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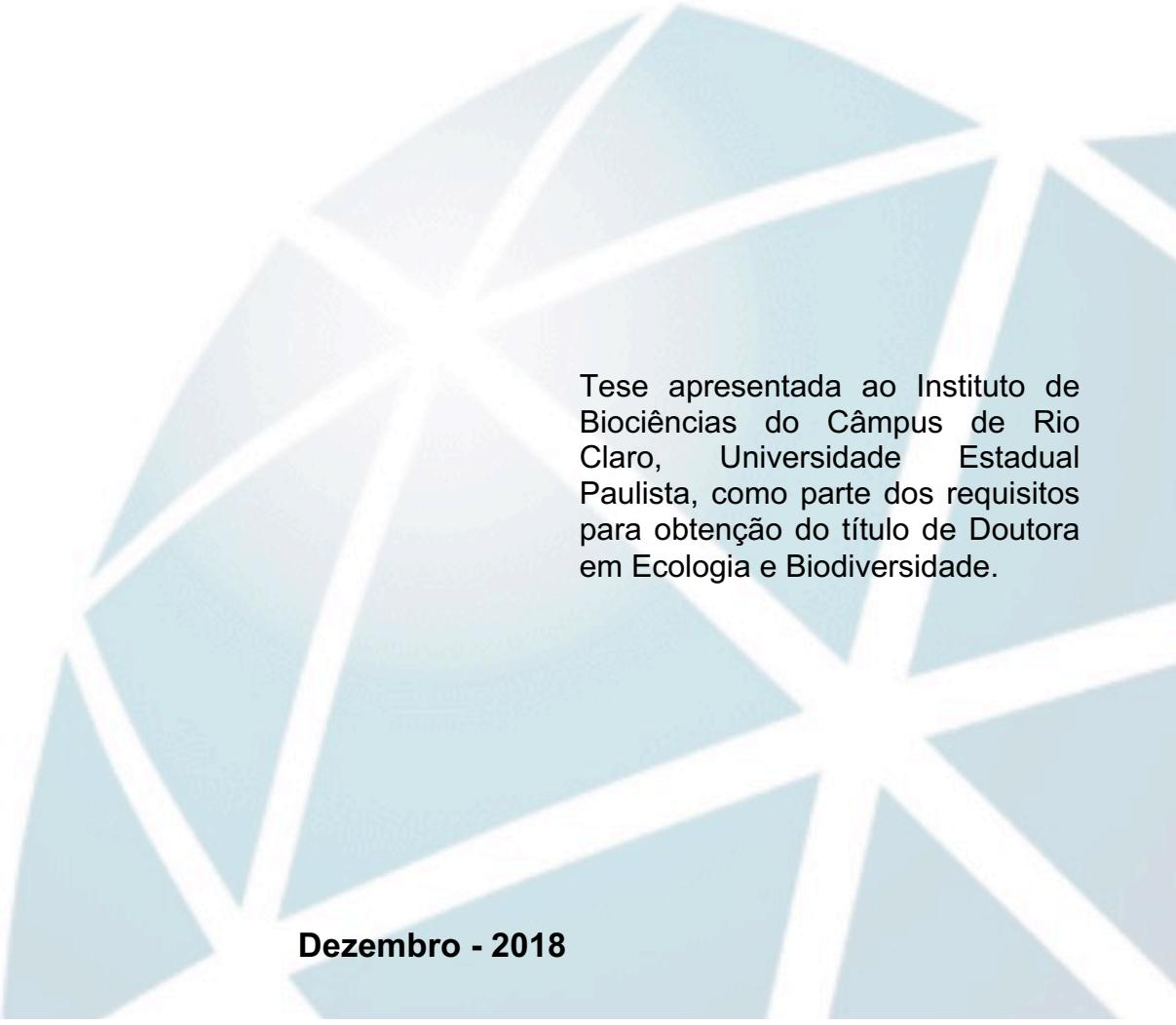
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PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E BIODIVERSIDADE

**PHENOTYPIC AND OPTICAL PLANT TRAIT VARIATION ACROSS SPACE AND
TIME IN THE SEASONAL TROPICS: PATTERNS, DRIVERS AND
CONSEQUENCES**

ANNIA SUSIN STREHER

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Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutora em Ecologia e Biodiversidade.

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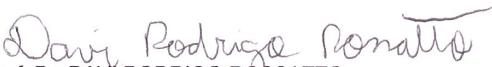
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Rio Claro, 14 de dezembro de 2018

This work is dedicated to all women in science. You are a true inspiration.

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A learning experience is one of those things that says,
‘You know that thing you just did? Don’t do that’

