MIGUEL ÂNGELO TEIXEIRA DA SILVA

INFLUÊNCIA DA ALTITUDE EM INDICES ESPECTRAIS DE PLANTAS VASCULARES DE CAMPOS DE ALTITUDE

Dissertação apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Botânica, para obtenção do título de *Magister Scientiae.*

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APROVADA: 19 de novembro de 2018.

João Augusto Alves Meira Neto

Eduardo Gusmão Pereira

Andreza Viana Neri
(Orientadora)

Dedico este trabalho à minha família, em especial aos meus pais,

que me ensinaram a importância dos estudos para

o crescimento pessoal e realização dos meus sonhos.

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RESUMO

DA-SILVA, Miguel Ângelo Teixeira, M.Sc., Universidade Federal de Viçosa, novembro de 2018. **Influência da altitude em índices espectrais de plantas vasculares de campos de altitude.** Orientadora: Andreza Viana Neri. Coorientadora: Cibele Hummel do Amaral.

Os campos de altitude são ecossistemas de montanhas acima de 1700 m de altitude em meio à Floresta Atlântica brasileira, com alta diversidade e altos níveis de endemismo de táxons de plantas. Para se evitar a perda de espécies e se manter o funcionamento destes ecossistemas frente a mudanças climáticas é preciso conhecer melhor os aspectos ecológicos e desenvolver métodos eficazes de monitoramento dos campos de altitude. O objetivo deste trabalho foi investigar características foliares através do cálculo de índices de reflectância espectral de vegetação (IEVs) entre espécies de diferentes tipos de distribuição ao longo de um gradiente de altitude em campos de altitude. A altitude é um fator determinante na condição fisiológica das plantas dessas comunidades de altitude? Em relação aos diferentes grupos de espécies de acordo com a distribuição no gradiente, a hipótese é de que espécies indicadoras de faixas de altitude, selecionadas pelo método IndVal, possuem maior número de mecanismos adaptativos constitutivos às condições das altitudes do que as espécies generalistas. Os valores encontrados dos índices *red-edge vegetation index* (RVSI) e *normalized difference vegetation index* (NDVI) correlacionaram positiva e significativamente ($p<0,05$) com a altitude quando analisamos o grupo de espécies indicadoras e o conjunto completo de espécies amostradas, que indicam ajustes das plantas a condições ambientais mais restritivas nas altitudes mais elevadas, *e.g.* baixas temperaturas, radiação solar excessiva e solos pobres e rasos. Essa observação tem potencial em abordagens de sensoriamento remoto por imagens para descrição e monitoramento dos campos de altitude. O índice *photochemical reflectance index* (PRI) foi positivamente correlacionado à altitude de forma significativa ($p<0,05$) em espécies generalistas. *Hippeastrum glaucescens*, mostrou valores de RVSI e PRI que indicam maiores traços de estresse em altitudes mais baixas, diferente de *Baccharis platypoda* e *Eryngium elegans* que indicaram maiores taxas de estresse por meio dos IEVs nas elevações maiores. Os grupos indicadoras e generalistas apresentaram comportamentos morfofisiológicos distintos em relação à altitude dependendo do IEV utilizado. O estudo das características espectrais de plantas através de IEVs mostrou-se uma ferramenta eficaz para investigação e monitoramento de espécies dos campos de altitude, com especial importância no contexto de impactos de mudanças climáticas nesses ecossistemas únicos.

ABSTRACT

DA-SILVA, Miguel Ângelo Teixeira, M.Sc., Universidade Federal de Viçosa, November, 2018. **Influence of altitude on spectral indices of vascular plants from high altitude grasslands.** Advisor: Andreza Viana Neri. Co-advisor: Cibele Hummel do Amaral.

Brazilian highland grasslands, the *campos de altitude*, are unique grassland-heathland ecosystems found in the middle of the Atlantic Forest on the highest mountains above 1700 m, which contains high levels of endemism and diversity. In order to avoid the loss of species and to maintain the ecosystem functioning in the face accelerated of climate change it is necessary to know better the ecological aspects and to develop efficient methods of monitoring the high-altitude grasslands. The aim of this work was to investigate foliar characteristics by calculating hyperspectral vegetation indices (HVIs) among species of different distribution types along an altitudinal gradient in high-altitude grasslands. Is altitude a determining factor in the physiological condition of the plants in these high-altitude communities? In relation to the different groups of species according to their distribution in the gradient selected by IndVal method, the hypothesis is that species indicatives of specific altitudinal ranges possess more adaptative mechanisms to the conditions of the altitudes than the generalist species. The red-edge vegetation stress (RVSI) and normalized difference vegetation index (NDVI) values correlated positively and significantly to altitude when analysed the group of indicator species and the complete set of species sampled, indicating plant adjustments to more restrictive environmental conditions at higher altitudes, *e.g*. lower temperatures, excessive solar radiation and shallow, poor soils. This finding is potentially useful in remote sensing imaging approaches for describing and monitoring high-altitude grasslands. The photochemical reflectance index (PRI) was positively and significantly correlated to altitude in generalist species, indicating less stress in higher elevations. *Hippeastrum glaucescens*, showed values of RVSI and PRI indicating higher stress at lower altitudes, unlike *Baccharis platypoda* and *Eryngium elegans*, which indicated higher stress rates through the HVIs at higher elevations. Indicator and generalist species groups showed different morphophysiological behaviours in relation to altitude depending on the HVIs used. The study of spectral characteristics of plants through HVIs has proved to be an effective tool for research and monitoring of

high-altitude field species, with special importance in the context of impacts of climate change on these unique ecosystems.

SUMÁRIO

Spectral vegetation indices as a tool for functional studies on altitudinal gradient in Brazilian *Páramos*

1. Introduction

On the highest areas of southern and south-eastern Brazil high altitude grasslands and shrublands dominate the landscape above 1700-2000 m, an ecosystem known as *campos de altitude* (Hugh DeForest Safford, 2007). This ecosystem is amid the Atlantic Forest, one of the global hotspots of biodiversity (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). Some authors have referred to *campos de altitude* as *Brazilian Páramos* (Carneiro, Dolibaina, Mielke, & Casagrande, 2014; Coelho, Carneiro, Branco, Borges, & Fernandes, 2017; Hugh Deforest Safford, 2001; Hugh DeForest Safford, 1999a, 1999b, 2007) due to their floristic and physiognomic resemblances to the vegetation found in higher and more extensive areas of equatorial Andes mountain range. *Campos de altitude* ecosystems are considered a “refuge vegetation or relict” among a forest matrix (Veloso, Rangel Filho, & Lima, 1991) and they harbour an expressive number of endemic or even micro-endemic species (Vinicius M. Benites, Schaefer, Simas, & Santos, 2007; Iganci, Heiden, Miotto, & Pennington, 2011; Martinelli, 2007).

