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Woody Species Richness and Precipitation as drivers of PrimaryProductivity in Dry Forests of Northeastern Brazil

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ABSTRACT

Although it is common sense in the scientific community that there is a correlation between species richness and primary productivity, empirically this is poorly addressed for semiarid ecosystems. In the present study (1) we correlate woody species richness with ~~a~~ vegetation index from satellite data (as a proxy for primary productivity); we also determined (2) the effect of rainfall on productivity, and (3) rainfall and productivity anomaly indices for 49 sites in Dry Forests of Northeastern semiarid region of Brazil. We show that both species richness and rainfall are positively correlated with productivity ($r^2 = 0,33$ and $p < 0,05$; $r^2 = 0,11$, $n = 49$ and $p < 0,05$, $n = 49$; respectively). Productivity has a significant one month lag in response to rainfall ($r^2 = 0.39 \pm 0.16$; $p < 0.001$; $n = 49$). We also found that rainfall shows an anomaly 3 times more intense thanthe productivity anomaly ($p < 0.001$, $r^2 = 0.5$). We conclude that at the regional level, woody species richnesshas a stronger effect than rainfall on productivity of Dry Forests of semiarid Brazil. In addition, the anomaly results showed the vegetation´s resistance to the semiarid harsh climate, an important result for conservation and policy under a climate change scenario.
Keywords: Caatinga, ecosystem productivity, remote sensing, enhanced vegetation index, climate change.

Riqueza de espécies lenhosas e precipitação como fatores de produtividade primária em florestas secas do Nordeste do Brasil

R E S U M O

Embora seja senso comum que riqueza e produtividade primária estejam correlacionadas, esta relação é pouco abordada empiricamente em regiões semiáridas. Neste presente estudo (1) relacionamos a riqueza de espécies lenhosas (utilizando dados secundários) com um índice de vegetação gerados por sensores satelitais (como um proxy para produtividade) para o semiárido brasileiro; determinamos também (2) o efeito da precipitação na produtividade para as mesmas localidades, e (3) os índices de anomalia tanto da precipitação quanto da produtividade para os 49 locais de Florestas Secas da região semiárida do Nordeste do Brasil. Os resultados mostraram que tanto a riqueza de espécies quanto a precipitação se correlacionaram positivamentecom a produtividade ($r^2 = 0,33$ e $p < 0,05$, $n = 49$; $r^2 = 0,11$ e $p < 0,05$, $n = 49$; respectivamente). A produtividade tem um atraso significativo de um mês em relação à precipitação ($r^2 = 0.39 \pm 0.16$; $p < 0.001$; $n = 49$). Quanto às anomalias, observamos que a precipitação apresentou extremos cerca de 3 vezes mais intensos do que a produtividade ($p < 0.001$, $r^2 = 0.5$), Concluímos que na escala da paisagem, a riqueza de espécies tem um efeito maior que a precipitação na produtividade em Florestas Secas da Caatinga. Além disto, através dos resultados dos índices de anomalia, determinamos a resistência da vegetação local perante o clima semiárido, resultado importante em um cenário de mudanças climáticas.
Palavras-chave: Caatinga, produtividade ecossistêmica, sensoriamento remoto, índice de vegetação, mudanças climáticas.

Introduction

It is highly plausible and projected by different climate models that until the end of the 21st century, terrestrial ecosystems will face higher temperature and more severe droughts (IPCC, 2021). Likewise, a decrease in rainfall is expected in semiarid, hot regions of Brazil. It is also expected, due to deforestation and degradation of native vegetation, a decline in species richness in the same region. In this study, we will show how species richness and rainfall control primary productivity in dry forests (regionally known as Caatinga) of Northeastern Brazil.

Caatinga ecosystems occur in very heterogeneous environments, with great biodiversity and high endemism (Da Silva *et al.,* 2018; Da Silva e Cruz, 2018; Leal *et al.,* 2003; Leal *et al.,* 2005; Moro *et al.,* 2014; Moro *et al.,* 2016; Sobrinho *et al.,* 2016).

Although with a considerably smaller productivity than other tropical forests, it is essential for the maintenance of its ecosystems and also for the livelihood of extensive human populations in semiarid Brazil (Erasmi *et al*., 2014).