-Douglas Adams-

DECLARAÇÃO

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RESUMO

O objetivo geral dessa tese foi explorar os conceitos da ecologia baseada em atributos a fim de entender como o ambiente modula a variação de atributos funcionais em diferentes escalas espaciais e temporais, combinando sensoriamento remoto e ecologia vegetal. No segundo capítulo da tese, avaliou-se os padrões de fenologia remota do mosaico de vegetação na montanha do Espinhaço, investigando quais os agentes ambientais são responsáveis pelos padrões observados. O algoritmo TIMESAT foi utilizado para extrair os indicadores fenológicos de uma série temporal de 14 anos de imagens de satélite MODIS/NDVI. A disponibilidade de água e luz, modulada pela topografia, foram os principais responsáveis pelas respostas da fenologia remota na região, determinando o início, fim e comprimento da estação de crescimento. A temperatura teve um papel importante na determinação das taxas de desenvolvimento das folhas e na força da sazonalidade da vegetação. No capítulo três, testou-se a generalidade dos padrões globais de estrutura e função da vegetação na escala da paisagem, na porção sul do Espinhaço, conhecida como Serra do Cipó em Minas Gerais. Também buscou-se determinar a relação dos atributos funcionais que representam as dimensões de estrutura e função da vegetação com os gradientes de elevação e topo-edáficos encontrados na região. Foram coletadas características funcionais (LMA, LDMC – relacionados à economia foliar, área foliar e altura da planta – relacionados com a estrutura da vegetação) de 1650 indivíduos, compreendendo todas as formas de vida, em cinco locais ao longo de um gradiente de elevação, abarcando os diferentes tipos de vegetação encontrados em cada elevação. A organização fenotípica na estrutura e função das plantas encontrada em escalas globais foi análoga à encontrada entre as espécies que co-ocorrem localmente nos campos rupestres. A dimensão relacionada a estrutura da vegetação apresentou variação ao longo dos gradientes ambientais, porém as relações alométricas foram igualmente importantes para explicar as variações encontradas nessa dimensão funcional. A dimensão fenotípica relacionada a função foliar não apresentou variação relacionada a nenhum dos gradientes ambientais avaliados, indicando que os atributos funcionais, LMA e LDMC, não estão relacionados com as estratégias de aquisição e uso dos recursos em ambientes sazonalmente secos. No capítulo quatro, utilizou-se os dados funcionais de folhas coletados no capítulo três, para testar a capacidade da espectroscopia de solo em estimar as características funcionais foliares e diferenciar plantas com diferentes formas de crescimento. Os espectros de reflectância foliar foram capazes de predizer com precisão as características funcionais de folhas da vegetação independente da forma de crescimento, porém os modelos apresentaram imprecisão em torno dos valores maiores de LMA. Este resultado aponta para uma limitação ou do método da espectroscopia e/ou do método de modelagem utilizado neste estudo. Gramíneas e plantas lenhosas apresentaram respostas espetrais mais dissimilares, enquanto as herbáceas representam um tipo espectral intermediário, parcialmente semelhantes as gramíneas (no visível) e

parcialmente semelhantes às plantas lenhosas no infravermelho médio. No capítulo cinco foi investigada a influência dos níveis taxonômicos na relação entre a diversidade espectral e funcional em um subconjunto de plantas coletadas no capítulo três. A variação interespecífica foi maior que a variação intraespecífica para todas as características funcionais e espectrais da vegetação, mas o tamanho da influência intraespecífica foi uma resposta específica de cada espécie. Os resultados indicaram também que a idade foliar pode estar contribuindo mais que o esperado na variabilidade espectral intraespecífica e assim, dificultando o delineamento de um paralelo com os processos reconhecidos pela ecologia baseada em atributos que geram a variação intraespecífica (i.e., plasticidade). A partição da variância mostrou que tanto os atributos funcionais quanto os atributos espectrais variaram principalmente no nível de família, indicando que ambos são conservados evolutivamente. Este estudo contribui para a construção de teorias ligando a diversidade espectral com a diversidade funcional e taxonômica, os quais são muitas vezes difíceis de quantificar nos trópicos, auxiliando a impulsionar um sistema de monitoramento da biodiversidade baseado em sensoriamento remoto hiperespectral.

Palavras-chave: ecologia baseada em atributos, sensoriamento remoto, fenologia, atributos funcionais, LMA, LDMC, campo rupestre, espectroscopia.

ABSTRACT

Here, I explore trait-based ecology to understand how the environment shapes plant trait variation at multiple scales, combining remote sensing technologies and plant ecology. In the second chapter, the patterns and drivers of land surface phenology were assessed for the Meridional Espinhaço Range in Brazil. The TIMESAT algorithm was used to extract the phenological indicators from a 14-year time series of MODIS/NDVI satellite images. Water and light availability, modulated by topography, are the most likely drivers of land surface phenology in the region, determining the start, end, and length of the growing season, while temperature had an important role in determining the rates of leaf development and the strength of vegetation seasonality. In chapter three, I tested if the generalities of global patterns of plant form and function dimension held in finer scales in the seasonally dry tropics, and its relation with the an elevational and topo-edaphic environmental gradient. Leaf functional data (LMA, LDMC and leaf area) and plant height from 1650 individual comprising all life-forms of locally co-occurring plants was gathered, at five sites along an elevational gradient, sampling all vegetation types found within each elevation, at the southern portion of the Espinhaço range, known as Serra do Cipó, in Minas Gerais. The phenotypic organization of plant form and function found at global scales was similar to the one found among locally co-occurring species in *campo rupestre*. The whole-plant size dimension varied along the elevational gradient, however, the leaf economics dimension (LES) behaved differently than plant size, and no variation of key LES traits along environmental gradients was found. In chapter four, the ability of spectroscopy to estimate leaf functional traits and to differentiate plants comprising different growth forms was investigated. Leaf reflectance spectra was able to accurately predict leaf functional traits from different growth forms, but the models lost precision towards higher LMA values, pointing out a saturation point from spectroscopy and/or a limitation from the modelling approach adopted in this study. Grasses and woody plants were the most spectrally dissimilar, while forbs represented an intermediary spectral group. In chapter five the influence of taxonomic levels on the relationship between spectral and functional diversity was investigated. Interspecific variation was greater than intraspecific variation for functional and spectral traits, but the amount of intraspecific variation was a specific response of each species. Leaf age may be contributing more than expected to intraspecific spectral variability, hampering the delineation of a full parallel with trait-based ecology. The variance partition showed that both, functional and spectral traits varied mainly at the family level, indicating that both are evolutionary conserved. This study contributes to the construction of theories linking spectral to functional and taxonomic diversity, helping to build a biodiversity monitoring system based on remote sensing.

Keywords: trait based ecology, remote sensing, phenology, functional traits, LMA, LDMC, spectroscopy.

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1. GENERAL INTRODUCTION

This thesis is a tale of two stories. The first story is about a tropical mountain of recognized ecological importance as an ecotone among three tropical biomes, and how the environment shapes functional traits and ecosystem function across scales. The second story is about a less known biodiversity component, the spectral component, and its links with functional and taxonomic diversity, providing a fresh perspective on how we understand key plant structural and physiological features, emerging as an important piece of the puzzle that is ecology.