The *campos de altitude* are a series of humid tropical and subtropical, subalpine grasslands associated with granite and gneiss rocky outcrops (Hugh DeForest Safford, 1999a; Vasconcelos, 2011). The plant communities are dominated by herbaceous and shrubby components distributed in a mosaic, according to a complex of environmental gradients that operate on a short spatial scale (Campos et al., 2018; Neri et al., 2016). These gradients are a result of variation in altitude and topography, as well as soil characteristics (Vinicius M. Benites et al., 2007; Neri et al., 2016). For instance, in higher altitudes temperature, atmospheric pressure and clear sky turbidity decreases, and also factors not specifically related to altitude may vary: moisture, hours of sunshine, wind velocity increases (Körner, 2007). The soils in *campos de altitude* are mainly shallow, acidic, with low nutrient content (dystrophic), high aluminium toxicity as well as low water retention capacity (Vinicius M. Benites et al., 2007; Vinicius Melo Benites, Caiafa, Mendonça, Schaefer, & Ker, 2003). These soil limitations, low temperatures and intensive solar radiation work as strong environmental filters (Vinicius M. Benites et al., 2007; Neri et al., 2016), which in turn reflect in a range of physiological, phenological and morphological adaptations of plant species found in these tropical grasslands (Aparecido et al., 2018; Camerik & Werger, 1981; Vitarelli, Riina, Cassino, & Meira, 2016).

In regard to mountain rocky outcrops complexes, in the Brazilian territory most of them are protected by law under conservation units; nevertheless, the biodiversity of these ecosystems is especially vulnerable to climate change and disturbance (Bitencourt, Rapini, Santos Damascena, & De Marco Junior, 2016; Leão, Fonseca, Peres, & Tabarelli, 2014). Similarly to what Porembski (2007) suggests for *inselbergs* in the Atlantic Forest, the peaks where *campos de altitude* occur are mostly isolated from each other, what limits the potential dispersion and genetic exchanges by native populations and contributes to the high level of endemism and higher susceptibility of these plants to be extinct. Furthermore, these areas have a role in maintaining and regulating the hydrological cycle which gives them a great social and environmental importance close to the most populated region of Brazil, making them a priority for conservation (Assis & de Mattos, 2016).

For the conservation of *campos de altitude,* an effective monitoring of the vegetation status/health requires linking different approaches, by *in-situ* species approaches and remote-sensing approaches (Lausch et al., 2018). Many studies have demonstrated the efficiency of leaf reflectance spectrometry as a promising method for vegetation monitoring and for functional ecology, contributing to remote sensing of spatial distribution of vegetation types, as well as recognition of plant functional types (Roth et al., 2016; Schweiger et al., 2017; Ustin & Gamon, 2010). A common spectrometry approach in vegetation studies is the use of Hyperspectral Vegetation Indices (HVIs), which are measurements of vegetation properties by converting a reflectance spectrum into a single number value (Roberts, Roth, & Perroy, 2011). These HVIs are relatively simple and effective algorithms for qualitative and quantitative evaluations of vegetation traits, such as cover, types, growth dynamics and vigour, among other applications (Ali, Darvishzadeh, Skidmore, & van Duren, 2017; Xue & Su, 2017), and therefore hyperspectral remote sensing began to be used as a tool for functional characterization of grassland ecosystems (Van Cleemput, Vanierschot, Fernández-Castilla, Honnay, & Somers, 2018).

The aim of this study is to investigate and analyse patterns of leaf traits and spectral reflectance response through HVIs among species of different distribution ranges along an altitudinal gradient in *campos de altitude* ecosystem. We hypothesized that altitude is a determinant factor on the physiological condition and adaptations of these high-altitude plant communities. Therefore, the higher the elevation, the harsher are the conditions for plant growth and so the plants will show HVI values corresponding to leaf physiological stress. We also had the hypothesis that indicator species have more specific mechanisms that reflect adaptations to the conditions of those high altitudes than the generalist species do.

2. Material and Methods

2.1. Study site

This study was conducted in a mountaintop grassland – *campos de altitude* physiognomy – at the Caparaó National Park, south-eastern Brazil. The area is surrounded by the Atlantic Rainforest domain, a high degraded and threatened ecosystem considered one of the hotspots of diversity (Myers et al., 2000). This park has a total area of 31,853 ha and is located between Minas Gerais and Espírito Santo states (20˚19' - 20˚37' S and 41˚43'- 41˚53' W) (ICMBIO, 2015). This area has the highest altitudes in eastern South America and the third highest peak in Brazil, the *Pico da Bandeira* with 2892 m altitude (20˚26'04 S and 41˚47'47 W) (Figure 1). In addition, the area stands out for having vast extensions of rocky outcrops interspersed by grassy and shrub vegetation from around the elevation of 2000 m upwards, vegetation known as *Campos de Altitude* (Brade, 1942).

The local climate is considered of subtropical highland type (Cwc) according to Köppen's classification system, 13 ˚C as annual mean temperature (ca. -0.55˚/100 m of elevation) and mean precipitation of 1.300 mm (Alvares, Stape, Sentelhas, De Moraes Gonçalves, & Sparovek, 2013). The geological substrate is mainly composed by pre-Cambrian rocks, from medium to high-level of metamorphism, comprising Archean gneisses on uplifted blocks along geological faults during Tertiary and early Quaternary periods (Hugh DeForest Safford, 1999a).

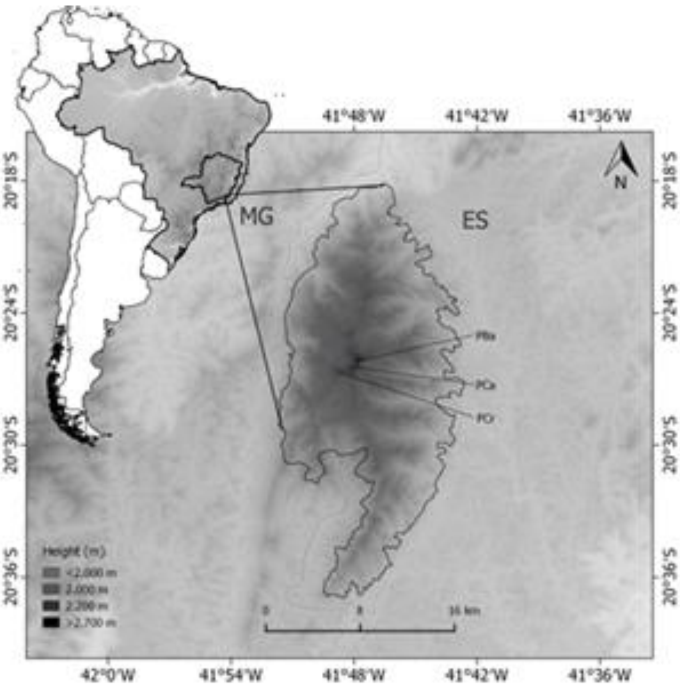

Figure 1 - Location of Caparaó National Park and the three highest peaks (PBa – Pico da Bandeira, PCa – Pico do Calçado, PCr – Pico do Cristal), Espírito Santo (ES) and Minas Gerais (MG) states, southeastern Brazil.