As for the climate in this semiarid region, climate models projections indicate an intense rainfall reduction, as well as an increase in aridity and surface temperatures by the end of this century (IPCC, 2021). Even at present, Northeastern Brazil has faced from 2012 to 2017, two of the most intense and severe droughts, with impacts on the regional economy and lives (Marengo *et al.,* 2017, 2019).

As a result, Caatinga ecosystems, which are already greatly impacted by anthropogenic activities (Antongiovanni *et al.,* 2020), will alsobe affected by the intensification of climatic extremes, which will ultimately lead to a decrease in its primary productivity, resistance and resilience (Alvalá *et al.,* 2017) - and as a consequence will also have an effect on the 27 million people who live in the semiarid region of Brazil (SUDENE, 2017) and benefit from these ecosystems for economic and subsistence purposes.

Although it is common sense that species richness and productivity are correlated (Tilman *et al.,* 2001; Whittaker, 2010), few studies show empirically such relation at the ecosystem level.

Isbell *et al.* (2015, 2018) argue that a greater biodiversity stabilizes ecosystem productivity during moderate to extreme climatic events and point out that species loss could lead to a decrease in ecosystem functioning. Ecosystems with greater plant diversity exhibit lower sensitivity to climate variability (Oliveira *et al.,* 2022), providing stability and improved functioning. Therefore, species richness has a fundamental and positive role in ecosystem productivity over time (Wagg *et al.,* 2022).

Specifically for the semiarid region of Brazil, this analysis is very little addressed or observed (*e.g.*: Araújo *et al.,* 2022; Mazzochini *et al.,* 2019; Medeiros *et al.,* 2019). It is important to emphasize that the semiarid region is highly vulnerable to current and projected climate changes. Therefore, determining the extent to which the species richness of the predominant ecosystem in this region is associated with its productivity can provide information related to its resistance and resilience, during and after periods of extreme climate events, especially considering that future projections indicate an intensification of these climate events.

The direct estimate or measurement of an ecosystem's productivity demands high cost equipment, complex operational skills and expensive temporal and spatial repetitions (Ran *et al*., 2016). In contrast, the use of remote sensing techniques allows the acquisition and quantification of reliable data on land cover over large areas, for a significant long period of time, in a relatively short period of data sampling (Salimon & Anderson, 2018). There are different methods of estimating ecosystem productivity through remote sensing, with different vegetation indices, which are considered very good indicators of leaf area, aboveground biomass and in extension, primary productivity of an ecosystem (Ma *et al.*, 2013; Wagle *et al.,* 2014).

While Medeiros *et al*. (2019) analyzed if spectral bands could be used to estimate species richness at the stand level, in the present study we focus on the use of satellite data as a proxy for productivity, similar to other studies (*e.g.:* Araújo *et al.,* 2022; Mazzochini *et al.,* 2019; Salimon & Anderson, 2017).

Due to constant anthropogenic pressures and to global climate change, considering that the Caatinga ecoregion is vulnerable to these factors, and little is known about the mechanisms that control its productivity, our goal was to determine how strongly woody species richness and rainfall drive primary productivity (using EVI2 as a proxy) in dry forests of the Northeastern Semiarid Brazil. Our hypothesis is that species richness and precipitation are positively correlated with the primary productivity of the Caatinga, with varying degrees of strength.

Material and methods

Our study area is the Brazilian semiarid, which covers 65% of northeastern Brazil (Figure 1). Due to its diverse geological settings, different soil types and rainfall regimes, the region presentsa variety of plant communities and vegetation types, from savannahs to forests (Moro *et al.,* 2016). This wide variety of vegetation types are regionally called "Caatinga" and it is the largest tropical seasonally dry formation in the Americas (De Queiroga Miranda *et al.*, 2020; Moro *et al.,* 2016), divided into nine ecologically distinct phyto physiognomic formations (Da Silva *et al.,* 2018).

Its climate is characterized by high average temperatures, from 26 to 28 ◦C (Zanella, 2014) and also by its low and irregular rainfall patterns (Nimer, 1972). Such rainfall patterns are spread throughout northeastern Brazil, posing a significant social and economic pressure on its States (Tinôco *et al.*, 2018). Such irregularity is due to the different atmospheric systems present over this region, mainly the Intertropical Convergence Zone ITCZ and the South Atlantic Convergence Zone SACZ (Zanella, 2014) and the El Niño Southern Oscillation ENSO (Marengo *et al.,* 2017). Such low and irregular rainfall, in addition to high temperatures leads consequently to high evapotranspiration, reducing soil humidity in short periods of time, causing a high water deficit at stand and regional level, posing a severe stress and limitation to vegetation structure.

