaceae	*Bowdichia virgilioides*	tree	1			0.24	0.10				
Fabaceae	*Caesaria sp.*	shrub	3	3.49	0.32	0.15	0.03	93.61	36.01	0.36	0.10
Fabaceae	*Chamaecrista*	shrub	1	3.07	0.50					1.05	0.30
Fabaceae	*Enterolobium gummiferum*	tree	3	3.34	0.41	0.16	0.02			0.80	0.29
Fabaceae	*Hymenaea courbaril*	shrub	3	3.17	0.26	0.64	0.14	108.00	23.44	1.53	0.78
Fabaceae	*Hymenaea courbaril*	tree	1	3.14	0.12	1.91	0.51				
Fabaceae	*Machaerium opacum*	tree	5	2.77	0.27	2.70	0.84	73.50	12.48	4.33	1.50
Fabaceae	*Pauteria romiflora*	shrub	2	2.83	0.31	0.22	0.06			0.63	0.25
Fabaceae	*Plathymenia reticulata*	shrub	1			1.49	0.54				
Fabaceae	*Pterodon pubescens*	shrub	3	2.93	0.07	0.48	0.11	82.09	3.75		
Fabaceae	*Pterodon pubescens*	tree	3	2.83	0.14	1.06	0.26	116.47	52.74	0.95	0.16
Fabaceae	*Qualea multiflora*	tree	3	2.73	0.46	0.29	0.05	97.16	16.93	0.52	0.10
Fabaceae	*Qualea grandifolia*	tree	2	2.11	0.54	1.65	0.77			1.08	0.20

Fabaceae	*Strychnophendron adstringens*	tree	3	3.25	0.13	0.30	0.12			1.44	0.19
Malpighiaceae	*Banisteriopsis sp. (unknown 1)*	liana	7	3.30	0.75	0.72	0.15	62.55	10.71	1.56	0.65
Malpighiaceae	*Banisteriopsis sp. (unknown 2)*	shrub	1	3.58	0.24	0.65	0.12				
Malpighiaceae	*Bunchosia sp.*	liana	2	2.02	0.32	0.31	0.05				
Malpighiaceae	*Byrsonima sp.*	shrub	5	4.52	0.66	0.46	0.14	32.43	10.57	1.04	0.51
Malpighiaceae	*Byrsonima verbascifolia*	shrub	6	3.38	0.39	1.92	0.56	155.82	38.09	6.51	2.66
Malpighiaceae	*Peixotoa tomentosa*	shrub	1			0.30	0.09				
Malpighiaceae	*Unknown*	shrub	1	4.20	0.18						
Asteraceae	*Eremanthus sp.*	shrub	1	3.53	0.24					0.43	0.09
Asteraceae	*Eremanthus cf elegaenus*	shrub	3	3.21	0.18	0.15	0.03	78.56	7.76		
Asteraceae	*Eremanthus erythropappus*	shrub	6	3.28	0.43	0.11	0.04	94.60	4.53	0.12	0.03
Asteraceae	*Eremanthus glomerulatus*	tree	1	3.86	0.29						
Asteraceae	*Erymanthus glomerulatus*	shrub	7	3.57	0.26	0.65	0.17	99.22	25.58	2.46	0.86
Asteraceae	*Gochnatia polymorpha*	shrub	2	4.34	0.75	0.70	0.23	30.03	11.80		
Asteraceae	*Piptocarpha rotundifolia*	shrub	4	3.42	0.72	0.49	0.11	68.32	9.64	0.80	0.30
Asteraceae	*Unknown*	shrub	2	3.22	0.17	1.22	0.33			1.92	0.53
Asteraceae	*Rudgea viburnoides*	shrub	1	3.24	0.42	0.78	0.28	65.32	10.40		
Apocynaceae	*Unknown*	shrub	1	3.58	0.13					0.94	0.45
Apocynaceae	*Aspidosperma sp1*	shrub	4	6.96	0.95	1.31	0.26	15.49	7.18	2.57	2.39
Apocynaceae	*Aspidosperma tomentosum*	shrub	3	3.74	0.23	1.99	0.51			7.99	3.14
Apocynaceae	*Campomanesia cf. pubescens*	shrub	1	3.75	0.35					0.50	0.07
Apocynaceae	*Forsteronia sp.*	liana	1	0.98	0.36					0.38	0.11
Apocynaceae	*Forsteronia sp1*	tree	2			0.29	0.03				
Apocynaceae	*Stipecoma peltigera*	liana	1	3.40	0.44	0.32	0.03				
Apocynaceae	*Tocoyena formosa*	tree	3	3.39	0.16	3.04	0.85			5.31	1.09
Apocynaceae	*Unknown*	liana	1	3.39	0.15					2.87	1.07
Combretaceae	*Unknown*	shrub	1	3.22	0.39	0.39	0.14				
Combretaceae	*Unknown*	shrub	1	3.04	0.20	0.33	0.06	63.61	2.24		
Combretaceae	*Unknown*	tree	1	2.55	0.54	1.01	0.42				