So far, most of the vegetation studies already carried out at Caparaó National Park have focused only floristic surveys of *campos de altitude* (Brade, 1942; Forster & Souza, 2013; Machado, Forzza, & Stehmann, 2016; Mazine & Souza, 2008) or on vegetation types other than *campos de altitude* (Zorzanelli, Dias, da Silva, & Kunz, 2016). Only recently researchers have shifted their focus to the ecological dimension of this ecosystem (Campos et al., 2018).

2.2. Data base

The data used for selection of indicator species were obtained from previous collections for composition and structure vegetation studies (Campos et al., 2018; Cordeiro, 2017). The altitudinal belts where the plants were collected were 2100, 2300, 2500, 2700 and the mountaintop at 2892 m of elevation along the main track to *Pico da Bandeira*. In both studies, all species of vascular plants found inside the plots were sampled and the abundance recorded.

2.3. Species selection for sample collection

To collect functional and leaf spectral data in a feasible time, we selected indicator species of *campos de altitude* (grassland physiognomy) prior to the field work. Therefore, the species selection must represent the whole altitudinal range and different frequencies of coverage and occurrence (González, Rochefort, Boudreau, Hugron, & Poulin, 2013; Ricotta, Carboni, & Acosta, 2015). To do this, from the obtained database will be carried out a selection of species indicative of each altitude quota and of the whole altitude gradient by means of the calculation of the Indicator Value (IndVal) (Cáceres & Legendre, 2009).

The indicator species analysis was carried out using the package 'indicspecies' in R environment (Cáceres, 2013), in order to relate species abundances to altitudinal heights by means of the Indicator Value index (IndVal). Indval is calculated for each species as a product of two variables: specificity (concentration of abundance of the species under analysis at a particular elevation) and fidelity (proportion of plots in a particular elevation containing the species under analysis) (Cáceres, 2013; Ricotta et al., 2015). The 95% significance level of the IndVal was assessed by a Monte Carlo test with 999 permutations (Bakker, 2008; González, Rochefort, Boudreau, & Poulin, 2014).

From the analysis results we selected three to five species per altitudinal quota, which were possible to confirm the identification in the field at the time we sampled (Table 1). For instance, we had to exclude from collection species difficult to be recognised from Poaceae and Cyperaceae families and those with undetermined species identity in the data base. The species here called 'generalists' are species found in the whole studied altitudinal range of *campos de altitude*, according to our data base, and which were indicators of at least two altitudinal quotas. *Baccharis platypoda* and *Eryngium elegans* were indicator of four altitudinal quotas; and *Hippeastrum glaucescens* was indicator of two quotas but it was considerably abundant along the gradient at the time of field collection.

Table 1 - Species selected by altitudinal range for the analysis and their respective Raunkiaer's life form.

Altitude	Species (Family)
2100 – 2890	*Baccharis platypoda* DC. (Asteraceae)
	Eryngium elegans Cham. & Schltdl. (Apiaceae)
	Hippeastrum glaucescens Mart. (Amaryllidaceae)
2100	*Gomesa barbaceniae* (Lindl.) M.W.Chase & N.H.Williams (Orchidaceae)
	Hesperozygis myrtoides (A. St.-Hil.) Epling (Lamiaceae)
	Myrsine coriacea (Sw.) R.Br. ex Roem. & Schult. (Primulaceae)
2300	*Achyrocline vargasiana* DC. (Asteraceae)
	Borreria capitata (Ruiz & Pav.) DC. (Rubiaceae)
	Doryopteris paradoxa (Fée) C. Chr. (Pteridaceae)
	Lucilia lycopodioides (Less.) S.E. Freire (Asteraceae)
2500	*Croton erythroxyloides* Baill. (Euphorbiaceae)
	Lycopodium clavatum L. (Lycopodiaceae)
	Oxalis calva Progel (Oxalidaceae)
	Plantago australis Lam. (Plantaginaceae)
	Trimezia campanula Lovo, J. & Mello-Silva (Iridaceae)
2700	*Baccharis opuntioides* Mart. (Asteraceae)
	Declieuxia coerulea Gardner (Rubiaceae)
	Oxalis confertissima A. St.-Hil. (Oxalidaceae)
	Paepalanthus acantholimon Ruhland (Eriocaulaceae)
	Stevia camporum Baker (Asteraceae)
2890	*Achyrocline satureioides* (Lam.) DC. (Asteraceae)
	Chionolaena arbuscula DC. (Asteraceae)
	Chusquea baculifera Silveira (Poaceae)
	Gaylussacia caparoensis Sleumer (Ericaceae)
	Oxypetalum leonii Fontella (Apocynaceae)

2.4. Leaf data collection and processing

The expedition for field collection of data was in January 2018, in the peak of the growing season. We collected fully expanded and sun-exposed leaves that represent the canopy and without conspicuous damage caused by pathogens or herbivores. For all indicator species we sampled randomly at least five individuals per species for each group of altitude level; for the generalist species we collected 25 individuals per species, five from each of the altitude levels. Due to the sensitivity of the spectral properties to the physiological status of the plants along the daytime, as far as possible we collected the samples around the same daytime. The single leaves or brunches (for species with small leaves) were wrapped in moistened paper towel and placed in closed plastic bags to avoid desiccation. Then, the samples were stored in a refrigerated container until the spectral measurement, done within 48 hours.

In the lab, we recorded the spectral signatures of the leaves using an ASD Pistol Grid attached to an ASD Field-Spec® 4 Hi-Res spectrometer (Analytical Spectral Devices, Boulder, CO, USA) (specifications in Table 2) and a spotlight (model, brand) adjusted a 45˚ angle to the surface as showed in Figure 2. We used three measurements per individual from the adaxial face of the leaves, using a bunch or a pile of small leaves or single leaves for those big enough to be captured by the spectrometer probe. In the case of aphyllous species *Baccharis opuntioides*, we used the tips of the photosynthetically active twigs as the representative of the plants' crown.