Woody Species Richness

All data on woody species richness were obtained in secondary data through bibliography search of published indexed scientific papers on Scielo and ISI Web Of Knowledge, using as search criteria the terms: "caatinga", "plant community", "community structure", "woody species richness", "phytosociology", "Brazilian semiarid". All of these terms were searched in both Brazilian portuguese and english. The bibliographic search was carried out in 2017.

From a total of 1107 papers (618 in SCIELO and 489 in ISI Web Of Knowledge), only49 papers met the following inclusion criteria (1) valid geographical coordinates, explicitly corresponding to sampling site, (2) explicit inclusion criteria for woody species individuals in each sampling unit, such as DBH or other, (3) total sampling area and (4) results of species richness per area. These 49 papers (published between 1997 and 2015) were then the only selected and used in this present study (list of articles and location in Table 1 and all references included in the Reference Session).

EVI2 and rainfall

Although there are many vegetation indices and even though all seem to respond clearly to severe droughts (Wagle *et al.*, 2014), in this paper we used the Enhanced Vegetation Index EVI2 (Huete *et al.*, 1997; Freitas *et al.*, 2011) due to its greater where NIR corresponds to the near infrared reflectance and RED the red reflectance (Jiang *et al.*, 2008).

The EVI2 is functionally equivalent to EVI, although it can be estimated by sensors lacking the blue band as for MODIS sensors and can be calculated by the following formula (eq.1):

$$EVI2 = 2.5 \star \left(\frac{NIR-RED}{NIR+2.4\star RED+1}\right) \qquad (1)$$

where NIR corresponds to the near infrared reflectance and RED the red reflectance (Jiang *et al.*, 2008).

With the sampling lat/long coordinates of each of the selected 49 papers, we retrieved monthly EVI2 (Freitas *et al.*, 2011) and rainfall data, freely obtained from the MODIS/Terra Temporal Series Viewer from the National Institute for Space Research (INPE), available at: (http://www.dsr.inpe.br/laf/series/). The time window available for these two variables was from 2000 to 2017. Since the first and last years for the period did not have complete data, we used for all analyses the period of 2001 to 2016.

All data was processed in spreadsheets by sampling site (each sampling site was assigned from each of the 49 papers), containing a total of 192 paired data for rainfall and EVI2 (16 years x 12 months). Therefore for each site n = 192.

On the other hand, in order to include the species richness in the analyses, we had to use an average value of EVI2 and average annual rainfall, since there is only one value of species richness for each site, therefore for this analysis, our n = 49.

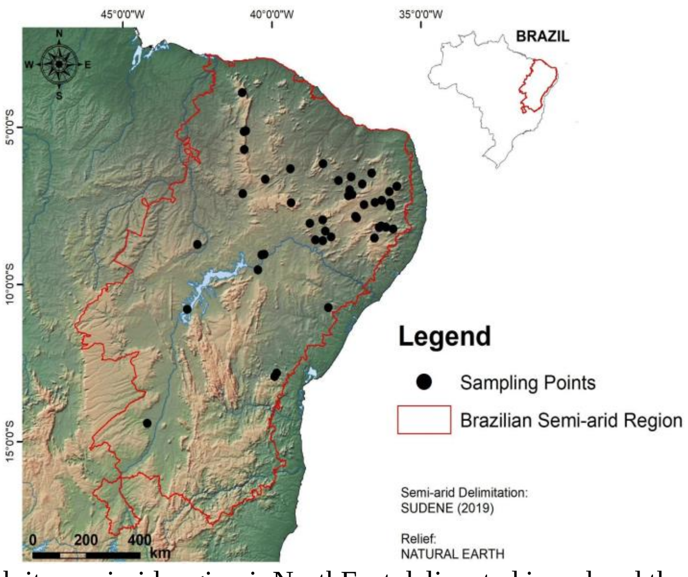


Figure 1 - Brazil's map, with its semiarid region inNorthEast delineated in red and the 49 sampling sites of the present study.

