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ABSTRACT

The capacity of ecological models to better capture and predict ecosystems variations and changes is dependent on the choice of its environmental inputs' variables, being precipitation the mostly used hydroclimatic variable. Yet, water available to plants is a function of rainfall and atmospheric evaporative demand. We assessed which hydroclimatic variable better explains variations in vegetation productivity in a seasonally dry tropical mountain system. We modeled NDVI temporal responses of different vegetation types to Climatic Water Deficit (CWD) and Precipitation, answering the following questions: 1) Are the responses of vegetation to different hydroclimatic variables specific for each vegetation type? 2) If so, which hvdroclimatic variable better explains vegetation productivity for each vegetation type? We found that seasonally dry vegetation types were more responsive to CWD, while moist vegetation productivity was poorly explained by all hydroclimatic variables. The timing of responses of vegetation to CWD or precipitation varied according to site specificity.

Key words — Evapotranspiration, Climatic Water Deficit, Mountain, NDVI, Vegetation productivity.

1. INTRODUCTION

In ecological studies, the identification of environmental variables that are ecophysiologically meaningful is crucial to improve models and better forecast ecosystem changes [1]. Hydrological dynamics are a major driver of ecosystem function, and yet, are usually oversimplified when studying species distribution and vegetation dynamics [2]. Given the importance of water to ecological processes, the choice of predictive hydrological variable is directly related to the capacity of models to capture and predict ecosystem dynamics [3].

Precipitation is frequently used as a predictor of plant water availability, but it is known that the water available to plants is a function not only of rainfall input, but of a set of other variables, such as atmospheric energy balance [4]. Stephenson (1998) advocates that many correlative studies on vegetation distribution and water availability do not make use of hydroclimatic parameters that are truly meaningful to plant physiology, and propose that Actual Evapotranspiration (AET) and Climatic Water Deficit (CWD) should be used instead of precipitation, since both variables provide a reasonable biological interpretation, and have shown good correlation with the distribution of different vegetation types, from local to continental scales [5]. Both CWD and AET estimate the length and magnitude of hydroclimatic conditions to plants; CWD is related to drought, and AET represents favorable conditions of availability for biologically usable water and energy inputs to the environment [4].

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In the tropics, vast areas experience seasonally dry climates, which are well-defined by a wet season during which most of the annual precipitation occurs, followed by a prolonged dry season. These areas harbor a great variety of vegetation types, from semi-deciduous to dry forests and savannas [6]. Seasonally dry tropical environments are expected to experience future changes in periodicity due to climate change, with stronger impacts predicted for higher elevations [7]. Among other impacts, tropical montane ecosystems will potentially suffer an acceleration of their hydrological regimes, caused by an increase on the variability of precipitation patterns [8], leading to, among others effects, changes in ecosystem functioning and productivity, or improvement of environmental conditions to invasive species, increasing mortality rates and, therefore impacting species diversity and distribution. For this reason, understanding and quantifying the spatial and temporal patterns of seasonal plant water use can provide important insights on how tropical mountainous ecosystems will respond to climate change.

The Espinhaço Range is a seasonally dry mountainous region feeding the watersheds of three large river basins in Brazil (São Francisco, Atlântico Leste and Atlântico Sul), with a primary S-N direction. This region is an ecotone of semi-deciduous moist forests, savannas, dry forests and mountain vegetation (Figure 1). This ancient landscape, dating back to 640 Mya, has ample topographic and altitudinal variation, with mountain peaks reaching over 2000 meters a.s.l [9]. A recent analysis of spatial precipitation patterns in the Espinhaço Range showed that there is no significant difference in total annual rainfall between eastern and western sides, which are occupied by semi-deciduous forest and savanna vegetation, respectively [10]. For this reason, here we propose an analysis to assess which hydroclimatic variables better explain vegetation dynamics in the Espinhaço Range.

To understand the relations between vegetation productivity and hydroclimatic variables in this tropical mountainous system, and improve variables choice for bioclimatic studies, we addressed the following questions: 1) Are the responses of vegetation to different hydroclimatic variables specific for each vegetation type? 2) If so, which hydroclimatic variable better explains vegetation productivity for each vegetation type?

2. MATERIAL AND METHODS

We adjusted pixel-wise linear regression models between an NDVI dataset, a proxy of vegetation productivity, and two layers of hydroclimatic variables (precipitation and CWD) to assess the temporal vegetation responses to water availability. The linear regression models were fitted using monthly pairwise observations, with 0, 1 and 2-month lags for precipitation and CWD, to capture possible lagged vegetation responses to climate. All datasets covered the period between January/2001 and December/2017, at monthly intervals, with a 1 x 1 km spatial resolution. To ensure we were sampling natural vegetation, we fitted the models to all pixels within the studied region to reveal broad spatial patterns, but then evaluated model fit only for regions corresponding to known protected areas within the Espinhaço Range.