1.1 The appeal of trait based ecology

Predicting species abundances is one of the most fundamental pursuits in ecology, and despite over a century of scrutiny, understanding the drivers of species diversity across space and time remains a crucial research area (Whittaker, 1967; McGill *et al.*, 2006; Kraft *et al.*, 2011), given the accelerated biodiversity losses during the Anthropocene era (Schimel *et al.*, 2013). Although the early plant geographers had perceived that species phenotypic variability influenced their abundance and distribution (Schimper, 1903; Grime, 1974), the species-centric approach, in which the numbers and types of specimens were compared within and between environments (Whittaker, 1967), was adopted in ecology's early phases as a way of understanding diversity. Recently, it has been argued that the focus on species identities has led to a loss of ecological generality and predictability (McGill *et al.*, 2006), especially in highly diverse systems, where using species as the working unit is often overwhelming (Messier *et al.*, 2010).

The shift from a species-centric view to a trait-based approach was the conceptual framework proposed to reconcile long-standing hypotheses within ecology (Lavorel & Garnier, 2002; McGill *et al.*, 2006) and enhance predictability (Houlahan *et al.*, 2017). The appeal of the so called “trait based ecology” resides in its promise of generality, by providing a common basis for the comparison of individuals, populations and species from different phylogenetic histories and environments (Shipley *et al.*, 2016). This new type of ecology seems curiously similar to the older functional ecology and comparative ecology, and the boundaries between such disciplines are not clear (Shipley *et al.*, 2016). For the sake of simplicity, I use functional ecology and trait-based ecology as synonyms. I use the definition of trait-based ecology as a description of organisms that emphasizes the values of their phenotypic traits over their taxonomic or phylogenetic affiliations (thus “trait-based” ecology), allowing for the explicit comparison of trait values between many species, environments and ecological scales in order to elucidate general trends (McGill *et al.*, 2006; Garnier *et al.*, 2015; Shipley *et al.*, 2016).

The advantages of the trait-based approach are threefold. First, a summarized list of plant traits that are good indicators of ecological strategies, easily available to plant ecologists (Westoby *et al.*, 2002). Second, traits are usually straightforwardly measured by following standardized protocols, allowing the comparison of multiple trait values using a common basis, across multiple scales, even in highly diverse communities (i.e. Kraft *et al.* 2008). This approach thus provides a link between population, community, and ecosystem processes (e.g., growth, metabolism, reproduction; McGill *et al.* 2006). Third, since traits are closely coupled to the environment and to interactions, their use improve our understanding of the selective pressures constraining species distributions, and provides a mechanistic plant-environment relationship (McGill *et al.*, 2006).

By defining trait-based ecology, a second question emerges: what is a *trait*? Many definitions can be found in the current literature, causing some confusion not only in the use of the term “trait” itself, but also in the underlying concepts it refers to (Violle *et al.*, 2007). Originally, traits were defined by Darwin as proxies for organismal performance (Violle *et al.*, 2007; Garnier *et al.*, 2015). Over the last three decades, the “trait bandwagon” in ecology (McGill, 2015) has pushed the concept of traits beyond these original boundaries, and trait-based approaches are now used in studies ranging from organismal to ecosystem levels. Unarguably, the two key aspects defining a trait are: 1) something measured from a single individual, and 2) this measure can be conceivably linked to function or performance (e.g fitness or a component of it such as growth rate). In this thesis, I use the definition of *trait* as any morphological, physiological or phenological feature measurable at the individual level, without need to reference the environment or any other level of organization (Violle *et al.*, 2007; Garnier *et al.*, 2015), which can be understood as a “performance currency” derived from the processes of acquiring, allocating and/or spending energy and resources (McGill *et al.*, 2006).

Our understanding of the functional component of biodiversity has been advanced by the concept of strategy dimensions (Grime, 1974), and a core assumption of trait-based ecology is that trade-offs and constraints have shaped phenotypic variation in different trait dimensions (Westoby *et al.*, 2002). *Trait dimensions* are sets of correlated phenotypic traits that reflect distinct aspects of a plant’s ecological strategy (Westoby *et al.*, 2002), representing the continuous functional variation among plants, relevant to growth, survival and reproduction. Across broad spatial and taxonomic scales and/or large environmental gradients, trait dimensions describe global trends in phenotypic diversity (Wright *et al.*, 2004; Reich, 2014; Díaz *et al.*, 2016). Our understanding of several plant traits has taken substantial advances in the last two decades, in the light of

empirical data, and ecologists have used these resources to make remarkable progress in understanding plant ecological strategies at large scales (Moles, 2018). However, it is widely understood that patterns and processes change with spatial, temporal and biological scales (Wiens, 1989; McGill, 2010). In fact, recent studies have suggested that relationships among traits detected in large scale studies cannot be interpreted in the context of the predicted tradeoffs at local scales (Messier *et al.*, 2010; Funk & Cornwell, 2013; Messier *et al.*, 2017b; Anderegg *et al.*, 2018), and it remains unclear whether trait dimensions are also present at the smaller spatial and biological scales that are relevant for community assembly processes.

The knowledge gap in the scaling of trait relationships exists not only because we do not know the nature of trait-trait relationships across scales, but also because spatially and temporally explicit information on plant traits is still lacking in ecology (Asner & Martin, 2009; Schimel *et al.*, 2015; Jetz *et al.*, 2016). Although trait databases keep continuously expanding, available global data on plant functional biodiversity are grossly incomplete and non-representative taxonomically, geographically, environmentally, and temporally (Jetz *et al.*, 2016). Most of our theoretical and empirical understanding of trait-trait and trait-environment relationships comes from broad species-level studies. We do not know what to expect in terms of local and regional diversity of traits. According to Jetz et al. (2016), only 2% of currently known vascular plant species have any trait measurements available at the regional scale. This gap is even larger across the tropics. Existing trait databases often overlook tropical regions, and trait sampling is still biased towards the northern hemisphere, yielding a gap of local observations of plant functional traits exactly where available trait data is relatively small when compared to the high level of taxonomic diversity (Schimel *et al.*, 2015; Jetz *et al.*, 2016). This limits our ability to generalize how variation in trait values changes across environmental gradients and ecological scales.