Figure 2 - ASD Spectrophotometer with the spectral probe. A detail of the material at the moment of spectra capture.

Later, the raw data recorded were converted from radiance to reflectance data with the ViewSpecPro software provided by the manufacturer of the ASD. In order to identify outliers in the spectra, all spectra of each species were plotted, and obviously, deviating spectra were deleted manually. Offsets produced in the spectra by the shift of sensors of the spectrometer were corrected by splice correction using the software RS^3 ™ (Analytical Spectral Devices, Boulder, CO, USA). There were 555 spectra collected and processed altogether, and an averaged spectrum was calculated for each individual, species or altitudinal level.

Table 2 - Technical specifications of the spectroradiometer used for data sampling.

Portable Spectroradiometer ASD FieldSpec 4 Hi-Res	
Spectral cover	350 - 2500 nm
Spectral resolution	3 nm (350-700 nm) 8.5 (700-1400 nm) 6.5 nm (~2100 nm)
Spectral intervals	1.4 and 2.0 nm
Number of bands	2151

2.5. Spectral indices

The Hyperspectral Vegetation Indices (HVIs) used in this work were selected based on their proved efficiency on detecting subtle changes in physiological status and plant stress parameters (Roberts et al., 2011; Xue & Su, 2017).

The Red-Edge Vegetation Stress Index (RVSI) is an index that captures variation in the shape of “red-edge” band associated with plant physiological stress (Table 3), which is based on the chlorophyll content – in the *red* region – and leaf structure – in the *near-infrared* region – (Horler, Dockray, & Barber, 1983; R Merton & Huntington, 1999; Ray Merton, 1998; Roberts et al., 2011). Slightly negative or positive RVSI values are found in stressed plants (upward concavity in red-edge band), while a concave downward red-edge, and strongly negative values occur in unstressed plants (R Merton & Huntington, 1999).

One of the most used plant physiology indices, the Photochemical Reflectance Index (PRI) is a carotenoid index that shows high correlation with plant stress-induced change in the state of xanthophylls (Gamon, Peñuelas, & Field, 1992; Garbulsky, Peñuelas, Gamon, Inoue, & Filella, 2011). The PRI is designed to capture the shift from violaxanthin to zeaxanthin, and so it is an indicator of photosynthetic efficiency and radiation use efficiency (RUE) (Gamon et al., 1992). This shift is a result of a subtle decrease (<1%) in the reflectance at 531 nm of wavelength, which can be quantified using a difference normalized index and 570 nm as reference band. Therefore, PRI values progressively negative will occur in more stressed plants (Roberts et al., 2011). Garrity et al. (2011) found that the PRI is significantly influenced by both chlorophyll and carotenoid contents, but the PRI-carotenoid/chlorophyll ratio relationship is the most consistent in all the analytical approaches.

The Normalized Difference Vegetation Index (NDVI) is calculated from hyperspectral radiance as a normalized ratio between the reflectance at the red (680 nm) and the reflectance at the near infrared band (800 nm) (Karnieli et al., 2010). NDVI is one of the most used indices for vegetation studies as a direct proxy of canopy growth and vigour, due to its power in predicting wet and dry green biomass (Galvão, Vitorello, & Almeida Filho, 1999; Tucker, 1979). In general, NDVI values are positively correlated to green biomass, photosynthetic activity and growth vigour, and may also be correlated to higher land surface temperature (Karnieli et al., 2010); low values near zero represent low photosynthetic rate, characteristics of more stressed vegetation (Roberts et al., 2011).

Table 3 - Hyperspectral Vegetation Indices investigated and their respective formulas.

Vegetation Index	Formula[1]	Reference
Red-Edge Vegetation Index (RVSI)	$RVSI = (R_{714} + R_{752})/2 - R_{733}$	(Ray Merton, 1998)
Photochemical reflectance Index (PRI)	$PRI = (R_{531} – R_{570})/(R_{531} + R_{570})$	(Gamon et al., 1992)
Normalized Difference Vegetation Index (NDVI)	$NDVI = (R_{800}-R_{680})/(R_{800}+R_{680})$	(Gago et al., 2015; Rouse, Haas, Schell, & Deering, 1974)

1) Where: R_{714}, R_{752}, R_{733}, …, and R_{680} indicates the spectral reflectance at 714, 752, 733, …, 680 nm, respectively.

2.6. Data Analyses

The data produced were subjected to analysis of variance (ANOVA) of linear regressions using Generalized Linear Models (GLM), and Linear mixed models with species as random factor (five altitude levels, three generalist species and 22 indicator species, five repetitions for each of them), all using 5% as the significance level. Prior to the ANOVA, all data were checked for the normality of the distribution of the residuals by Shapiro-Wilk test. We used Tukey HSD test for comparative analyses between pairs of means. All statistical analyses were done using the R statistical software (R Core Team, 2017), implemented in RStudio (RStudio Team, 2018). Packages in R used: *car*, *indicspecies, MuMIn*, *multcomp*, *lme4*, *lfe*.

3. Results

The resulting averaged spectra is plotted in Figure 3. We detected a more evident differentiation between the plant species sampled from the lowest and the highest altitudes in the Near-Infrared wave region.

Figure 3 - Spectral reflectance recorded (in nm*) from species along an altitudinal gradient from campos de altitude grasslands, Caparaó National Park, Brazil.*

3.1. Red-edge Vegetation Index (RVSI)

RVSI values were positively and significantly correlated with altitude when considering all the species sampled in the plant community of *campos de altitude*, what indicates that plant traits are responding to an increase of harsh conditions related to altitude (Table 4; Figure 4.a). However, the RVSI values obtained were slightly negative values, indicating that no strong stress condition was detected in the physiological status of the plant species sampled.

Table 4 - Red-edge Vegetation Stress Index (RVSI) values and the respective analyses results obtained from plant species and groups sampled along an altitudinal gradient in campos de altitude, Caparaó National Park, Brazil.