Vegetation types at each protected area were classified following the Brazilian official biome classification, and then attributed to the protected areas. To delineate the "Campos Rupestres" classification, which is not an official biome, we identified all protected areas that overlaid the Silveira et. al (2016) "Campos Rupestres" delineation, and reclassified it as "Campos Rupestres" protected areas. The vegetation types found on the study area are, hereafter, classified as "Caatinga" (5014 pixels), "Campos Rupestres" (8041 pixels), "Cerrado" (7900 pixels) and "Mata Atlântica" (11572 pixels).

We used a time-series of NDVI images generated from Moderate Resolution Imaging Spectroradiometer (MODIS) images. Data was obtained from the Land Process Distributed Active Archive Center (LP-DAAC – USGS/NASA). Monthly NDVI pixels values result from the best pixel composite of two 16-day composite periods. To improve the quality of pixels, and minimize atmospheric and cloud effects, the 16-day period algorithm chooses the best available pixel within all the acquisition dates. All monthly images were downloaded, mosaiced and transformed to GeoTIFF format using the "MODIStsp" package of the R programming language [11].

Precipitation was obtained from the Climate Hazards Infrared Precipitation with Stations (CHIRPS) dataset [12]. CHIRPS is a quasi-global precipitation dataset which incorporates satellite data of cold cloud duration and gauge stations. Using an interpolation approach between cold cloud duration rainfall estimates and gauge station data, CHIRPS provides daily, pentadal, monthly, 2 and 3 months aggregated and annual precipitation gridded datasets at a 5 x 5 km spatial resolution. We disaggregated the data to 1 x 1 km spatial resolution to match the NDVI dataset. CHIRPS is freely available at http://chg.geog.ucsb.edu/data/chirps/.

We used the TerraClimate dataset [13] to obtain CWD values, which are gridded (~ 4km) monthly data products. TerraClimate products are generated from the interpolation of different global weather station databases from WorldClim (version 1.4 and version 2.0), CRU Ts4.0 and JRA-55. To calculate AET and CWD, TerraClimate uses a onedimensional modified Thornthwaite-Mather climatic waterbalance model, with CWD given as the difference between (PET) Potential Evapotranspiration and Actual Evapotranspiration (AET). We also disaggregated the data to 1 x 1 km spatial resolution to match thr NDVI dataset. TerraClimate freely available is at http://climatologylab.org/terraclimate.html.

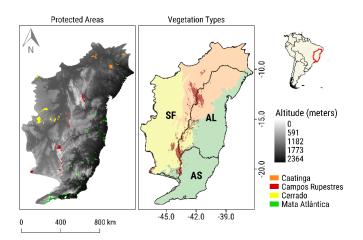


Figure 1. Overview of the Espinhaço mountain range in Brazil. On the left panel, the topography and extent of the Espinhaço Mountain Range and the protected areas classified by vegetation types, in Brazil. On the right, the Espinhaço Range as an ecotone of vegetation types, and as the watershed of São Francisco (SF), Atlântico Leste (AL) and Atlântico Sudeste (AS) basins.

3. RESULTS

The pixel-wise linear regression between NDVI and either precipitation or CWD showed an inverse vegetation response to hydroclimatic variables (Figure 2). We found a general spatial pattern of higher responses of NDVI to CWD for monthly pairwise linear regressions, while the highest explained variance for precipitation was found using a 2-month lagged regression (Figure 2 A and 2 C).

"Caatinga" vegetation productivity better responded to pairwise CWD (median $r^2 = 0.87$) and had the worst results when using 2-month lag CWD (median $r^2 = 0.14$). "Campos Rupestres" was most responsive to 1-month lag CWD (median $r^2 = 0.80$) and least to 0-lag pairwise precipitation (median $r^2 = 0.12$). "Cerrado" productivity was better explained by 1-month lag CWD (median $r^2 = 0.92$) and had the lowest responses to pairwise precipitation (median $r^2 = 0.18$). "Mata Atlântica" productivity was the least responsive to hydroclimatic variables among all vegetation types, with its largest amount of variance explained by 2-month lag CWD (median $r^2 = 0.40$) and the smallest by the pairwise precipitation regression (median $r^2 = 0.05$).