1.2 Trait based ecology in a remote sensing era

The term remote sensing usually refers to the measurement of reflected, emitted, or backscattered electromagnetic radiation from the Earth's surface, using instruments stationed at a distance (far or close range) from the object of interest (Jensen, 2007). The remote sensing definition sounds like a theoretician's dream: a way to obtain data without leaving their chair (Roughgarden *et al.*, 1991). Unfortunately, while many remote sensing activities can be done in a chair, remote sensing analysis is far from simple and straightforward, and substantial legwork is still needed to ensure the accurate interpretation of remotely sensed signals (Roughgarden *et al.*, 1991). Also, many ecologists seem to ignore the physical principles behind remote sensing, which allow reliable retrieval of biophysical properties from the Earth's surface, generating products that go beyond "pretty study area pictures" or land cover maps (Milton *et al.*, 2006; Jensen, 2007). To put it another way, plants can be understood essentially as solar energy factories with leaves and canopies structured to optimize sunlight capture within existing resource constraints, shaping phenotypic variability (Ustin & Gamon, 2010). Consequently, by inverting the viewpoint and looking down from above, remote sensing can assesses key plant structural and physiological features related to its interaction with electromagnetic radiation, giving a new perspective to plant ecology studies (Ustin & Gamon, 2010).

Generally, the link between remote sensing and plant biodiversity is twofold (Turner *et al.*, 2003). First, we can obtain direct remote sensing measurements of optical properties (reflectance, absorbance and transmittance) from individual organisms, species assemblages, or ecological communities from hand-held, airborne, or space-borne sensors (Turner *et al.*, 2003). Data on ecosystem structure (such as ecosystem extent and fragmentation, or land cover types),

ecosystem function (net primary productivity, land surface phenology or disturbance regimes) and community composition can be derived from satellites and are key to understand large-scale processes, currently comprising the so-called Remotely Sensed Essential Biodiversity Variables (RS-EVB) (Paganini *et al.*, 2016). The second link is the indirect remote sensing of biodiversity by deriving environmental variables, such as topography, cloud cover, climate and others, and using them as proxies for estimating species distribution and abundances (Turner *et al.*, 2003).

Another important approach is to retrieve temporal information from “historical remote sensing” (Reed *et al.*, 2009a). For example, one of the most challenging aspects of understanding vegetation phenology in the tropics is the lack of long-term monitoring datasets (Morellato *et al.*, 2013, 2016). Through the use of remotely sensed information of vegetation dynamics, known as *land surface phenology* (LSP), ecologists can have a glimpse of otherwise unknown patterns. For instance, by retrieving information from the *Moderate Resolution Imaging Spectrometer* (MODIS), we can access LSP information every eight days from approximately 20 years back, or even more than 30 years back with more sparse images available from the Landsat series sensors or coarser spatial resolution from the AVHRR series. LSP is defined as the seasonal pattern of variation in vegetation “greenness” of vegetated land surfaces (de Beurs & Henebry, 2004), and although not a trait *per se*, (because is not measured at the individual scale - while ground-based phenology is), it allows us to infer landscape-scale patterns about the timing of phenological events and duration of growing seasons, which are important features of the temporal niche. Nevertheless, our ability to apply remote sensing to map and retrieve plant traits is still a challenge to be conquered, and has been limited by the spatial, temporal and spectral scales of the available technology, combined with the fact that correlative models are also limited by the *in-situ* gaps in trait data (Jetz *et al.*, 2016; Cavender-Bares *et al.*, 2017).

Spectroscopy can be one solution to this challenge.

1.3 New avenues for remote sensing in a trait-based ecological era

With the goal of advancing trait-based ecology, spectrometers are a very promising avenue. Spectroscopy is the acquisition of reflected radiation measurements at contiguous narrow adjacent spectral bands (i.e. “full spectra”), providing a continuous representation of radiation reflectance across the full optical electromagnetic spectrum (Milton *et al.*, 2006; Goetz, 2009). Spectroscopy has already proven to be a ‘sharper tool’, making novel contributions to our understanding of functional traits (Milton *et al.*, 2006; Ustin & Gamon, 2010; Asner & Martin, 2016). The integration between remote sensing spectroscopy and plant ecology occurs mainly at the leaf level. Spatial and temporal variations in resource utilization by plants result in chemical, metabolic, structural, and phenological differences that ultimately influence leaf optical properties, namely reflectance, absorbance and transmittance (Ustin & Gamon, 2010; Cavender-Bares *et al.*, 2017). Leaf spectroscopy has shown the potential to link leaf optical properties to a wide group of foliar traits (Fig 1.1), including many of the traits used in leaf trait dimensions.

However, a small number of selected leaf traits are unlikely to fully capture the variation contributing to a particular phenotype. In this sense, leaf spectra has an advantage over commonly measured traits: it incorporates more of the total variation in function associated with leaf chemistry, anatomy and morphology, including variation that is difficult to measure as a single trait or may be of unrecognized importance (Cavender-Bares *et al.*, 2017; Schweiger *et al.*, 2018). Consequently, the leaf reflectance spectra are able to reproduce plant life-history strategy, and can be understood as an overall expression of a “leaf phenotype”.

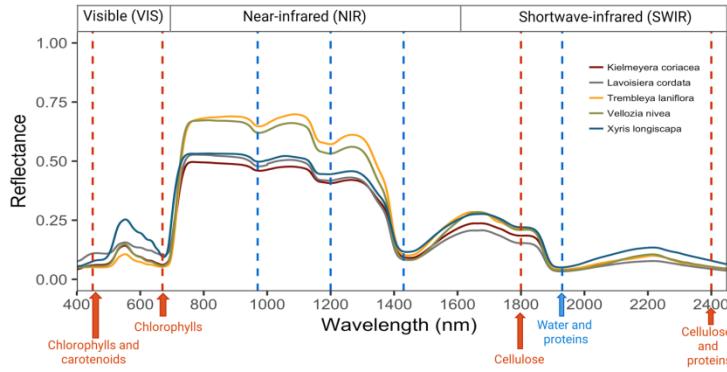


Figure 1.1: Full spectra of different *campo rupestre* plant species, corroborating the potential of spectroscopy for species discrimination. The visible (400–700 nm) region of the spectrum is dominated by leaf pigments absorption; the near-IR (700–1500 nm) region expresses leaf water content and leaf internal structural scattering; and the shortwave-IR (1500–2500 nm) regions are influenced by leaf water, nitrogen and carbon (e.g. lignin and cellulose) constituents. The blue vertical lines indicate water absorption bands.