Species group	***p*-value**	**r^2 altitude**	**r^2 altitude +species**
All species – altitude alone	<0.001*	0.1621	0.6691
All species – altitude + species as factor	<0.001*	0.0521	0.6377
Indicators – altitude alone	<0.001*	0.2311	0.7955
Generalists – altitude alone	0.025*	0.0665	0.1688
Generalists – altitude + species as factor	0.0171*	0.0633	0.1746
Baccharis platypoda	0.005*	0.2961	
Eryngium elegans	0.002*	0.3474	
Hippeastrum glaucescens	0.048*	0.1157	

When assessed separately, the group of indicator species also showed a positive significant correlation between RVSI and altitude, but with a steeper slope of the regression line and a greater coefficient of determination (Table 4; Figure 4.b). The generalist species group showed a similar trend, with positive and significant correlation of RVSI values with altitude, although the coefficient of determination of this group was lower than the other groups (Table 4; Figure 4.c).

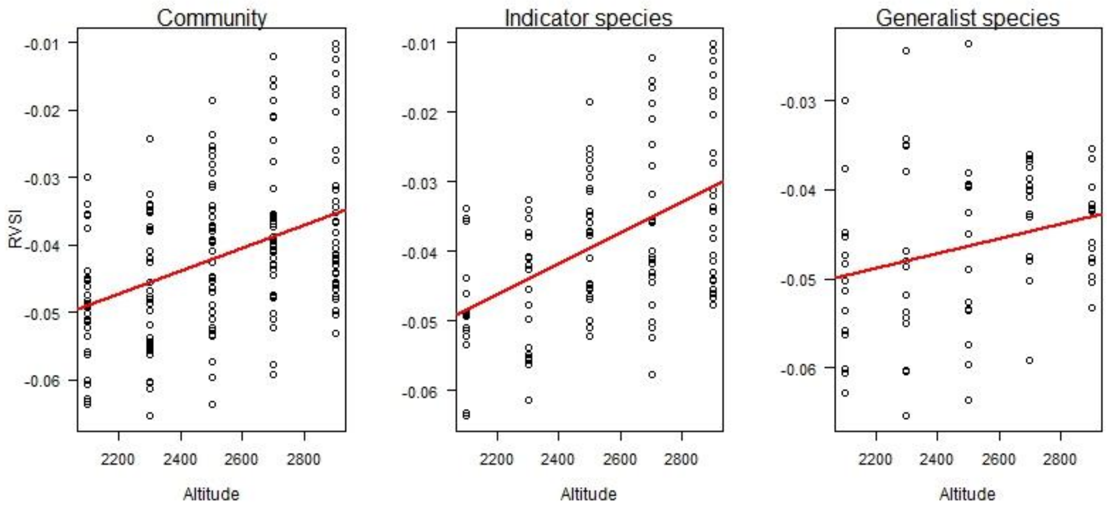

Figure 4 – Red-edge Vegetation Stress Index (RVSI) values found in the sampled species from campos de altitude, Caparaó National Park, Brazil, by species group: a) community, b) indicator species, and c) generalist species.

Analysing individually, the generalist species displayed different behaviours when comparing results of RVSI related to the altitude gradient (Table 4; Figure 5). For *Baccharis platypoda* and *Eryngium elegans*, the RVSI values were positively and significantly correlated to altitude (Table 4; Figure 5); *Eryngium elegans* had a greater coefficient of determination value and a steeper slope of the regression line, the highest among generalist species (Table 4; Figure 5.b). Therefore, *E. elegans* seems to be more affected negatively than *B. platypoda* in terms of environmental stressors in higher altitudes. Only RVSI values of *Hippeastrum glaucescens* showed a statistically significant negative correlation to the altitudinal gradient (Table 4; Figure 5.c). Thus, this species has more stressed individuals in lower altitudes, an opposite behaviour to the other species. *E. elegans* has lower mean RVSI values than the other two species, *B. platypoda* and *H. glaucescens* which have similar values.

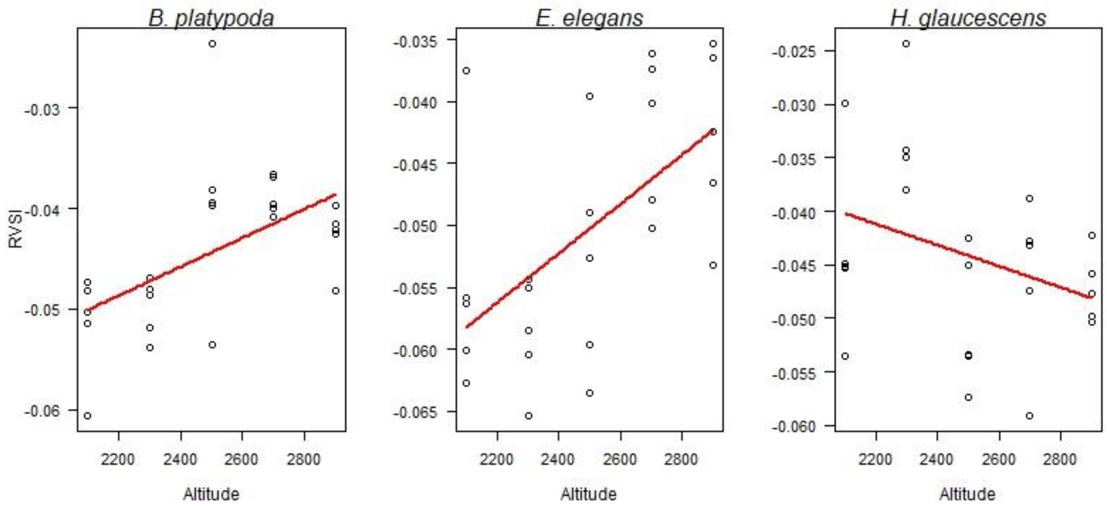

Figure 5 – Red-edge Vegetation Stress Index (RVSI) values found in the generalist species sampled from campos de altitude, Caparaó National Park, Brazil: a) Baccharis platypoda*, b)* Eryngium elegans*, c)* Hippeastrum glaucescens.

3.2. Photochemical Reflectance Index (PRI)

PRI values obtained did not show a significant (p>0.05) correlation with the altitude change when considering either the whole pool of species collected (Table 5; Figure 6.a) or the indicator species group (Table 5; Figure 6.b) (although it did show a negative correlation, marginally significant). On the other hand, the generalists group showed a significant positive correlation with the altitude when considering effect of species identity as factor (Table 5; Figure 6.c) and thus it represents slightly more stressed plant aspects in the lowest altitudes.

Table 5 - Photochemical Reflectance Index (PRI) values and the respective analyses results obtained from plant species and groups sampled along an altitudinal gradient in campos de altitude, Caparaó National Park, Brazil.