We estimated rainfall and EVI2 interannual variability for each site, using a Anomaly Index (z-score) which is a measure of how much each year differs from the average of the period studied (in our study, from 2001 to 2016), using the formula (eq.2):

$$A_I = \frac{V_i - \bar{X}_i}{\bar{X}_i} \quad (2)$$

where: A_i (I anomaly); V_i (ith value); $\bar{X}$ i (i average).

Since this is a normalized index (eq.2), we can compare different attributes and variables, independent of the different units of measure for each variable. Therefore, this index was calculated for both rainfall and EVI2 to estimate the amplitude of interannual variation and also to compare and correlate both variable's anomalies. Note that for this analysis $n = 784$ (16 years x 49 sites).

Data Analysis

With all data sampled for woody species richness, average EVI2 and average annual rainfall, we ran correlation and regression analyses in the statistical software environment *R* (*R* Development Core Team 2011). A synchronic and lag-type analyses were performed with 1, 2 and 3 months lag between precipitation and EVI2 for each site.

We also tested if there was a temporaltrend for both rainfall and EVI2, using time as the independent variable. This was needed in order to detect if there was land cover change during the 16 years studied independently at each site. If that was the case, such sites should be eliminated from our analyses. Nevertheless, no such trend was observed in any of the 49 sites.

We used Levene Test for variance homogeneity between EVI2 residuals and woody species richness (p = 0,01615) and EVI2 residuals with average annual rainfall (p = 0,01595). Since there was no homogeneity of variance, we used a non-parametric approach, a rank-based estimation regression (Kloke *&* McKean, 2012).

Results

Species Richness, Precipitation and EVI2

Among the 49 papers analyzed, we found an average woody species richness of 35±16 species per hectare. The greatest richness was 74 and the lowest was 11 species per hectare (Table 1). The site with lowest species richness also shows productivity (EVI2) and rainfall below the average (0,17 e 537 mm, respectively) while the site with the highest woody species richness showed values for both productivity and rainfall above average (0,38 e 972 mm, respectively).

The monthly average EVI2 for the whole time series and 49 sampling sites was 0,31 ± 0,11 (Table 1, Graph 1A), with average maximum value of 0,58 and average minimum value of 0,12. From 2001 to 2016, the year 2009 showed the highest average EVI2 (0.36), in contrast to the year 2012, which showed the lowest average value (0.25) - an average difference of 31% between average minimum and maximum.

Average annual precipitation (from 2001 to 2016 and all 49 sites included) was 758 ± 209mm (Table 1, Graph 1B). Average maximum and minimum values were 1075 mm e 329 mm, respectively, observed in years 2009 and 2012 (a 70% difference between average maximum and minimum).

We tested if there was a significant interannual trend in precipitation and EVI2. Nevertheless, the slope for neither variable was statistically different from zero. Therefore, we consider that between 2001 and 2016 there was neither an increase or decrease in precipitation and productivity, although there was interannual variability.

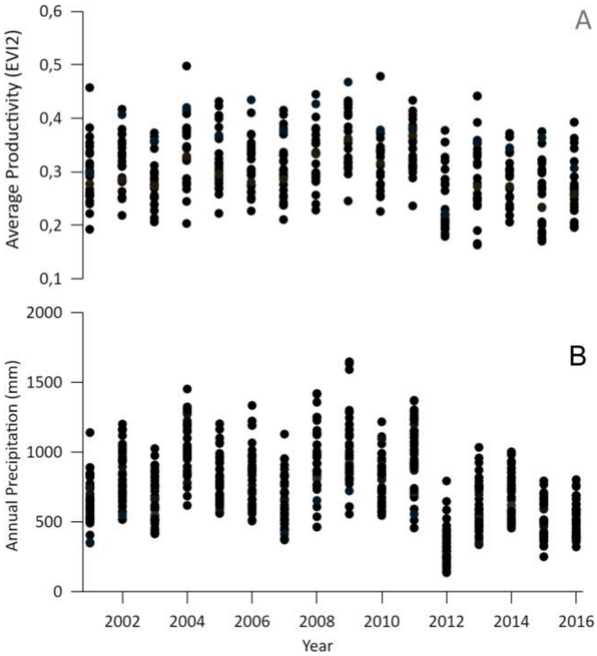
As we measured the anomaly index of the interannual variability, we noticed that precipitation maximum and minimum anomalies were always more extreme in amplitude (0.72 and -0.79) than productivity (EVI2) anomaly (0.42 and -0.54). Such difference implies a greater amplitude of variation in precipitation. The relationship between the two anomalies (precipitation and EVI2) was highly significant with a good coefficient of determination (Graph 2, $p < 0.001$, $r^2 = 0.5$, $n = 784$).

