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# Daily Variation on Soil Moisture and Temperature on Three Restinga Plant Formations

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**ABSTRACT:** *Restinga* forests and open scrubby formations establish on sandy well-drained soils alongside the Brazilian coastline. *Restinga* plants are exposed to extreme conditions and vegetation types are mainly structured by species access to groundwater. But to date, no systematic evaluations have been done in order to characterize soil microclimatic conditions and understand how they are associated with variations in climatic drivers. We evaluated hourly soil moisture and temperature along 84 days at *Restinga* Seasonal Dry Forest (SDF), sparse (Open *Clusia* Scrubs—OCS), and dense (Open Ericacea Scrubs—OES) tickets at Restinga de Jurubatiba National Park, at Rio de Janeiro state (Brazil). Due to distinctions on physical structure and access to groundwater between plant formations, we expected higher daily soil moisture and lower daily moisture and temperature variations on forests than on open vegetated areas. Daily soil moisture was higher, respectively, on SDF, OES, and OCS, whereas soil moisture and temperature variability presented the opposite trend (SDF < OES < OCS), supporting our hypotheses. Daily soil temperature dynamics are quite well predicted by solar radiation incidence patterns, whereas daily soil moisture is mainly regulated by precipitation at OCS, an interaction of precipitation and temperature at OES and delayed effects of precipitation at SDF. Our results corroborate our expectations that forests are more effective in buffering both air temperature and precipitation effects on soil conditions than open vegetated areas. They also indicate that soil moisture and temperature conditions are important aspects differentiating *Restinga* vegetation types.

**KEYWORDS:** Vegetation types, soil conditions, microclimate, ground water, forest, open scrubby

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## Introduction

Brazilian sandy coastal plain, originated by marine deposits during Quaternary sea-level changes, are locally called *Restinga*. It consists of a mosaic of ecosystems formed by dried bare sand with patches of creep or shrubby low vegetation, areas covered by dry or wet woods, swales, artificial channels, and coastal lagoons (Martin et al., 1993). On *restinga* terrestrial ecosystems, plant species establish on sandy well-drained soils, and are exposed to extreme micro-climatic conditions, such as drought, high temperature, oligotrophy, intermittent flooding, and even salinity (Scarano, 2002; Scarano et al., 2005). Distinct sets of these species are morphologically and physiologically adapted to support these stressful conditions (Dias & Scarano, 2007; Rosado & de Mattos, 2010; Scarano et al., 2005), originating distinct vegetation types, such as forests, open and closed scrubby formations (Assis et al., 2011; Henriques et al., 1986; Martins et al., 2008; Scarano, 2002; Scarano et al., 2005).

The access to water resources, driven by the distance from water table and community capacity to retain rain water, is one of the main characteristics that defines the occurrence of these distinct vegetation types among *restinga* areas (Dansereau, 1948; Henriques et al., 1986; Scarano, 2002). Forest formations usually occur in the swales between sandy ridges, near coastal lagoons, shallow pools, or ancient lagoons, on older ridges or are subject to uprising of the water table during the rainy

season (Kurtz et al., 2013; Magnago et al., 2010). On the other hand, open scrubs lie at the top of the sandy ridges, often more than 1-m above ground-water levels, while closed or dense scrubs are situated in the intermediate position or are restricted to post-beach ridges (Henriques et al., 1986). As a result, their community properties and functioning are very distinct, mainly between open scrubs and forests, which tend to be more distinct along gradients on soil conditions and are the most frequent formations along some of the most studied *restingas* in Brazil (Caris et al., 2013; Santos-Filho et al., 2010; Scarano, 2002).

Open scrub areas are formed by sparse vegetation patches varying from <1 to 1,100-m<sup>2</sup> and from 1.5 to 6-m tall, covering about half of the matrix made up of bare sand and sparse herbaceous vegetation (Montezuma & Araujo, 2007; Pimentel et al., 2007). Plant community composition in these systems may be regulated by nutrients and water use efficiency, mainly during the dry season (Rosado & de Mattos, 2007, 2010). The few species achieving high leaf water potentials, strong stomatal control, and deep roots to access humid regions in the soil profile may become more abundant (Rosado & de Mattos, 2010). In contrast, *restinga* forest is a predominantly arboreal vegetation, seasonally or permanently flooded, with tall trees interspersed by sparse scrubby vegetation, with close and open canopy, respectively (Kurtz et al., 2013; Magnago et al., 2010).



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Forests are situated in more acidic and humid soils, also composed of clay and with higher organic matter concentrations (Kurtz et al., 2013; Magnago et al., 2010), and in general, are richer in woody species than scrubby formations (Assis et al., 2011; Kurtz et al., 2013; Magnago et al., 2010; Martins et al., 2008; Montezuma & Araujo, 2007; Pimentel et al., 2007). The rates of ecosystem processes also vary considerably between these formations. For example, litter production—which is a good proxy for plant production (Clark et al., 2001; Malhi et al., 2011)—is 1.2 to 2 times larger in forests than in open scrubs (Brito et al., 2018). Litter decomposition and carbon (C) loss rates follow this same trend, and are mediated by accelerated microbial and soil fauna activity in *restinga* forests (Brito et al., 2018). As a result, C and nutrient accumulation is also larger on *restinga* forest soils (Magnago et al., 2010).