Species group	***p*-value altitude**	**r^2 altitude**	**r^2 altitude + species**
All species – altitude alone	0.361	0.0045	0.6302
All species – altitude + species as factor	0.2125	0.0063	0.6355
Indicators – altitude alone	0.0667	0.0308	0.7281
Generalists – altitude alone	0.079	0.0421	0.4172
Generalists – altitude + species as factor	0.035*	0.0345	0.4334
Baccharis platypoda	0.303	0.0459	-
Eryngium elegans	0.993	3.51e-06	-
Hippeastrum glaucescens	0.022*	0.2146	-

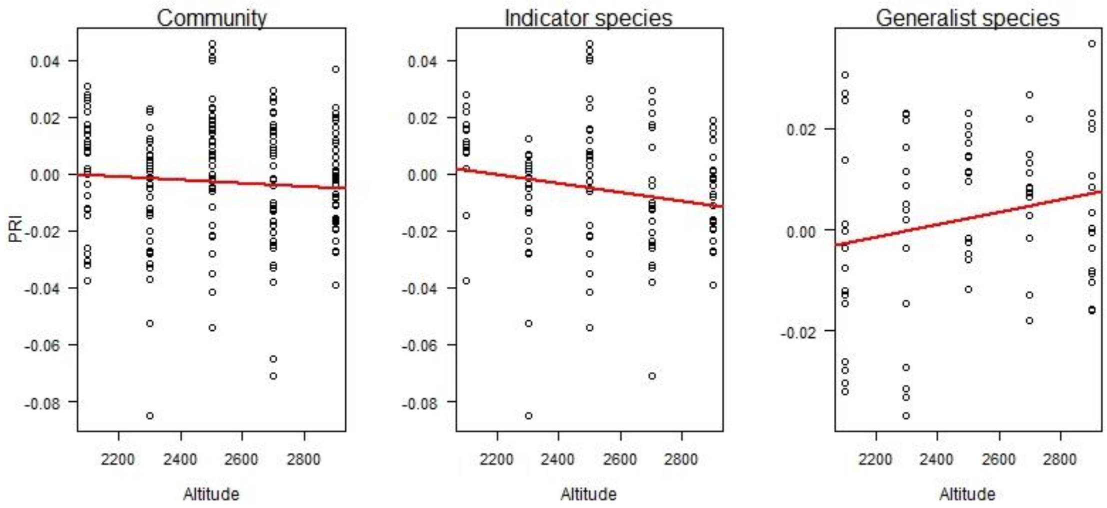

Figure 6 – Photochemical Reflectance Index (PRI) values obtained from plant species sampled along a altitudinal gradient in campos de altitude, Caparaó National Park, Brazil.

The generalist species *Baccharis platypoda* and *Eryngium elegans* analysed individually did not present a significant variation in the altitudinal gradient (Table 5; Figure 7). Conversely, *Hippeastrum glaucescens* presented a significant variation of PRI values along the altitude gradient, with a positive correlation (Table 5; Figure 6). This significant behaviour of *H. glaucescens* mainly contributed to the significant result of the generalist group – when considered the effect of the species identity apart from the effect of altitude. In average, *Eryngium elegans* presents higher PRI mean values than *B. platypoda* and *H. glaucescens*, which have no statistical difference.

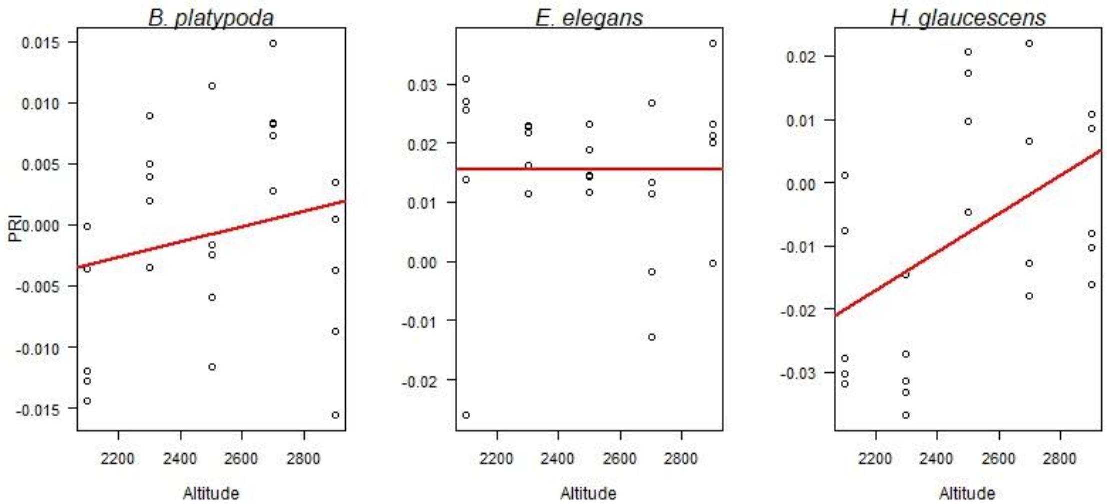

Figure 7 – Photochemical Reflectance Index (PRI) values obtained from generalist species sampled along an altitudinal gradient in campos de altitude, Caparaó National Park, Brazil: a) Baccharis platypoda, b) Eryngium elegans, c) Hippeastrum glaucescens.

3.3. Normalized Difference Vegetation Index (NDVI)

Regarding NDVI values, in the species pool collected we detected a significant negative correlation with altitude variation (Table 6; Figure 8.a); the indicator species group also showed a significant negative correlation but with a greater inclination of the regression line and a higher coefficient of determination (Table 6; Figure 8.b). These results show that plant species collected at the highest altitudes, especially the indicator group, tend to have characteristics of plants under more restrictive environmental conditions, fact that agrees to our initial hypothesis.

Table 6 - Normalized Difference Vegetation Index values and the respective analyses results obtained from plant species and groups sampled along an altitudinal gradient in campos de altitude, Caparaó National Park, Brazil.