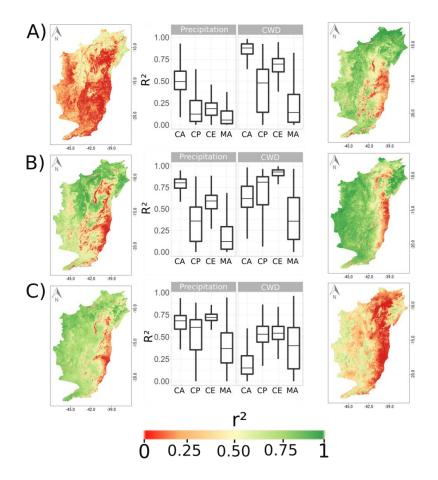


Figure 2. A) Pairwise linear regression; B) 1-month lag linear regression; C) 2-month lag linear regression. Maps resulted from the linear regression between NDVI (Jan/2001 to Dec/2017) and CHIRPS precipitation dataset (Jan/2001 to Dec/2017) (A; B and C left panels) and Climatic Water Deficit (Jan/2001 to Dec/2017) (A; B and C right panels), and boxplots of the r² resulted from the linear regressions (A; B and C middle panels) for each vegetation type sampled at known protected areas (CA = Caatinga; CP = Campos Rupestres; CE = Cerrado; MA = Mata Atlântica).

4. DISCUSSION

The amount of water available to plants is a result of the balance between hydrological inputs and outputs controlled by the amount of energy held in a system. Our results show that the most commonly used variable in ecological predictive models, precipitation, oversimplifies this hydroclimatic aspect, since vegetation productivity responses were poorly correlated to pairwise rainfall. Vegetation responses to CWD, a variable that accounts for the simultaneous availability of water and energy usable by plants, better explained NDVI variation in almost all cases.

"Caatinga" vegetation, which experiences seasonally dry to dry environments, was highly correlated with almost every hydroclimatic variable, with the exception of pairwise precipitation and 2-month lag CWD. Caatinga vegetation productivity is highly dependent on water, shedding their leaves to escape from drought, with the majority of plants presenting this drought avoidance strategy to periods of low water availability [10, 14]. The dry season experienced by caatinga is characterized by a long period of low to the absence of rainfall together with extremely high temperatures, that is, an excess of energy availability. Thus, the 1-month lag of precipitation explaining a greater variance on NDVI for this vegetation type, indicates that water takes around 1-month after the rainfall event to be available to plant use. This is a result of the first rainfall events in the beginning of the rainy season being rapidly evaporated to attend the high atmospheric evaporative demand from the dry season. However, caatinga vegetation is highly tuned to CWD, given the capacity of this variable to capture the coupling between small variations on water inputs and vegetation productivity, expressed by this balance between water inputs and atmospheric evaporative demand.

"Campos Rupestres" are found on mountaintops, associated with high topographic variation and rugged relief [15]. Runoff accounts for a major portion of the water balance in these environmental conditions, justifying the higher explained variance between vegetation productivity and the timing of precipitation. In addition, campos rupestres in high altitudes experience a near-constant presence of cloud cover, and consequently a lower amount of energy coming from solar radiation [10]. This way, "Campos Rupestres" productivity is better correlated to a 1-month lag CWD, demonstrating that this vegetation demands a certain accumulation of water and energy to be responsive.

The higher r² found for "Cerrado" productivity between 1-month lag CWD and 2-month lag precipitation is a function of the relations between topoedaphic conditions and energy availability. The "*Cerrado*" distribution is related to a region with high water retaining capacity, but the high irradiance and elevated temperatures during the dry season deplete the upper soil layers of water in this period [16]. Given the smooth topography and well-drained soils, deep-rooted plants can access water from the deeper soil layers even during the dry season, explaining the largest portion of productivity variance explained by the 2-month lag precipitation response. However, the best response was still found for the 1-month lag CWD, when there is a better balance between rainfall inputs and energy availability, especially during the rainy season.

The moist vegetation typical of the "Mata Atlântica" biome showed the lowest response between plant productivity and hydroclimatic variables, as a result of high-water availability throughout the year. This suggests that water availability may not be the main driver of vegetation productivity, in relation to other environmental conditions. Tropical moist forest phenology is usually characterized by continuous leaf flushing, as shown for Mata Atlântica [17] and Amazonia [18], with high influence of irradiance and cloud cover [10, 17].

5. CONCLUSIONS

The vegetation types analyzed across the study area, with exception of "Mata Atlântica", were highly correlated with hydroclimatic variables, especially with CWD, with variations in the timing of response regarding its experienced environmental conditions. We conclude that CWD is a better hydroclimatic predictive variable when analyzing vegetation dynamics in dry to seasonally dry regions, since it has the ability to capture plant response patterns to the amount of energy and water, in the spatial and temporal dimensions.

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