So, on *restinga* plant formations, water table variations may directly affect community structure and ecosystem processes by regulating plant species access to ground water, and indirectly by soil moisture conditions and vegetation cover and composition effects on the dynamic of other edaphic conditions, such as acidity, nutrient availability, and microclimatic amplitude and variability. Previous studies have discussed the implications of variations on edaphic conditions such as soil structure, pH, and nutrient cycling on distinct *restinga* vegetation types (Assis et al., 2011; Brito et al., 2018; Magnago et al., 2010; Santos-Filho et al., 2013), but neglected the importance of local moisture and temperature variations. Soil moisture is a complex attribute reflecting topographic conditions, canopy cover, evapotranspiration rates, climatic (mainly rainfall and temperature) patterns, as well as local hydrology (Bruno et al., 2006; Nijssen et al., 2001; Riggs et al., 2015), and is commonly referred as one of the main drivers of primary production, decomposition, and plant species diversity on natural ecosystems (Brunbjerg et al., 2020; Moeslund et al., 2013; Riggs et al., 2015). Soil moisture also affect temperature variations, which tend to be lower on more humid sites due to high water specific heat and consequent changes in soil temperature capacity and diffusivity (Abu-Hamdeh, 2003). Temperature magnitude and variation also affect soil communities and ecosystem processes, even at short temporal and/or spatial scales (Bell et al., 2009; Cookson et al., 2007; Karhu et al., 2014; Salmon et al., 2008; Sulkava et al., 1996). Variations in vegetation properties such as canopy cover, stratification and litter layer thickness can also alter light distribution and shading patterns, throughfall interception, evapotranspiration, and soil structure, thus affecting soil moisture and temperature (Gray et al., 2002; Kim et al., 2011; Lin & Lin, 2010). Such effects may be more important under lower and sparsely distributed vegetation, where plant canopies have a limited capacity to modulate the effects of climatic variations on microclimate, than in taller and denser vegetated areas. Thus, understanding how soil moisture and temperature vary in *restinga* is an important step to understand feedback mechanisms that affect or regulate community and ecosystem

processes. But to date, no systematic measures of soil moisture and temperature have been done on *restinga* ecosystems in order to characterize distinct plant formations.

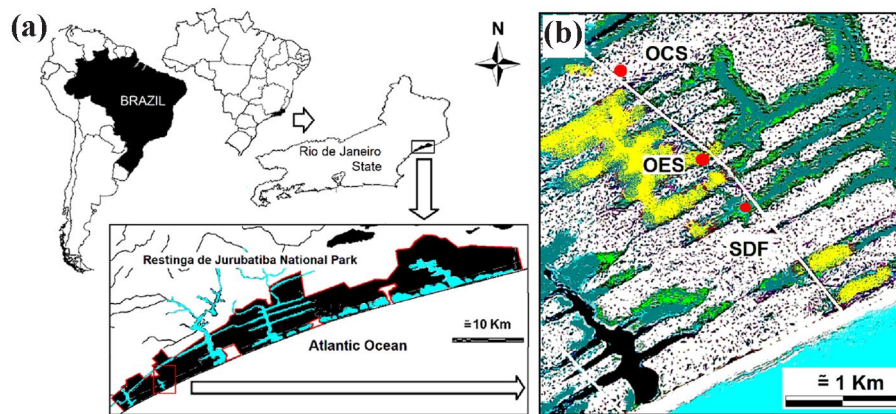
Here we aim to characterize the dynamics of soil moisture and temperature on open scrubs and forested *restinga* formations, and evaluate how they are associated with or driven by variations on air temperature, humidity, and precipitation. Because open scrubby formations tend to have only a limited capacity to modulate the effects of climatic variations on patch microclimate, we expect higher soil moisture and lower variations in soil moisture and temperature on *restinga* forest than on scrubby-dominated areas.

## Material and Methods

### Study area

The study site is situated in the Restinga de Jurubatiba National Park (22°00′–22°23′S; 41°15′–41°45′N), the largest protected area preserving *restinga* ecosystems in Brazil. It has an area of about 14.86 km<sup>2</sup> and 44 km in length in the municipalities of Macaé, Carapebus, and Quissamã, along the northern region of Rio de Janeiro state coastline. For the evaluation of the objectives presented above, it was selected a representative area from each of the three most common plant formations in the park (Figure 1): the Open Clusia Scrub (OCS), the Open Ericaceae Scrub (OES), and Seasonal Dry Forest (SDF), which cover 32%, 29.1%, and 15.7% of the park area, respectively (Caris et al., 2013). The fact that these plant formations are situated on a relatively small area on our study site (Figure 1) avoids great climatic variations, what allow us testing how climate drives microclimatic soil conditions.