Species group	***p*-value altitude**	***r^2* altitude**	***r^2* altitude + species**
All species – altitude alone	<0.001*	0.0715	0.5102
Indicators – altitude alone	<0.001*	0.1155	
Generalists – altitude alone	0.5102	0.0058	0.5394
Generalists – species as factor	0.3408	0.0047	0.6178
Baccharis platypoda	0.3501	0.0380	
Eryngium elegans	0.3315	0.0410	
Hippeastrum glaucescens	0.6804	0.0074	

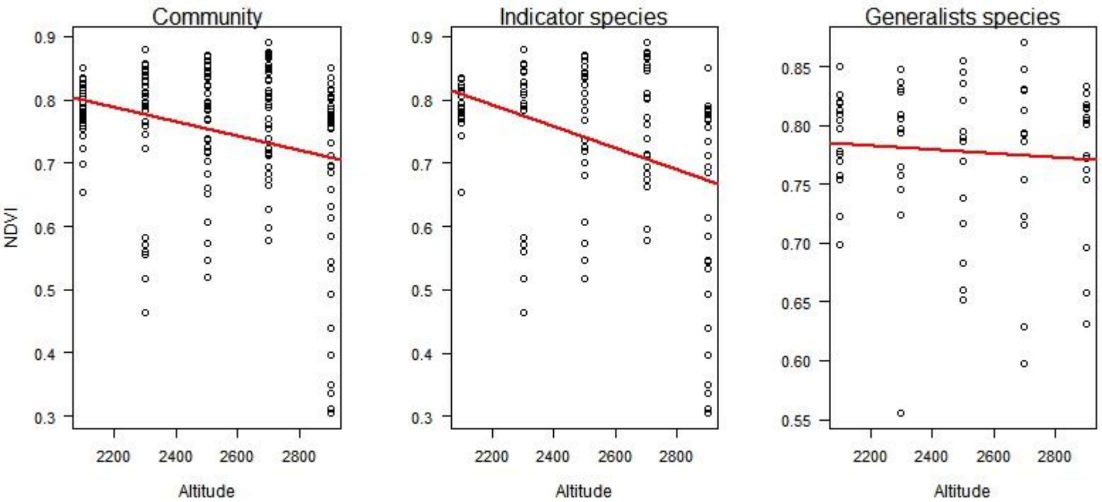

Figure 8 – Normalized Difference Vegetation Index (NDVI) values found from the species sampled along an altitudinal gradient in campos de altitude, Caparaó National Park, Brazil.

On the other hand, the generalist species group did not show a significant variation along the altitudinal gradient (Table 6; Figure 8.c). When analysing generalist species individually, none of them presented a significant correlation with altitude (Table 6; Figure 9). However, it was detected a significant difference among the species: *B. platypoda* showed lower mean values of NDVI than *E. elegans* and *H. glaucescens,* which were not significantly different from each other. From these results we see no intraspecific variation along the studied altitudinal range but an interspecific difference of the values among species, which means that the variance among species is determinant when comparing NDVI results.

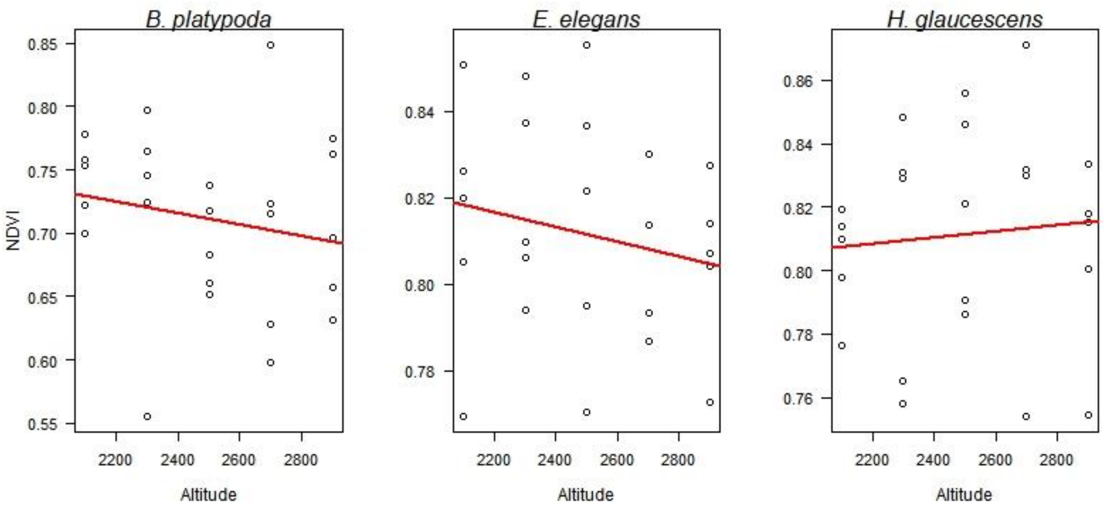

Figure 9 – Normalized Difference Vegetation Index (NDVI) values found in the sampled generalist species along an altitudinal gradient in campos de altitude, Caparaó National Park, Brazil.

4. Discussion

Our study is the first one to investigate the spectral properties of plant species and functional groups along an altitudinal gradient in Brazilian high-altitude grassland. The results revealed that altitude is a relevant factor in the spectral reflectance variation and that this spectral diversity is important to the understanding and the monitoring of grassland communities from tropical rocky outcrops at high altitudes. Three hyperspectral vegetation indices (HVIs) – RVSI, PRI, NDVI – were used for assessing the physiological status and morphological adaptations of the vegetation. Each of these HVIs presented some significant variation along the altitudinal gradient, in general showing correspondence of plant traits to the harsher conditions of high altitude.

The RVSI is the index that showed the strongest positive correlation with altitude considering the whole pool of species and the indicator species group. The higher RVSI values in plants at the highest altitudes indicate plant physiological stress through the variation in shape of the red-edge region, conventionally related to plant stress and chlorophyll's activity (Ju et al., 2010; Roberts et al., 2011). These RVSI results corroborate our initial hypothesis that higher altitudes have more restrictive environmental conditions typically found in mountaintop ecosystems (Carvalho et al., 2014; Fernandes, 2016; Leuschner, 2000) – and that this fact is detectable by a spectral vegetation index (Ray Merton, 1998; Roberts et al., 2011). These conditions, such as low mean temperatures, shallow and nutrient-poor soils, high solar radiation, limit the potential growth of native plants and the productivity of the community (Aparecido et al., 2018; Carvalho et al., 2014; Hugh DeForest Safford, 1999a).

It is important to notice that no species in our sample seems to be in a strong stressed status (RVSI values between -0.0652 and -0.01019) once we know that RVSI values slightly negative or positive are found in stressed plants and strongly negative values are found in unstressed plants (R Merton & Huntington, 1999; Roberts et al., 2011). This fact is probably associated with the time the species were sampled, which was mid-summer (January, 2018), the peak of the growing season with higher temperatures and precipitation (Hugh DeForest Safford, 1999b). In the first description of the RVSI, Merton (1998) verified that this index varies significantly according to the environmental conditions of the seasons and, therefore, it shows progressively positive values as the growing season comes to the end.