Combretaceae	*Buchenavia sp.*	shrub	4	3.00	0.17	0.40	0.08	58.60	7.31	0.42	0.13
Combretaceae	*Qualea grandifolia*	tree	1	3.39	0.10	1.72	0.42			3.94	0.90
Combretaceae	*Terminalia cf argentina*	tree	1	3.57	0.29						
Combretaceae	*Terminalia glabrescens*	tree	2	2.38	0.30						
Myrtaceae	*Campomanesia adamantium*	shrub	1	3.17	0.37	0.23	0.06	80.61	21.95		
Myrtaceae	*Campomanesia adamantium*	tree	1	2.79	0.14	0.23	0.05				
Myrtaceae	*Eugenia brasilensis*	shrub	2	2.01	0.61	0.49	0.12				
Myrtaceae	*Eugenia dysenterica*	tree	1	3.92	0.82	0.37	0.07	70.87	22.43	0.59	0.27
Myrtaceae	*Eugenia sp.*	tree	1	3.46	0.68	0.05	0.01	157.81	53.50	0.15	0.05
Myrtaceae	*Myrcia guianensis*	shrub	1	1.40	0.39	0.09	0.02				
Myrtaceae	*Myrcia tomentosa*	shrub	1	3.06	0.38	0.66	0.10				
Myrtaceae	*Myrcinaria delicatula*	shrub	3	2.44	0.31	0.03	0.01	91.56	10.72		
Caryocaraceae	*Caryocar brasilensise*	tree	10	3.35	0.25	1.21	0.37	74.06	21.42	2.75	1.15
Lamiaceae	*Eriope macrostachya*	tree	4	2.64	0.89	0.05	0.01			0.25	0.20
Lamiaceae	*Unknown*	shrub	3	3.02	0.49	0.51	0.13			1.18	0.30
Lamiaceae	*Hyptidendron cf. canum*	shrub	4	7.89	0.46	0.27	0.09			2.65	0.75
Lamiaceae	*Hyptis sp1*	shrub	1	4.21	0.95	0.12	0.18	0.18	0.04		
Lamiaceae	*Hyptis sp2*	shrub	1	4.79	1.40	0.08	0.04				
Sapindaceae	*Matayba mollis*	tree	2	2.60	0.37	0.36	0.13				
Sapindaceae	*Serjania*	liana	4	2.30	0.22	0.69	0.33	119.88	58.63	2.16	1.20
Sapindaceae	*Serjania*	liana	4	2.31	0.17	0.86	0.26	90.52	11.02		
Sapindaceae	*Serjania*	liana	8	2.30	0.19	0.77	0.29	105.20	34.83	2.16	1.20
Sapotaceae	*Unknown*	liana	1	2.22	0.40					1.63	0.94
Sapotaceae	*Himatanthus drasticus*	shrub	1	3.41	0.29	1.20	0.25				
Sapotaceae	*Mysine*	tree	2	3.06	0.14	0.54	0.09			0.95	0.21
Sapotaceae	*Pauteria sp1*	tree	2			0.30	0.07				
Sapotaceae	*Pauteria torta*	tree	2	3.82	0.05	1.00	0.13	77.92	24.98	2.75	0.66
Sapotaceae	*Pouteria ramiflora*	tree	2	2.91	0.12	0.55	0.17	77.94	31.30	1.21	0.23
Sapotaceae	*Pouteria sp1*	tree	1	3.20	0.13						
Sapotaceae	*Pouteria sp2*	tree	1	2.72	0.19	0.27	0.07				
Sapotaceae	*Pouteria sp3*	tree	1	3.46	0.09	1.18	0.15	23.51	12.52	1.04	0.58
Bigoniaceae	*Lundia*	liana	4	3.79	0.42	0.81	0.38	73.42	44.70	1.56	0.57
Bigoniaceae	*Pyrostegia venusta*	liana	3	3.05	0.26	0.19	0.10			0.44	0.09
Bigoniaceae	*Unknown*	liana	1	3.00	0.32						

Vochysiaceae	*Qualea*	tree	2			0.51	0.18				
Vochysiaceae	*Vochysia*	tree	3	4.51	0.68	1.18	0.26			3.48	0.84
Vochysiaceae	*Vochysia cf. elliptica*	shrub	2	3.53	0.37	0.40	0.17			0.81	0.25
Vochysiaceae	*Unknown*	tree	1	4.28	0.28						
Araliaceae	*Schefflera sp.*	tree	3	3.00	0.19	2.16	0.81			2.39	0.56
Araliaceae	*Schefflera sp.*	tree	3	5.06	0.26	0.85	0.24	41.17	3.02	2.83	1.43
Celestraceae	*Plenckia populnea*	tree	5	3.61	0.12	0.31	0.09	84.61	9.74	0.49	0.19
Celestraceae	*Roupala montana*	tree		2.93	0.12					2.06	0.92
Annonaceae	*Annona sp1*	tree	1	3.82	0.40	0.77	0.29				
Annonaceae	*Annona sp2*	tree	3	3.94	0.25	0.77	0.47			1.41	0.53