About 141 plant species have been registered on OCS, from which 62 are woody species (Pimentel et al., 2007); it is dominated by the CAM tree species *Clusia hilariana* Schltdl. (Clusiaceae), which nucleates most of the vegetation tickets, although other few species are also common (Dias & Scarano, 2007; Pimentel et al., 2007). At OES, there has been registered 105 species; it is dominated by species from Myrtaceae family and is characterized by the great abundance of *Calyptanthus brasiliensis*, *Agarista revoluta* and mainly *Humiria balsamifera* (Montezuma & Araujo, 2007). In addition to the distinctions in the dominance of species in their tickets, OCS and OES differ by the fact that OCS patches are more stratified, while OES patches are flatter, have a higher vegetation density and their tickets are interspersed with areas of sparse and dense-shrubby herbaceous vegetation, respectively (Montezuma & Araujo, 2007; Pimentel et al., 2007). SDF supports 91 plant species, from which 84 are woody species, with no clear dominance; vegetation is dominated by trees, that can reach up to 20 m height (Kurtz et al., 2013). For this study, the selected area is close to Comprida lagoon (Figure 1), and the sampling sites were chosen due to the dominance of representative species, mainly for OCS and OES, for which *C. hilariana* and *H. balsamifera* dominated tickets were selected, respectively.



**Figure 1.** Representation of (a) Restinga de Jurubatiba National Park, situated at the northeastern region of Rio de Janeiro state, Brazil; and (b) study sites (red circles) on the three *restinga* vegetation types evaluated: Open *Clusia* scrub (OCS; small dots, white matrix), Open *Ericaceae* scrub (OES; yellow), and Seasonal dry forest (SDF, dark green).

Spodosols and Quartzarenic Neossols are the main soil classes underlying *restinga* vegetation, and the latter are often in an initial process of podzolization (Bonilha et al., 2012; Gomes et al., 2007). Organic matter and nutrient content are higher in *restinga* soil surface layers (0–20 cm), where root systems are concentrated and litter decomposition are more pronounced (Bonilha et al., 2012; Brito et al., 2018). The mean annual rainfall in the region varies between 1,100 and 1,250 mm (Alvares et al., 2013), concentrated between November and January. The mean annual air temperature varies between 21.3°C and 22.4°C, with small oscillations between minimum and maximum temperatures, but January to March tends to be slightly hotter. It is characterized as an Aw climate (Tropical with dry winters) according to Köppen classification (Alvares et al., 2013).

### Data sampling

Soil conditions were monitored by volumetric soil moisture sensors S-SMC-M005 and temperature sensors S-TMB-M002, Onset®. A kit containing one soil moisture sensor and one temperature sensor were implemented on each of our three sampling sites (Figure 1), totalizing three kits and six sensors considered on our study. Data were stored on HOBO Micro Station dataloggers (H21-002). On each sampling site (Figure 1), sensors were deployed at about 5 cm depth on the horizon A of the soil, below litter layer, to better capture climatic effects on soil surface layers, where soil biota abundance and activity are concentrated. Specifically for OCS and OES sites, sensors were deployed on the middle of the tickets, considered as the most representative place to evaluate climatic effects on soil microclimatic conditions on open vegetated areas. We monitored soil conditions for 84 days (from December 17, 2019 to March 09, 2020), at 1-hr intervals during the summer, when variations in soil microclimate are expected to be sharper due to increases in precipitation and temperature variations. The field capacity of soil was approximately  $0.6\text{ m}^3\text{ m}^{-3}$  and was

nearly uniform between vegetation types. Soil moisture values, measured as water content in  $\text{m}^3\text{ m}^{-3}$  were converted to percentage (%) of soil moisture.