Besides the potential to retrieve the functional component of biodiversity, the spectral domain is also tied to the taxonomic component of plant diversity (Asner & Martin, 2009; Asner *et al.*, 2014a; Schweiger *et al.*, 2018) and niche theory. According to the spectral or optical diversity hypothesis (Palmer *et al.*, 2002; Rocchini *et al.*, 2015; Schweiger *et al.*, 2018), the larger the spectral heterogeneity, the higher will be niche availability for different organisms, suggesting that species within a plant community occupy unique spectral spaces delineated by their chemical, anatomical and morphological characteristics. The precept for the optical diversity hypothesis is the same underlying classical niche theory, and more recently, trait-based ecology: interspecific variability in spectral reflectance exceeds intraspecific variability. Hence, the higher the spectral variability of an environment, the higher would be species diversity. Such a hypothesis has been tested with taxonomic data (Rocchini *et al.*, 2015, 2018; Schweiger *et al.*, 2018) and often resulted in a positive statistical relationship, although this link does not always hold (Schmidlein & Fassnacht, 2017).

Plant spectra can be sampled at different spatial scales, providing the means to link an array of biological disciplines at different ecological scales (Asner *et al.*, 2015, 2016b; Cavender-Bares *et al.*, 2016). The comparisons between field sampling of functional traits and leaf-level reflectance measured using imaging spectrometers, be it airborne (including UAV-based) or spaceborne, are still lacking. There is a major knowledge gap between small-scale field studies (≤ 1 ha) of plant functional traits and broad-scale, remotely sensed estimates of vegetation properties (Asner *et al.*, 2016b). We still do not know how traits vary across scales (Messier *et al.*, 2010), and we do not know how pixel grain size (spatial resolution) will shape our perception of trait distributions (Asner *et al.*, 2015), but the few results already found in the literature are encouraging (Asner *et al.*, 2016b; Schweiger *et al.*, 2018). Assessing all components of biodiversity in a concise and scalable manner is increasingly urgent. The only low-Earth orbit spectroscopic satellite available is the low-fidelity Hyperion-1, which has proven difficult for estimate functional traits and species composition (Townsend & Foster, 2002; Asner *et al.*, 2016b). Recently, researchers have envisioned a global biodiversity observatory by integrating remotely sensed information on functional traits (through an imaging spectroscopy mission) with other remotely sensed information and *in situ* observations of phylogenetic relationships, functional traits and species distributions (Jetz *et al.*, 2016; Cavender-Bares *et al.*, 2017).

Trait-based ecological studies can be greatly improved by multiscale spectroscopic studies, but to fully realize the potential of spectroscopy, data must be combined with sound ecological theory to pave the way for a more integrated global assessment of plant functional biodiversity (Ustin & Gamon, 2010; Jetz *et al.*, 2016; Cavender-Bares *et al.*, 2017). While I do not directly address the multiscale relationship of trait based ecology and spectroscopy in this work, my thesis touches on both worlds: ecology and remote sensing. By combining trait-based ecology

with the physical basis of remote sensing, I was able to assess trait-trait, trait-environment and trait-spectra relationships of individual plants. I contribute not only with ecophysiological trait sampling at the individual level, helping to fill the existing gap of local trait observations in tropical regions, but also with standard spectroscopy measurements. Together, these results allowed me to draw some first-order inferences about the shape of the environment-phenotype-spectral relationships for tropical seasonal environments across scales.

1.4 Study scales

My thesis is built around a specific study area (Fig 1.2). To “move” research across scales is not something straightforward (Wiens, 1989). The nomenclature of scales is ambiguous and not well defined across the literature. The term “ecological scales” refers here to biological, spatial, and temporal scales on which ecological processes act (Chave, 2013). For this thesis, I will use the term “spatial scales” as the spatial extent defining the range over which a pattern or process occurs. I thus define my spatial scales of interest in three levels: **a) regional:** representing patterns often spanning large geographical areas and multiple biomes (Fig. 1.2a); **b) landscape:** representing the different elevational bands along a small geographical area, with high environmental heterogeneity, where the main ecological mechanisms (environmental filtering) is expected to occur at the species level; and **c) local:** representing local interaction at the individual level (e.g. within a transect), where the main ecological mechanisms are expected to act at the individual level (Fig 1.2c). In addition, ecological scales also include the nested hierarchical nature of “biological scales”, and in this thesis, they will be referred to as the levels of individual, species, genus and family.

The Espinhaço Range (*Cadeia do Espinhaço*) is one of the most important biogeographic regions

of South America, so much that in 2005 it was designated as a Biosphere Reserve by UNESCO (UNESCO 2005) (Fig 1.2a). The unique location of the Espinhaço Range places this mountain within an ecotone among three biomes: Atlantic Rainforest to the East and South, Cerrado to the West, Caatinga to the North and, on the highlands, the *campos rupestres*, a montane vegetation mosaic comprising mainly non-forest formations (Silveira *et al.*, 2016; Streher *et al.*, 2017). Mean elevation is over 1000m above sea level, with peaks reaching 1800 to 2100m, and the rugged topography produces a wide diversity of soils and micro-environmental conditions (Giulietti & Pirani, 1988; Schaefer *et al.*, 2016a,b).

The southern portion of the Espinhaço Mountain Range, known as “Serra do Cipó”, was chosen for this study as it comprises a large range of environmental heterogeneity within a small geographical area, hosting a megadiverse flora with more than 1800 species recorded within 200 km² (Alves *et al.*, 2014). Variations on vegetation structure and growth form turnover occur naturally across two nested scales associated with distinct environmental gradients: (i) a *landscape* scale, along a short elevational gradient (~600m, from 800m to 1400m) (Fig 1.2b), where subtle changes from forest-*cerrado* (savanna) formations towards grassy-shrubby *campo rupestre* vegetation can be observed Fig. 1.2b); and (ii) a *local* scale within each elevational band, where vegetation mosaics characterized by a high number of endemic plant species and lineages can be associated with soil conditions mostly determined by local topography and microenvironmental aspects (Fig 1.2c). The *campo rupestre* is considered, alongside the *fynbos* (Cape Floristic Region) and *kwongan* (south-western Australia), as an example of the old climatically-buffered infertile landscapes (OCBILS) theory on which infertile soils and climatic stability are the core explanations for the high floristic richness and levels of endemism (Silveira *et al.*, 2016).