Annonaceae	*Unknown*	tree	1	4.14	0.12	1.08	0.24				
Clusinaceae	*Kielmeyera*	tree	4	3.60	0.12	1.69	0.36			4.29	2.04
Clusinaceae	*Kielmeyera petrolaris*	tree	2	2.98	0.13	0.58	0.09	1.62	0.09		
Dilleniaceae	*Curatela americana*	tree	2	3.25	0.37	1.21	0.50	79.42	22.27	4.01	1.13
Dilleniaceae	*Davilla rugosa*	tree	2	3.61	0.61	0.46	0.12			0.66	0.12
Dilleniaceae	*Tabebuia aurea*	tree	1	8.14	0.15	1.89	0.59	45.21	27.13	3.74	1.57
Loganiaceae	*Strychnos cf Pseudoquina*	tree	5	4.15	0.18	1.02	0.21	50.56	5.26	1.49	0.27
Mimosidae	*Caliandra*	shrub	5	2.47	0.30	0.22	0.07			2.08	0.54
Acanthaceae	*Justicia*	liana	3	1.25	0.77	0.08	0.02			0.17	0.03
Acanthaceae	*Ruellia sp.*	shrub	2	4.73	0.88					0.14	0.06
Acanthaceae	*Unknown*	shrub	1	1.67	0.45						
Cecropiaceae	*Cecropia glazioui*	shrub	3	3.56	0.40					29.37	20.82
Erythroloxyaceae	*Erythroxylum suberosum*	shrub	1	3.60	0.10	0.51	0.14			2.14	0.86
Erythroloxyaceae	*Erythroxylum tortuosum*	shrub	3	2.55	0.86	1.18	0.31			2.02	0.34
Lorantheaceae	*Struthanthus*	liana	4	3.65	0.45	0.11	0.03			0.43	0.14
Lorantheaceae	*Unknown*	shrub	1	4.33	0.88						
Mysinaceae	*Myrsine cf. umbellata*	shrub	1	2.71	0.35	0.22	0.07				
Mysinaceae	*Myrsine coriacea*	tree	1			0.10	0.01	135.11	8.92		
Mysinaceae	*Myrsine sp*	tree	1	3.38	0.16	0.16	0.03	79.70	4.81		
Siparunaceae	*Siparuna cf guianensis*	shrub	4	2.88	0.26	0.81	0.19	110.80	25.70	2.28	0.63
Solanaceae	*Solanum lycocarpum*	shrub	4	4.00	0.38	0.77	0.25			1.06	0.23
Symploceae	*Tapirira guianensis*	tree	3	3.38	0.22	0.41	0.11	83.93	17.98	0.55	0.18
Caesalpinoideae	*Chamaecrista*	tree	2	2.79	0.58	0.13	0.04			0.29	0.06
Lythraceae	*Lafoensia cf. pacari*	shrub	2	4.01	0.16	0.47	0.14	72.86	23.23	1.22	0.21

Nyctafinaceae	*Unknown*	tree	1	1.10	0.14	0.14	0.03				
Nyctafinaceae	*Guapira cf. graciliflora*	tree	3	3.10	0.14	0.92	0.21				
Polygalaceae	*Bredemeyera*	liana	1	3.12	0.25	0.19	0.05	93.81	10.10		
Polygalaceae	*Securidaca sp*	liana	1								
Rutaceae	*Zanthoxylum*	tree	2	3.48	0.12	1.04	0.29	59.96	31.60	1.64	0.63
Saliaceae	*Casearia cf obliqua*	shrub	1			0.13	0.01			1.73	0.57
Smilaceae	*Smilax*	liana	2	2.69	0.33	0.30	0.06			0.98	0.27
Anacardaceae	*Tapirira guianensis*	shrub	1	3.65	0.18	0.50	0.19				
Anacardaceae	*Tapirira guianensis*	tree	1	3.71	0.27	0.32	0.09				
Aquifoliaceae	*Unknown*	shrub	1			0.06	0.01	142.85	7.12		
Aquifoliaceae	*Unknown*	tree	1	3.43	0.17	0.27	0.05				
Lauraceae	*Ocotea*	shrub	1			0.38	0.09	73.88	4.65		
Rubiaceae	*Psychotria*	liana	1			0.14	0.24				
Unknown	*Unknown 1*	liana	1			0.17	0.04				
Unknown	*Unknown 2*	liana	1	2.58	0.26	0.31	0.15				
Unknown	*Unknown 3*	shrub	1	2.80	0.16	1.51	0.51				
Unknown	*Unknown 4*	tree	1	3.95	0.77	0.16	0.04				
Unknown	*Unknown 5*	tree	3	3.22	0.22	0.63	0.20			0.79	0.21
Viscaceae	*Phorandendron*	liana	2	2.46	0.48	0.63	0.12			2.57	0.44
Unknown	*Unknown 6*	tree	1			1.20	0.40	59.81	6.36		
Flacourtiaceae	*Casearia cf arborea*	shrub	1	1.76	0.14	0.18	0.05				