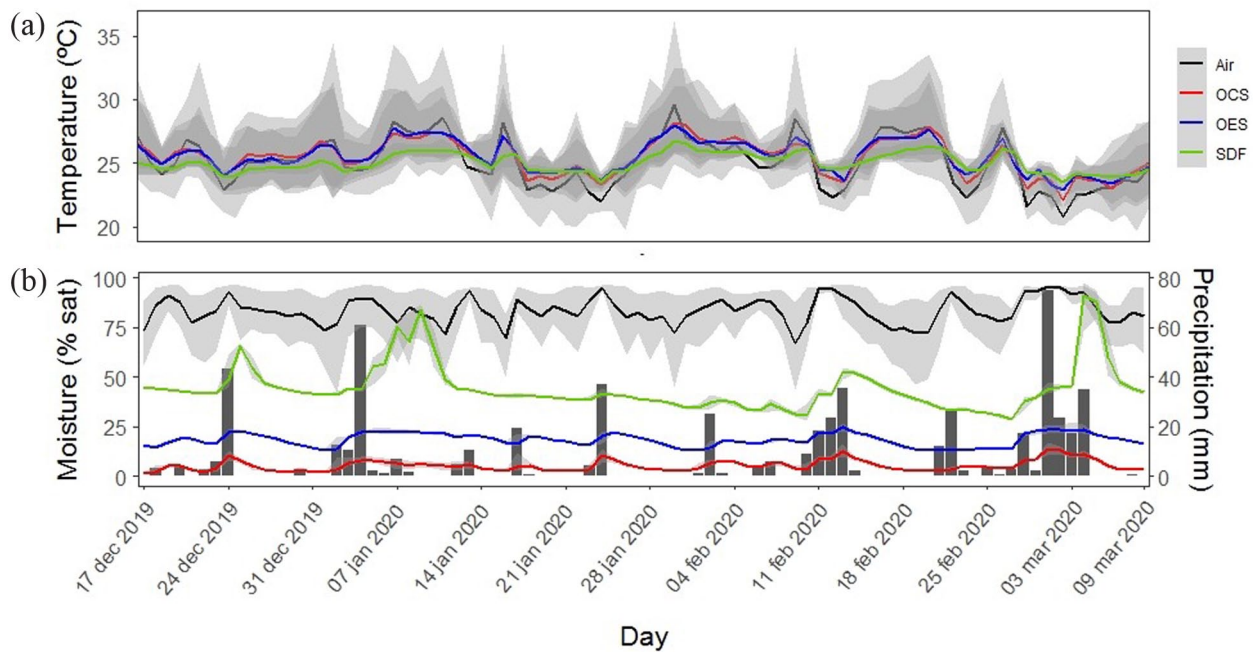
Small gaps in data were fulfilled using linear interpolation techniques (Baltazar & Claridge, 2006). They accounted for about 6% of the data (155 out of 2,016 records), and only occurred in SDF. We obtained climatic data—precipitation, air temperature, and humidity—for the same sampling period from Brazilian National Institute of Meteorology (INMET), station 86891—Macaé, situated about 20 km far from our sampling sites.

### Data analysis

To test the hypothesis that daily soil moisture is higher on *restinga* forest, we estimated 95% confidence intervals (95% CI) based on daily soil moisture (24 registers) for all vegetation types and compared the superposition on 95% CI along time between them. We also estimated 95% CI for daily air humidity data and plotted it in order to visualize the dynamic of daily soil moisture compared to atmospheric conditions. We also used this approach to explore general trends on daily soil temperature data.

To address the second hypothesis that soil moisture and temperature variations are lower on *restinga* forest, we first estimated the daily coefficient of variation (CV) of soil moisture and temperature, and considered it as a proxy for daily variation. Then, we evaluated differences in CV using a mixed-effect model. We used daily CV of soil moisture and temperature as response variables. Values of CV were *logit* transformed previous to analysis (Warton & Hui, 2011). Plant formation was considered a fixed factor and the sampling day a random intercept.

To evaluate how climate (precipitation and air temperature) drive the dynamics of soil conditions in OCS, OES, and SDF, we used multiple linear regressions. They were carried out to investigate the relationship between values of daily soil



**Figure 2.** Time series of daily (a) temperature and (b) moisture on the atmosphere and soil from three *restinga* vegetation types: Open *Clusia* scrub (OCS), Open *Ericaceae* scrub (OES), and Seasonal dry forest (SDF), along 84 days (from 17-December-2019 to 10-March-2020). Lines indicate mean daily values and gray hatch indicate daily 95% confidence intervals (CI). The grayer the hatches, the greater the overlap of 95% CI values. Precipitation is also represented, as dark bars on (b).

temperature and soil moisture on each plant formation based on air temperature, precipitation, and daily differences in air temperature and precipitation ( $\Delta$ Temperature and  $\Delta$ Precipitation, respectively).  $\Delta$ Precipitation and  $\Delta$ Temperature were estimated based on the difference between, respectively, precipitation or temperature of a specific day and that from the day before, and were considered in the analyses as a proxy for delayed responses of soil conditions to climatic variations.

Model selection were done using AIC values. For each selected model, the variance inflation factor (VIF) was used to investigate collinearity between explanatory predictors. Variables with VIF values  $>2$  were excluded. All models' predictors attended this requisite, except for precipitation and  $\Delta$ Precipitation on OCS and OES on soil moisture models. So, we re-analyzed these data sets, keeping only precipitation (besides temperature and  $\Delta$ Temperature) in the models. For all data sets, outliers were identified using R's *mahalanobis* function and excluded from the models. All analyses were done using R Program v. 4.0.2 (R Core Team, 2020) with support of the packages nlme (Pinheiro & Bates, 2022), MASS (Venables & Ripley, 2002), and car (Fox & Weisberg, 2019).