Table 1 - Enhanced Vegetation Index (EVI2) for 49 sites in Northeastern Brazil as a proxy for primary productivity and its relationship with species richness and rainfall. Where: Lat and Long, latitude in decimal degrees; State, abbreviation of Brazilian States where samples were collected; Species, species richness per hectare; EVI2, monthly average EVI2; Rainfall, annual average rainfall; Reference, articles used to extract information on species richness for each sampling site (all listed in Reference section at the end of the article).

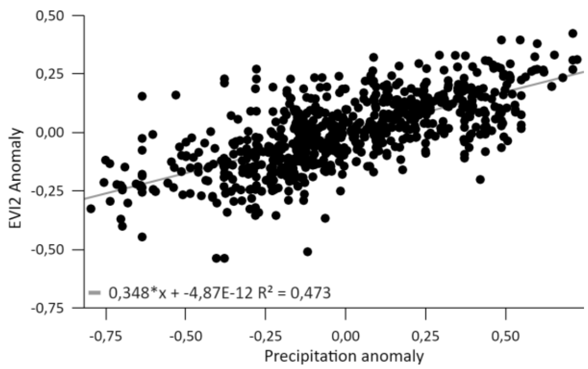
Sample	Lat	Long	State	Species	EVI2	Rainfall	Reference
EVI1	-9.048	-40.245	PE	48	0.317	515	Nascimento *et al.*, 2003
EVI2	-7.420	-36.027	PB	43	0.276	610	De Carvalho *et al.*, 2012
EVI3	-12.823	-39.828	BA	51	0.321	674	Farias, 2003
EVI4	-12.932	-39.899	BA	55	0.335	674	Farias, 2003
EVI5	-6.330	-39.377	CE	52	0.353	930	Guedes *et al.*, 2012
EVI6	-6.703	-37.754	PB	23	0.268	978	Dantas *et al.*, 2010
EVI7	-6.810	-36.961	PB	22	0.238	786	Fabricante *et al.*, 2007
EVI8	-6.881	-35.795	PB	54	0.385	789	Pereira *et al.*, 2002
EVI9	-7.000	-37.383	PB	16	0.292	940	Queiroz de Souza *et al.*, 2010
EVI10	-7.420	-36.027	PB	17	0.277	610	Trovão *et al.*, 2010
EVI11	-8.238	-35.922	PE	55	0.332	944	Alcoforado-Filho *et al.*, 2003
EVI12	-7.147	-37.296	PB	28	0.290	940	Souza *et al.*, 2009
EVI13	-8.734	-42.489	PI	56	0.358	667	Lemos e rodal, 2001
EVI14	-8.312	-38.196	PE	28	0.258	649	Rodal *et al.*, 2008
EVI15	-8.179	-36.169	PE	14	0.283	837	Silva, 2012
EVI16	-8.532	-36.550	PE	34	0.364	874	Silva, 2009
EVI17	-6.168	-38.279	RN	17	0.341	884	De Souza e De Medeiros, 2013
EVI18	-10.743	-38.098	SE	63	0.385	541	Ferreira, 2011
EVI19	-7.837	-37.192	PB	37	0.320	766	Júnior *et al.*, 2012
EVI20	-6.660	-40.216	CE	47	0.304	639	Lemos e Meguro, 2015
EVI21	-7.520	-36.000	PB	29	0.259	792	De Carvalho *et al.*, 2012
EVI22	-6.583	-37.333	RN	15	0.273	968	Amorim *et al.*, 2005
EVI23	-9.542	-40.457	BA	39	0.231	492	Souza *et al.*, 2012
EVI24	-5.117	-40.873	CE	25	0.329	739	Costa e Araújo, 2012
EVI25	-7.895	-37.143	PB	35	0.290	766	Pegado *et al.*, 2006
EVI26	-7.186	-37.426	PB	46	0.365	940	Leite *et al.*, 2015
EVI27	-9.066	-40.335	PE	27	0.225	509	Fabricante *et al.*, 2012
EVI28	-8.186	-36.396	PE	62	0.403	780	Nascimento e Rodal, 2008
EVI29	-7.407	-39.350	CE	43	0.403	976	Costa e Araújo, 2007
EVI30	-8.150	-36.321	PE	32	0.378	780	Nascimento, 1998
EVI31	-7.117	-40.967	PI	57	0.271	695	Sampaio *et al.*, 1997
EVI32	-6.889	-35.799	PB	53	0.329	789	Pereira *et al.*, 2003
EVI33	-8.591	-38.534	PE	11	0.174	546	Santos *et al.*, 2009
EVI34	-14.424	-44.172	MG	47	0.380	872	Dos Santos *et al.*, 2011
EVI35	-8.500	-38.000	PE	23	0.255	644	Rodal *et al.*, 2008
EVI36	-6.460	-36.641	RN	17	0.263	763	Andrade *et al.*, 2009
EVI37	-8.617	-38.283	PE	26	0.198	569	Rodal *et al.*, 2008