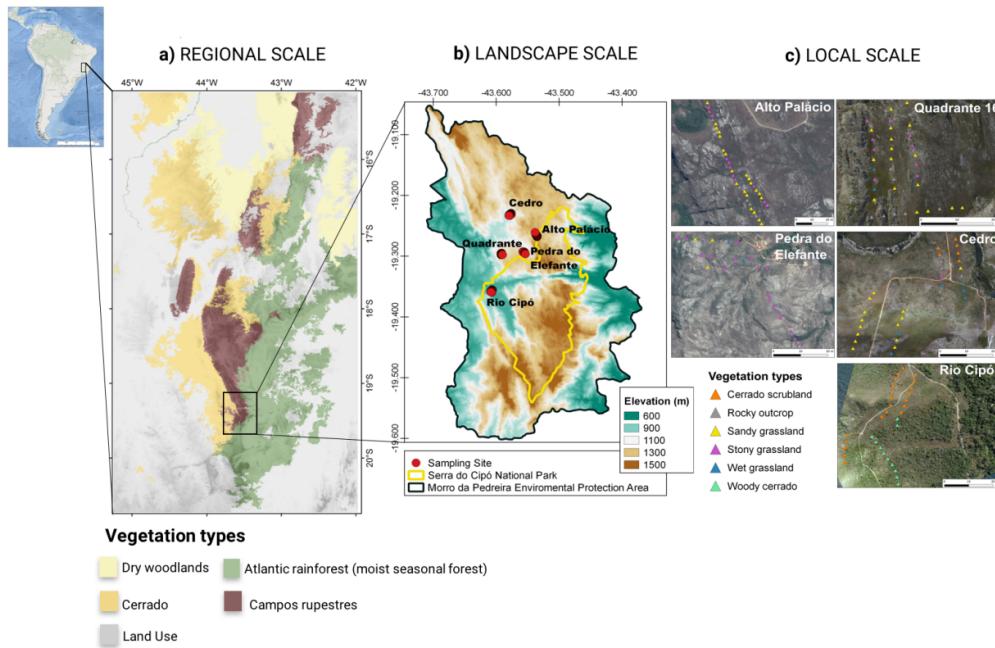


Figure 1.2: Upper left the location and extension of the Espinhaço Mountain Range in South America. The regional scale (a) assessed in this study, comprise the meridional portion of the Espinhaço Mountain Range in the state of Minas Gerais, and its unique location as an ecotone of vegetation types: Atlantic rainforest (moist seasonal forest) to the east and south, cerrado vegetation types to the west, dry woodlands in the north and, on the highlands, *campos rupestres*. The landscape scale (b) shows an overview of the extension and the topography of Serra do Cipó. The red dots mark the locations of the sampling sites along the elevational gradient. Within each sampling site, the local scale (c) comprise a mosaic of microenvironment conditions and vegetation types found across the elevational gradient, and the transects established at each sampling site, with the corresponding vegetation types found at each plot. The UAV images used on (c) are a courtesy of Dr. Patricia Morellato.

1.5 Overview of thesis goals, assumptions and general outline

My overarching thesis goal was to explore trait-based ecology to understand how the environment shapes trait variation at multiple scales, from leaves to ecosystems, and from space to species, by combining remote sensing and plant ecology. Together, the work presented here explores three assumptions that are largely untested along the Neotropics, resulting in four chapters. This thesis was written under a format where each chapter comprises a journal manuscript, so the reader may find some redundancy among chapters, especially within the methods section. First, I present the assumption that drove my research question, followed by a

small description of each chapter.

1.4.1 The temporal dimension

Time represents an important resource axis, that may be partitioned by an assemblage of competing species, thus reflecting different selective forces in assemblages of plants (Gotelli & Graves, 1996a). Leaf phenology represents a major temporal component of ecosystem functioning, regulating processes such as carbon, water and energy exchange, forage availability, competition, and coexistence (Cleland *et al.*, 2007; Polgar & Primack, 2011). The degree of partial or full loss of leaves is an indicator of shifts in the intensity and timing of species activities (Camargo *et al.*, 2018) and changes in leaf deployment and leaf lifespan are therefore likely to have far reaching implications at a wide range of spatial scales. At large scales, vegetation units are better defined by structural and functional attributes rather than by species composition (Higgins *et al.*, 2016), consequently phenology is a key component of biomes, and has even been considered as way of delineating and classifying biomes, the so-called *phenomes*, which are based on the link between physiological niche space and leaf habit classes (Givnish, 2002; Buitenwerf & Higgins, 2016).

However, our understanding of where and why different leaf habits are favored is incomplete. In tropical ecosystems, phenology might be less sensitive to temperature and photoperiod, and more tuned to seasonal shifts in precipitation, but we still have a poor understanding of the climatic drivers of tropical phenology (Cleland *et al.* 2007, Chapter 2), which can be linked to the overall paucity of long-term ecological monitoring. Along the Neotropics, few studies have addressed leaf exchange patterns at the community (Camargo *et al.*, 2018) and biome levels - with the exception of the Amazon - (van Leeuwen *et al.*, 2013). This knowledge gap is more acute for

tropical mountains, since patterns from temperate mountainous regions are not readily transferrable, as the dominant topography-induced controls on phenology in the tropics are not related to snow cover. Identifying patterns and constraints regulating leafing phenology, and how these mechanisms differ among tropical vegetation types, is therefore critical for understanding vegetation dynamics and for accurately forecasting future changes on tropical mountain ecosystems (Polgar & Primack, 2011).