## Results

The time series of temperature data indicate that daily soil temperature are cyclical, increasing during the day and reducing at night, following daily trends on air temperature (Figure 2a). Daily average soil temperature tended to be slightly higher at OCS ( $25.5^{\circ}\text{C} \pm 2.21^{\circ}\text{C}$ ) and OES ( $25.1^{\circ}\text{C} \pm 1.91^{\circ}\text{C}$ ) and lower at SDF ( $25.1^{\circ}\text{C} \pm 0.87^{\circ}\text{C}$ ) along time, with some minor

periods during rainy days, where the opposite trend was registered (Figure 2a). We found that relative increases in mean soil temperature on SDF than on open vegetated areas were positively associated to precipitation ( $R^2 = .133$ ,  $F = 12.6$ ,  $p = .0007$  and  $R^2 = .162$ ,  $F = 15.9$ ,  $p = .0001$  for OCS and OES, respectively; Supplemental Figure S1). However, soil temperature is considerably similar among vegetation types as can be noticed by comparing superposition on 95% CIs (Figure 2a).

Soil moisture is completely distinct between *restinga* plant formations; it is always higher at SDF ( $44.2\% \pm 12.1\%$ ) than OCS ( $5.3\% \pm 3.0\%$ ) and moderate at OES ( $18.4\% \pm 3.4\%$ ; Figure 2b). Daily soil moisture is on average 9.2 and 1.4 times larger on SDF than OCS (varying from 1.6 to 28.3 times) and OES (till 3.4 times). Air humidity presents a daily cycle, increasing at night and reducing during the day (Figure 2b). It is always higher than OCS and OES soil moisture, but not than on SDF. During a few days after intense precipitation events (more than 60-mm along a few day intervals), SDF soil moisture is almost saturated, and is comparable to air humidity (Figure 2b).

Daily variability in temperature and moisture are also considerably different between *restinga* plant formations and atmosphere, being always larger on this last compartment ( $F_{3, 249} = 415.3$ ;  $p < .0001$  and  $F_{3, 235} = 101.6$ ;  $p < .0001$ , respectively; Table 1; Figure 3). An exception was daily CV of OCS soil moisture, which was similar to daily variations on air humidity (Figure 3c and d). Daily variations in soil temperature and moisture are larger on OCS than OES, and on both of them are larger than on SDF (Figure 3a–d).

There was a considerable daily variability in soil temperature for all plant formations, mainly driven by air temperature and, to a lesser extent, to daily differences on air temperature (Table 2). These variables accounted for about 90% of daily variability for OCS and OES on soil temperature and 80% on SDF (Table 2). On all plant formations, soil temperature is positively correlated with air temperature and negatively to  $\Delta$ temperature, but is not related to precipitation nor  $\Delta$ precipitation (Table 2).

Daily soil moisture variability resulted from significant correlations with most of the meteorological drivers evaluated, but the contribution of the climatic predictors were much lower than for daily soil temperature (Table 3). Daily precipitation, air temperature, and  $\Delta$ temperature were the best predictors of soil moisture on OCS and OES, with an adjusted  $R^2$  value equal to .42 and .18, respectively (Table 3). Precipitation was the most important predictor of OCS soil moisture variability, explaining 30.6%, whereas air temperature and  $\Delta$ temperature

together explained 14%. But for OES soil moisture, all the predictors had a similar contribution (~7%). For SDF soil moisture, daily precipitation,  $\Delta$ precipitation, and  $\Delta$ temperature were the best predictors, but accounted for only 3.3%, 8.7%, and 1.7% explained variation, respectively (Adjusted  $R^2$  = .104; Table 3). Along the 84 days studied, accumulated rainfall accounted for 574.8 mm, averaging 6.8 mm per day, and the maximum value (74.8 mm) were registered on March, 1st 2020.