Table 1 - continued.

Sample	Lat	Long	State	Species	EVI2	Rainfall	Reference
EVI38	-7.053	-36.052	PB	37	0.286	629	Andrade *et al.*, 2007
EVI39	-6.703	-37.754	PB	23	0.268	978	Dantas *et al.*, 2010
EVI40	-8.060	-38.719	PE	18	0.293	725	Pinheiro e Alves, 2007
EVI41	-6.583	-37.333	RN	15	0.273	968	Amorim *et al.*, 2005
EVI42	-7.950	-38.283	PE	22	0.316	857	Nogueira Ferraz *et al.*, 2003
EVI43	-7.471	-36.898	PB	20	0.311	689	De Vasconcellos Barbosa *et al.*, 2007
EVI44	-3.909	-40.990	CE	74	0.376	1004	De Araújo *et al.*, 1999
EVI45	-5.146	-40.929	CE	39	0.385	739	De Vasconcelos *et al.*, 2010
EVI46	-5.717	-40.917	CE	54	0.329	652	Araújo *et al.*, 1998
EVI47	-7.333	-36.300	PB	22	0.248	586	Santos e Santos, 2008
EVI48	-10.800	-42.833	PB	22	0.351	678	Rocha *et al.*, 2004
EVI49	-7.400	-36.533	PB	17	0.204	628	De Andrade *et al.*, 2005



Graph 1 - Average productivity (EVI2, A) and annual precipitation (B) between 2001 and 2016 (*n* = 49), where no statistically significant interannual trend was detected for both variables.



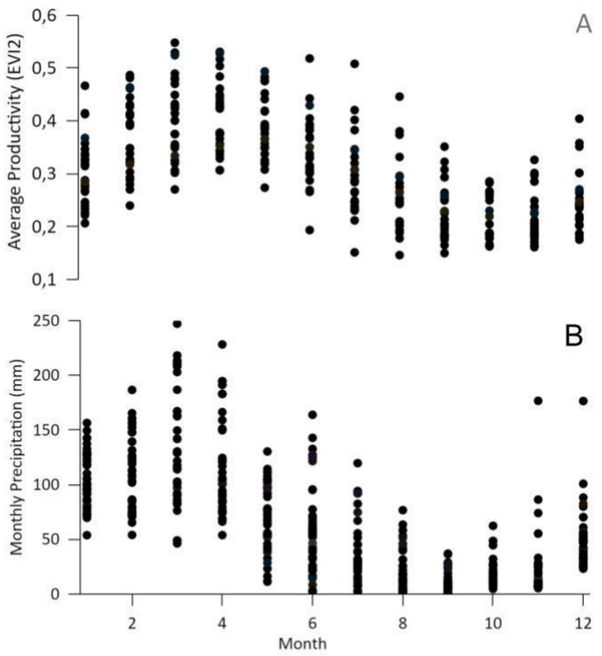
Graph 2 - Relationship between anomaly indices ofprecipitation and productivity (EVI2), equation 0,348*x + -4,87E-12; $p < 0.001$, $r^2 = 0.5$, $n = 784$.