Chapter 2:

The second chapter is based on assumption 1.4.1. We used LSP as a proxy for large-scale phenology to evaluate how a mountainous environment, the Espinhaço range (Fig 1.2a), shapes the timing of leaf phenological events across multiple tropical vegetation types. This chapter consists of a remote sensing analysis of vegetation phenology for the meridional portion of Espinhaço mountain range. I produced a regular time series of vegetation activity based on 15 years of NDVI/MODIS satellite images, acquired from the University of Natural Resources and Life Sciences, Vienna, (<http://ivfl-info.boku.ac.at/index.php/eo-data-processing/dataprocess-global/master-global>). Leaf phenology metrics, such as start and end of the growing season, peak growing date, season length and amplitude, and rates of growing and senescence were assessed using the TIMESAT 3.2 algorithm (Jönsson and Eklundh 2004). Also based on remote sensing, I produced environmental datasets of clear sky radiation budget, cloud cover, precipitation, topographical soil moisture and temperature, and tested the association between these variables and the satellite-derived metrics of leaf phenology.

1.4.2. Functional trait dimensions

Díaz et al. (2016) showed that most variation in plant form and function could be capture by only

two trait dimensions: the first reflecting variations in whole-plant size, broadly understood as architectural constraints (Niklas, 2004; Price *et al.*, 2014), and the second representing the construction costs for photosynthetic leaf area, known as the leaf economics spectrum (Wright *et al.*, 2004). Although the database used in Díaz *et al.* (2016) study represents one of the largest compilations of global trait data, it is still lacking in measurements from the tropics (Brian J. McGill personal communication). Furthermore, it is unclear whether global-scale interspecific trait correlations will hold at smaller spatial scales. Indeed, recent studies have questioned if the LES dimension is expressed within communities (Messier *et al.*, 2017b; Anderegg *et al.*, 2018). While the suite of traits used to describe the two-dimensional global spectrum of plant form and function have been extensively used, the processes of interest at smaller scales might not affect those specific traits and /or affect other traits more strongly. We still lack theoretical and empirical understanding of trait-trait and trait-environment relationships at smaller spatial scales.

Chapter 3:

The third chapter of my thesis is based on assumption 1.4.2. I tested if the LES and the plant-size trait dimensions (Díaz *et al.*, 2016) are present at the landscape and local scales (Fig 2b and 2c), and how the key traits from both dimensions are related to the environment. I sampled traits from 1650 individual plants, two representing the LES - leaf mass per area (LMA), leaf dry matter content (LDMC), and three representing the plant size dimension- leaf dry mass, leaf area, and plant vegetative height. I expected the patterns of both dimensions to emerge, due to the high phenotypic diversity; I also had expectations regarding the structure of variance of traits in relation to the environmental gradients: (1) if the elevational gradient (landscape scale) is responsible for filtering trait values, then I would expect large differences in modal trait values

and narrow variances among elevations, specifically showing an increasing trend for leaf traits values associated with greater conservation of nutrients, and a decrease trend for plant height, due to a decline in temperature and differences in precipitation with the increase of elevation (Read *et al.*, 2014; Pescador *et al.*, 2015); and (2) if plant-soil associations (vegetation types) are the major source of variation in trait distributions, I expect modal trait values to vary by vegetation type, and larger variances within elevations largely independent of elevation. I expect that leaf traits and plant height will vary accordingly with the dominant growth form of each vegetation type: higher mean values for vegetation types dominated by woody growth forms, while lower values would be associated with the different grasslands types independent of elevation (Rossatto & Franco, 2017).

1.4.3. The spectral dimension

The assumption that plants can be positioned along an axis of “light” is based on the fact that leaf optical properties are a function of leaf structure, water content, and concentration of biochemical elements (Curran, 1989; Curran *et al.*, 2001; Asner *et al.*, 2011a; Asner & Martin, 2016). Along an environmental gradient, changes in the use of sunlight and other resources by plants will likely change trait ecophysiological values and so the full-spectrum reflectance profile. This means that, analogous to the functional trait space, spectral space is conceptually an *n*-dimensional hypervolume populated by spectra of individual plants measured at the leaf level or through remote sensing (Schweiger *et al.*, 2018). There is sufficient theoretical basis linking the spectral, chemical, and taxonomic diversity of tree species, but our general knowledge is hindered by too few and spatially clustered measurements and also by the lack of measurements of other growth forms and deciduousness strategies. Major advances are still required for a deeper understanding and wider application of the spectral domain as a biodiversity component.

Chapter 4:

The fourth chapter is based on assumption 1.4.3. Here I tested if leaf level spectra is able to predict the two key LES traits (LMA and LDMC) in a seasonally dry tropical vegetation and if the spectra profile is able to reflect the expected functional changes among growth forms. For the same set of samples from Chapter 3, I measured high-fidelity leaf reflectance spectra and used a partial-least square modelling approach to predict leaf functional traits from spectra. I used the Bhattacharya distance to measure the dissimilarities among growth forms and draw further insights in leaf ecophysiological differences between them.

Chapter 5:

The fifth chapter is also based on assumption 1.4.3. Here I explore the hypothesis of the optical diversity, testing (1) if interspecific variations surpass intraspecific in spectral variability, and 2) if the trait x spectral relationship holds across biological scales. From the 1650 individuals sampled for chapter 3, I selected 231 individuals from 31 different species. I used ideas from the remote sensing community and methods widely used in ecology. I describe the spectral diversity based on the distances among individuals, species, genus and families in a spectral space and tested the convergence with the functional dissimilarities for each biological scale. I expect interspecific variation to exceed intraspecific variation, as predicted by classical niche theory. I also expect that convergence of spectral x trait dissimilarities are stronger at the species and genus level (Asner & Martin, 2009).

6. Concluding remarks:

The final chapter synthesizes the findings and limitations of this research and outlines current shortcomings for future research.

6. Concluding Remarks

This study has established an important link between trait based ecology and remote sensing, combining sound ecological theory to the physical basis of remote sensing. By addressing the multidimensional and integrated nature of the plant phenotype, and examining similarities and differences between trait-trait, trait-environment, and trait-spectra relationships across ecological scales, this work contributes to a more integrated assessment of tropical plant biodiversity.