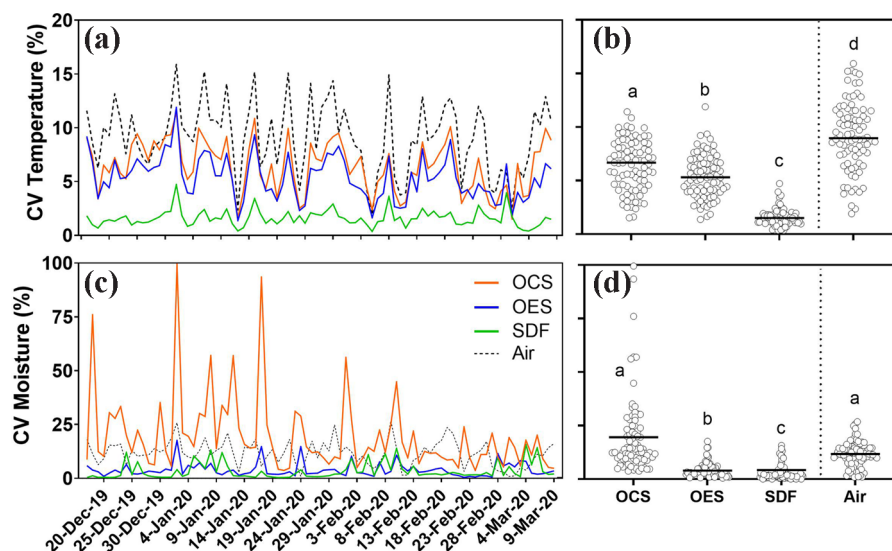
## Discussion

The exposure to different edaphic and microclimatic conditions and biological community structures, even at very short spatial scales, makes the *restinga* a natural laboratory for the study of biodiversity and functioning of tropical ecosystems. The local variation on edaphic conditions and vegetation communities between *restinga* plant formations has been one of the main research topics in Brazilian sandy coastal environmental studies (Assis et al., 2011; Magnago et al., 2010; Santos-Filho et al., 2013; Scarano, 2002), specially in Restinga de Jurubatiba National Park (Brito et al., 2018; Henriques et al., 1986; Kurtz et al., 2013; Montezuma & Araujo, 2007; Pimentel et al., 2007; Scarano, 2002). However, previous studies neglected microclimatic soil conditions. Studying microclimatic variations across *restinga* plant formations is fundamental to understand the differences in their ecological processes rates, such as primary production, seedling germination, decomposition, nutrient cycling, and carbon sequestration.

By recording hourly soil moisture and temperature during the rainy and hotter season, we could detect clear trends on daily magnitude and variation on these parameters for the three most common plant formations at Restinga de Jurubatiba National Park, and identify some of their climatic drivers. Assuming that climatic conditions are equal along the study site,

**Table 1.** Summary of the Mixed-Effects Models Testing the Effects of Plant Formations on Daily Coefficient of Variation (CV) of Temperature and Moisture. Significant Statistical Effects ( $p < .05$ ) Are in Bold.

SOURCE OF VARIATION	DF	F	P
<i>CV temperature</i>			
Plant formation	3	415.28	<b>&lt;.001</b>
Error	249		
<i>CV moisture</i>			
Plant formation	3	101.6	<b>&lt;.001</b>
Error	235		



**Figure 3.** Daily variation on temperature (a and b) and moisture (c and d), on the atmosphere and soil from three *restinga* vegetation types: Open *Clusia* scrub (OCS), Open Ericaceae scrub (OES), and Seasonal dry forest (SDF). On (b and d), the bars indicate mean coefficient of variation (CV) values and distinct letters indicate significant differences at  $p < .05$ .

**Table 2.** Results of Multiple Regression Analysis for Predicting Daily Soil Temperature on OCS, OES, and SDF From Climatic Variables. Only Selected Variables Are Depicted in the Table.  $R^2$  (%) Indicates the Contribution (and Percent Contribution) of Each Selected Variable to Model  $R^2$ . AIC Indicates the Akaike's Information Criterion Value for the Selected Model, While  $\Delta$ AIC Indicates the Difference Between the Selected Model From the Model Containing All Climatic Variables.

VARIABLE	COEFFICIENT	STD ERROR	T VALUE	P VALUE	$R^2$ (%)	AIC	$\Delta$ AIC
<i>Model—OCS</i>							
$(R^2 = .904; \text{Adj } R^2 = .902; F(2, 78) = 368.8; p < .001)$						-136.42	3.27
Temperature	0.6995	0.0265	26.36	<.001	88.9 (98.3)		
$\Delta$ Temperature	-0.1174	0.0329	-3.57	<.001	1.56 (1.73)		
Intercept	7.9136	0.6708	11.8	<.001			
<i>Model—OES</i>							
$(R^2 = .911; \text{Adj } R^2 = .909; F(2, 78) = 400; p < .001)$						-159.06	2.14
Temperature	0.6336	0.0232	27.264	<.001	90.1 (98.9)		
$\Delta$ Temperature	-0.0859	0.0288	-2.985	.0038	1.01 (1.11)		
Intercept	9.6249	0.5874	16.387	<.001			
<i>Model—SDF</i>							
$(R^2 = .797; \text{Adj } R^2 = .792; F(2, 78) = 153.4; p < .001)$						-167.92	2.47
Temperature	0.3841	0.022	17.49	<.001	71.7 (89.9)		
$\Delta$ Temperature	-0.1513	0.0272	-5.56	<.001	8.03 (10.1)		
Intercept	15.3944	0.555	27.74	<.001			

we hypothesized that *restinga* soil moisture would respond to topographic, hydrological, and biological conditions, thus would be higher on densely covered areas where groundwater level are closer to the soil surface—such as forests—than on open vegetated areas. In fact, we observed that soil moisture conditions are permanently higher on SDF than on open scrubby areas, and also higher on dense (OES) than sparse (OCS) open plant formations. *Restinga* forests are typically associated with saturated or inundated soils, due to high water table conditions (Kurtz et al., 2013; Magnago et al., 2010). It also presents taller trees, higher litter bed, and litter input rates to the soil along the year (Brito et al., 2018; Kurtz et al., 2013), what may restrict solar incidence, water evaporation, and favor the conservation of soil moisture conditions, even compensating for high plant root absorption and forest evapotranspiration rates (Scheffer et al., 2005). On the other hand, OCS are typically situated on the top of the sandy strips, distant more than 1-m from the water table, with sparse tickets, specially on our study site (Pimentel et al., 2007) and present lower litter input rates to the soil and litter layer thickness (Brito et al., 2018). OES are situated on topographically lower strips over a deep soil layer resistant to water infiltration, consequently flooding in the periods of increased rainfall (Caris et al., 2013; Montezuma & Araujo, 2007).