RVSI is one of the key vegetation indices indicated to assess health condition of tropical and subtropical forests (Kalacska & Sanchez-Azofeifa, 2008) and it is also known to be related to leaf nitrogen content, as RVSI values decreases with higher N content (Perry & Roberts, 2008). Therefore, our results from RVSI may also reflect the nutritional condition of the soil with possibly lower nitrogen contents in higher elevation in the gradient, as expected from other studies on soil nutrients of Brazilian high altitude grasslands (Vinicius M. Benites et al., 2007; Carvalho et al., 2014; Neri et al., 2016).

The generalist group also responded to altitude in RVSI values, although with a lower correlation to the elevation, mainly as an influence of the behaviour of *B. platypoda* and *E. elegans*. These two species had a similar trend of the indicator species, which presents more stressed traits in individuals from the highest altitudes. *B. platypoda* is a shrub with perennial leaves commonly found in grasslands and shrublands associated with rocky outcrops and savanna ecosystems in eastern Brazil and *E. elegans* is a perennial bromeliad-like herb found grasslands associated with high altitude rocky outcrops and subtropical *Pampas* grasslands in southern/south-eastern Brazil (Jardim Botânico do Rio de Janeiro, 2018). Caparaó mountains are the highest elevations where these species occur naturally and thus the leaf stress traits saw in our measurements may represent phenotypical plasticity limits and growth limitations in this harsh environment (Aparecido et al., 2018; Valladares, Gianoli, & Gómez, 2007).

The third generalist species *Hippeastrum glaucescens*, on the other hand, had a singular response of RVSI that contrasts with the other two generalist species, which indicates more stress related traits in lower altitude individuals than in higher altitude. *H. glaucescens* is a geophyte species – bulbous and deciduous plant – that occurs in open plant physiognomies in a wide range of biomes of south, southeast and mid-west Brazil (Jardim Botânico do Rio de Janeiro, 2018). The loss of leaves during the limiting season reduces the impact of the stressing conditions on the aerial parts and consequently the need of investing in protective leaf traits, such as xeromorphic adaptations (Dickison, 2000; Silva, Meira, Azevedo, & Euclydes, 2006). Accordingly, the stress detected in the RVSI values in *H. glaucescens* plants of lower elevations may due to warmer spring temperatures that induces the natural phenological cycle of the leaves to grow and to die earlier than in the ones in the higher altitudes (Körner, 2007). This PRI trend may also be caused by stressing conditions, because from personal observations, we noticed that the lower altitude sampled areas, around 2100 to 2350 m, had drier conditions of the soils and vegetation, which seems to be a result of the higher temperatures than in the high altitudes and high solar radiation due to the west facing slope.

The measurements of PRI in the whole group of species studied did not show a significant variation and evidences of stress adaptations of plants along the altitude, and so the community do not seem to have very different strategies related to carotenoids and chlorophyll contents detectable through PRI measurements (Garrity, Eitel, & Vierling, 2011; Wong & Gamon, 2015). PRI is an index developed as a surrogate for measuring Radiation Use Efficiency (RUE), based on the proportion of chlorophylls and carotenoids and the xanthophylls cycle (Gamon, Serrano, & Surfus, 1997). The shift of violaxanthin to zeaxanthin works as an energy sink when the chlorophyll molecules are overloaded, which prevents photooxidation in the photosystem II (Demmig-Adams & Adams, 1992; Latowski, Kuczyńska, & Strzałka, 2011). These values vary among species, functional type and level of available nutrients (Gamon et al., 1997). There is evidence that PRI values are also correlated to the proportion of chlorophyll and carotenoids content (Garrity et al., 2011).

PRI results only showed a significant variation along the altitudinal gradient for the generalist species *H. glaucescens*, which affected directly the significant variation in the generalist group when analysed considering the effect of species identity. This species seems to be affected by environmental changes along the altitudinal gradient so that the individuals found in lower altitudes have lower radiance use efficiency (RUE) due stressing conditions (Gamon et al., 1997). This trend corroborates to the results found in RVSI measurements that indicates stress in *H. glaucescens* at lower altitudes and thus contradicts our initial hypothesis that the most stressing conditions are found in the highest altitudes.

According to the NDVI and RVSI results, the indicator species from higher altitudes present ecophysiological adjustments to cope with the more stressing conditions of mountain-top ecosystems, in general reducing the RUE and the productivity (Gamon, Kovalchuck, Wong, Harris, & Garrity, 2015; Ray Merton, 1998). The same result was observed when assessed all the species sampled together but not in the generalist species group. NDVI is an index developed as a measure of vegetation greenness, and it is typically used to evaluate seasonal phenology or productivity of vegetation as it changes gradually with the growth and senescence of vegetation (Gamon et al., 2015). Previous studies have shown an existing trade-off relationship between the maximum photosynthetic rate and the investment in protecting characteristics associated with leaf longevity (REF). NDVI varies according to the altitude, however this variation is more likely to be due to the shift in species composition (especially in the indicator species group) than due to species intraspecific variation from acclimation to the environmental conditions (Stoms & Hargrove, 2000).

The indicator species group showed a stronger correlation between RVSI and NDVI and altitudinal range. The three species here selected as generalists due to their wider occurrence area showed a behaviour according to the altitude distinct from the indicators group and also different behaviour among themselves. Thus the selection of indicator species by IndVal calculation seems to be an effective tool for detecting plant strategies related to an environmental gradient (Cáceres & Legendre, 2009; González et al., 2013). Plant species of different size of distribution range inhabiting the same grassland vegetation have diverging morpho-physiological stress strategies, for instance micro-endemic species possess high nutrient use efficiency and shoot architecture that minimizes the excessive light absorption at midday (Pereira, Siqueira-Silva, Souza, Melo, & Souza, 2017), which may be the case of some of the indicator species we studied here. In addition, the interpretation of the data from the whole pool of species sampled in this study contributes to remote sensing imaging approaches that use the indices RVSI and NDVI, and it also gives the possibility of monitoring the stress conditions of the whole community of plants of *campos de altitude* (Van Cleemput et al., 2018).

The different spectral characteristics of the species allow us to conclude that altitude is a determinant factor on the development of the flora on these high-altitude grasslands, as described in the literature in other tropical mountain ecosystems (Körner, 2007; Krömer, Acebey, Kluge, & Kessler, 2013; Leuschner, 2000; Neri et al., 2016). The index that showed the most prominent results was RVSI and, therefore seems to be an effective tool for plant strategies investigation and monitoring of the conditions of *campos de altitude,* with special importance in the context of climate change impacts on these unique ecosystems. Further spectral and morphophysiological studies should be conducted in these plant communities in different climate seasons, and investigating the environmental attributes themselves, *e.g.* atmospheric temperature, soil characteristics and water availability, as well as approaches that use other spectral regions or indices not evaluated here.

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