Four main messages emerge from this body of work: i) defining vegetation units at regional scale by their phenological traits rather than by floristic composition enables the depiction of mechanisms determining the duration of leaf deployment and its geographical distribution, which are closely linked to large scale environmental gradients; ii) the global pattern of plant form and function from Díaz et al (2016) can be detected at the landscape scale in the seasonally dry tropics, but there is no simple relationship between traits, performance, and environment; iii) embracing the multidimensionality of the leaf full-reflectance spectra as a “leaf phenotype” provides different insights into plant ecology that are not accessible by a handful of individual leaf traits; iv) relationships among functional and spectral diversity reflects a rather similar taxonomic organization and evolutionary constraints, and endorse the spectral diversity concept as an important component of biodiversity.

Commonly, phenological patterns and its environmental relations are inferred from generalized climatic variables, such as total amount of precipitation and temperature means (Waldock *et al.*, 2018). However, at a snow-free tropical mountain, topography played a key role in shaping light and water availability for leaf development, allowing the co-occurrence of highly diverse vegetation types that partition the resources across space and time (Chapter 2). The interaction between precipitation and topographic wetness index (a proxy for soil moisture availability), and

light availability, given by the combination of incoming insolation and spatial and seasonal cloud coverage patterns, were the most likely drivers of land surface phenology in the Espinhaço range, determining the start, end, and length of the growing season. Although temperature is not usually acknowledged as an important cue for tropical phenology (Cleland *et al.*, 2007), it had an important role in determining the rates of leaf development and the strength of vegetation seasonality, suggesting that tropical vegetation is also sensitive to latitudinal temperature changes. Temporal displacement in the start date of the annual growth season was more evident than variations in season length among vegetation types, indicating a temporal separation in the use of resources (Chapter 2).

A closer look into the emergent patterns of leaf traits (chapters 3, 4 and 5) resulted in the following reasoning: yes, the LES is observable at local scales, but the two key traits from this dimension, LMA and LDMC, do not map the resource-use strategy as predicted by the fast-slow continuum theory at the studied site. This may be a result from the climatic stability under which the Serra do Cipó flora has evolved, favoring the persistence of old lineages that continue to diversify but conserve the traits and environmental tolerances of their ancestors (Chapter 3). These same traits, which are usually measured in ecological studies, also did not show ecologically significant variations (average and range) among plant growth forms. Leaf-reflectance spectra, however, was able not only to accurately predict functional traits, but also to discriminate major *campo rupestre* growth forms, despite the lack of LMA and LDMC variability. This indicates that neither trait fully captures the ecophysiological variation contributing to a particular leaf phenotype (Chapter 4), and that the full leaf spectra is integrating more information about chemical and structural leaf properties than isolated traits.

By placing functional and spectral diversity in an evolutionary context, we confirmed that not only functional traits are evolutionarily conserved in *campo rupestre* vegetation, but also the leaf reflectance spectra, as most of the variance for both biodiversity components were found deep in the phylogeny (*i.e.* at the family level, Chapter 5), thus corroborating findings from Chapter 3. Moreover, the relationship between functional and spectral diversity was confirmed in the seasonally dry tropics, but intrinsic leaf age differences may impact intraspecific spectral variability more strongly, and hamper the understanding of intra-to-interspecific relationships as we know it from trait based ecology.

As the world enters the Anthropocene, ecology faces the challenge of transitioning from a descriptive science into a predictive one, in time to provide relevant understanding of how ecosystem structure and function will be altered by global environmental change (Schimel *et al.*, 2013; Higgins *et al.*, 2016; Jetz *et al.*, 2016; Houlahan *et al.*, 2017). Taken together, the findings from this thesis imply that changes in the length and intensity of the dry season may act as a severe threat to all vegetation types found along the Espinhaço range, but particularly for the seasonally dry vegetation at Serra do Cipó, which comprises one of the richest floras of the world (Silveira *et al.*, 2016). The strongly conservative nature of leaf traits, combined with effects of temperature amplitude over the rates of green-up and senescence indicates that climatic stability is an important element in this region. These observations provide one more piece of evidence corroborating the OCBIL theory (Hopper, 2009), and highlights the peculiarities of the Espinhaço Mountain Range, but also show that this vegetation may not be plastic enough to keep up with the fast pace of anthropogenic climate change. Fernandes *et al.* (2018) show that 82% of *campo rupestre* areas along the Espinhaço range may be lost within the next 50 years due to climate change only. No specific information has been provided by the Brazilian panel of climate

change to the Espinhaço Mountain Range (Fernandes *et al.*, 2018), but it should be an important goal on the future research agenda of ecologists to address the impacts that climatic changes will have on vegetation structure and function in this unique system.

Predicting the future of ecosystems will increasingly require species- and trait-level data. This study works towards predictive ecology by empirically testing the generalities of ecological theory at the undersampled dry tropics and examining some of the foundational assumptions of trait-based plant ecology. A deeper understanding and wider application of leaf reflectance spectra can help integrate components of biodiversity that are difficult to assess, and help promote a global biodiversity monitoring system.

The only universal rule in ecology seems to be that nothing is universal, and the most common ecological result by far is “it depends on the scale”. While our current ecological understanding is still far from a “Newtonian unifying theory”, remote-sensing approaches are likely the best option to address the scale dependence of ecological process (Kerr & Ostrovsky, 2003; McGill, 2010; Schimel *et al.*, 2013; Jetz *et al.*, 2016). Currently, we lack a clear understanding of scale dependences in the spectral–biodiversity relationship (but see Asner *et al.*, 2016; Wang *et al.*, 2018), and this is likely to vary for different ecosystems. Nonetheless, this thesis has yielded encouraging findings by linking spectra to plant function and diversity at the leaf level in a tropical system, combining traditional field approaches with innovative remote observation techniques. In doing so, it attempts to contribute to the theory that guides future trade-offs for the scalability of biodiversity through remote sensing, and provides a positive encouragement for future studies to focus in comparisons between field sampling and reflectance measured across spatial and temporal scales using imaging spectrometers, be it airborne (including UAV-based) or (future) spaceborne, to greatly enhance our understanding in our rapidly changing planet.

7. References

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