These distinct topographic, hydrological, and biological conditions may also influence daily soil moisture and temperature

variability. Both were significantly lower in SDF than in open vegetation, and also lower in OES than OCS, corroborating our expectations. It suggests that these plant formations have distinct capacities to buffer the effects of abiotic external factors on soil conditions. In forests, the dense canopy and stratification of plant cover may act in thermal damping and solar radiation interception, delaying the heating of the soil in the early morning and cooling it in the early evening, in contrast to open scrubbies, that are composed of lower and less stratified vegetation (Antonić et al., 1997; Devkota et al., 2009; Song et al., 2013; Zhao et al., 2011). Even though greater canopy cover and darker canopies in SDF may have lower albedo, and therefore absorb much solar radiation, this energy is largely used for water evaporation (Scheffer et al., 2005), restricting soil heating. A greater canopy cover in forests may also provide a greater canopy storage capacity and precipitation interception (Baiaomonte, 2021), reducing the amount of water reaching the soil. As a result, improved thermal damping in SDF is particularly clear as daily rainfall increases; in such days, soil takes longer to cool down on SDF if compared to open vegetated areas (Supplemental Figure S1). Other forest features, such as a greater litter bed cover, also may be more efficient on mitigating the effects of air temperature on soil (Ogée & Brunet, 2002). In addition, the intrinsic high soil moisture of the *restinga* forests can act as a strong buffer for the daily soil temperature variation due to high

**Table 3.** Results of Multiple Regression Analysis for Predicting Daily Soil Moisture on OCS, OES, and SDF From Climatic Variables. Only Selected Variables Are Depicted in the Table.  $R^2$  (%) Indicates the Contribution (and Percent Contribution) of Each Selected Variable to Model  $R^2$ . AIC Indicates the Akaike's Information Criterion Value for the Selected Model, While  $\Delta$ AIC Indicates the Difference Between the Selected Model From the Model Containing All Climatic Variables.

VARIABLE	COEFFICIENT	STD ERROR	T VALUE	P VALUE	$R^2$ (%)	AIC	$\Delta$ AIC
<i>Model—OCS</i>							
$(R^2 = .4446; \text{Adj } R^2 = .423; F(3, 77) = 20.55; p < .001)$						106.18	0
Precipitation	0.1033	0.0188	5.501	<.001	30.6 (68.8)		
Temperature	-0.4942	0.1247	-3.963	<.001	7.6 (17.1)		
$\Delta$ Temperature	0.4507	0.1525	2.955	.0041	6.3 (14.2)		
Intercept	16.99	3.18164	5.34	<.001			
<i>Model—OES</i>							
$(R^2 = .211; \text{Adj } R^2 = .180; F(3, 77) = 6.85; p < .001)$						176.04	0
Precipitation	0.0593	0.0289	2.051	.044	6.85 (32.5)		
Temperature	-0.6266	0.1919	-3.265	.0016	6.94 (33.0)		
$\Delta$ Temperature	0.6251	0.2347	2.663	.0094	7.27 (34.5)		
Intercept	33.72	4.897	6.886	<.001			
<i>Model—SDF</i>							
$(R^2 = .137; \text{Adj } R^2 = .104; F(3, 77) = 4.085; p = .0095)$						400.22	1.67
Precipitation	0.463	0.1474	3.14	.0024	3.33 (24.3)		
$\Delta$ Precipitation	-0.289	0.1038	-2.786	.0067	8.70 (63.4)		
$\Delta$ Temperature	1.393	0.888	1.568	0.1209	1.70 (12.4)		
Intercept	41.3624	1.5471	26.736	<.001			

water specific heat (Abu-Hamdeh, 2003). These buffering properties of vegetation cover, stratification, litter layer, soil moisture, and water table distance may be determinant for distinctions in soil moisture variability between *restinga* plant formations (Antonić et al., 1997; Ogée & Brunet, 2002; Zhao et al., 2011), reducing losses by evaporation and drastic increases by rainfall infiltration on the forests, but not on open sparsely covered areas. Although OCS and OES share several characteristics related to their vegetation type and edaphic conditions, a considerable variation on their soil moisture may be explained by topography, vegetation cover, and litter bed properties (Caris et al., 2013; Montezuma & Araujo, 2007), what explain the differences in thermal variability between these open plant formations.

Even though the soil itself is a source of heat and moisture (as water vapor) to the atmosphere (Ogée & Brunet, 2002), soil temperature is primarily driven by patterns of solar radiation incidence (Gray et al., 2002). That is why we found a consistent daily variation in soil temperature for both OCS, OES, and SDF, following daily air temperature trends. As a result, soil temperature is quite well predictable (80%–90% of the

variation in daily soil temperature explained by the models) on a daily basis by climatic factors (mainly temperature and daily differences in temperature— $\Delta$ temperature), indicating a high temporal coherence in the soil temperature dynamics on all plant formations. On the other hand, soil moisture did not present a daily cyclic pattern as found for temperature and air humidity. It may result from the interplay between climate and plant communities, edaphic, and hydrological soil properties on each vegetation type, some of which are considerably variable along time. Assuming that climatic conditions are homogeneous along the study site, we found they explain from 15% (on SDF) to 42% (on OCS) of soil moisture variability. Precipitation is the main climatic driver of soil moisture variability, but for OES and mainly SDF, its effects take some time to appear. Variations in vegetation structure such as cover, stratification, and litter layer properties and its effects on throughfall interception and energy and heat exchanges with the atmosphere seems to play an important role on these patterns also. While the sparse vegetation cover and low litter layer on OCS may have limited capacity to intercept throughfall, dense vegetated areas may restrict rainfall infiltration. So, lagged responses on



SDF soil moisture to precipitation may reflect the late response on water table fulfilling and rain drops, dew drips, and stem flow to cross the vegetation stems, leaves, and the litter layer (Gray et al., 2002; Van Dijk & Bruijnzeel, 2001; Z. Wang et al., 2018). We also do not ignore that the exclusion of some outliers may have even improved our capacity to predict climatic effects on OES and SDF soil moisture. Thus, the temporal soil moisture dynamic is quiet hard to predict due to the distinct importance of plant communities, edaphic, and hydrological soil properties in these plant formations.

Our findings may help to elucidate some previous reported patterns for *restinga* plant communities and ecosystem functioning. For example, low soil moisture concentrations and high temperature variability on OCS may favor the dominance of *Clusia hilariana* in most vegetation patches, since it is a CAM photosynthesis species (Scarano et al., 2005), a characteristic commonly associated with the avoidance of water stress by plants; while in OES and SDF, C3 species dominate (Dias et al., 2005). Also, a slow development of C3 woody species seedlings in *C. hilariana* understory was previously reported (Dias & Scarano, 2007; Dias et al., 2005). Besides competitive interactions with *C. hilariana*, a lower and intermittent water availability at the soil surface to shallow root seedlings may restrict their growth on OCS. It has been previously demonstrated that litterfall rates are correlated to air temperature and precipitation in OCS and, to a lesser extent, in SDF (Brito et al., 2018; Gripp et al., 2020). When temperature increases and rainfall becomes lower than evapotranspiration, soil moisture is depleted, increasing tensions in the xylem sap that can trigger stomatal closure and other physiological responses (Nepstad et al., 2002), limiting tree growth and promoting litterfall peaks (Lawrence, 2005). Litter decomposition is also limited by water availability (Petraglia et al., 2019; X. Wang et al., 2017; G. Wang et al., 2019; Zhang et al., 2016), what may explain the differences in decomposition rates between these plant formations (Brito et al., 2018; Djukic et al., 2018). Finally, soil conditions may contribute to explain the distinctions in woody vegetation structure and diversity (composition and species richness) between plant formations (Kurtz et al., 2013; Montezuma & Araujo, 2007; Pimentel et al., 2007).

## Conclusions

Our study provides more information about the strong role of vegetation types on the dynamics of soil moisture and temperature in distinct *restinga* plant formations, and reinforces that these vegetation are good predictors of water table (Henriques et al., 1986), soil moisture conditions and moisture and temperature variations. It also provides clear evidences about how climate affect microclimatic conditions on *restinga* forests and open formations, even though it is restricted to a single rainy and hot season. In addition, our study calls attention to the necessity to consider vegetation structure and litter properties to understand temporal and spatial variations in soil microclimatic conditions.

Future studies should concentrate on evaluating how hydrological (water table variation), edaphic (soil structure, chemical and physical composition, etc), vegetation structure (cover, stratification, etc), and litter (shape, amount, etc) properties interact with each other and with climate to regulate throughfall, radiation interception, evaporation, and soil microclimatic conditions, and affect water and energy exchange between the soil and the air, within and between vegetation types in *restinga*.

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## Author Contributions

All authors contributed to the study conception. A.R.G., Q.S.S. and R.L.M. outlined the study design. Material preparation and data collection were done by A.R.G., J.G.F.G. and Q.S.S. Data analysis were performed by A.R.G. and J.G.F.G. The first draft of the manuscript was written by A.R.G., J.G.F.G. and C.A.M.B, and all authors revised previous versions of the manuscript. All authors approved the final manuscript.

## Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

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## Supplemental Material

Supplemental material for this article is available online.

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