In the years of 2004 and 2009, both EVI2 and precipitation showed the highest values. On the other hand, in 2012 we saw a significant decrease (more than two standard deviations below average) in precipitation, caused by a region wide extreme drought event. The drought also affected the vegetation, demonstrated by the decrease in EVI2.

As for the response lag in EVI2 to precipitation, the best coefficient of determination was when applied a one month lag ($r^2 = 0.39 \pm 0.16$; $p < 0.001$; $n = 49$), which was better than theregressions with no lag, 2 and 3 months lag. Therefore, all correlations and regressions presented hereafter, are with a one month lag.

Seasonality was also very clear for all sites and years. We found greatest productivity (EVI2) for the months April and May and lowest in October and November (Graph 3A).

Precipitation showed the same pattern, and with one month peak prior to productivity (as expected), with highest rains in March and April and lowest in September and October (Graph 3B).

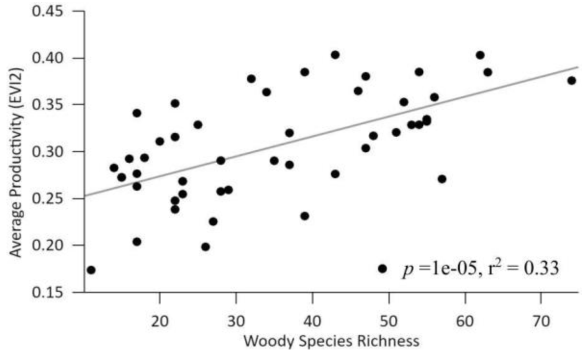


Graph 3 - Average monthly productivity (EVI2 in A) and precipitation (in B) from the years 2001 and 2016 (n = 49), with clear seasonality for both variables.

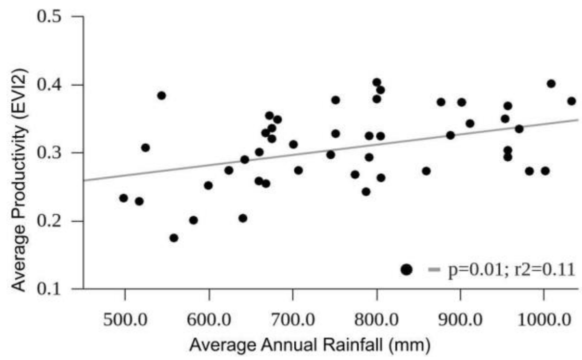
Relationship among Productivity (EVI2), woody species richness and annual rainfall

Woody species richness explained (when being the single independent variable) positive and significantly 33% of EVI2 (p = 1e-05, r^2 = 0.33, n = 49, Graph 4). Since we only have a single species richness value for each sampling site, it was not possible to determine the species richness effect on productivity per site.

When analyzed as the single independent variable, average annual precipitation explained little, but significant and positively 11% of the productivity (EVI2; p = 0.01, r^2 = 0.11; n = 49, Graph 5). In contrast with this low region wide coefficient of determination, the average coefficient of determination per site was 0.62±14 (p < 0.01; n = 192 [16 years x 12 months]). Such adifference could be explained by the fact that locally other variables are fixed and seasonality plays a more important role.



Graph 4 - Rank-based estimation regression between average productivity (EVI2) and woody species richness (p =1e-05, r^2 = 0.33, n = 49).



Graph 5 - Rank-based estimation regression between average EVI2 and annual average precipitation for all sites (p = 0.01, r^2 = 0.11, n = 49).

Together, in a multiple regression, the combined effect of species richness and rainfall explains 47% of EVI2 (p < 0.01, r^2 = 0.47; n = 49). On the other hand, we did not find a significant relationship between species richness and rainfall (p = 0.75).

Discussion

It is well established that species richness increases with stand age (Chazdon *et al.*, 2007) and inversely, anthropogenic impact has a negative effect in species richness, making it decline (Chase *et al.*, 2019; Yaynemsa *et al.*, 2023), leading to the imbalance of biological diversity at multiple spatial scales (Storch *et al.*, 2022). Both stand age and human impact have an indirect influence in our study and its results, since a great part of semiarid ecosystems in Brazil have been intentionally or accidentally burned, clear cut and used for pastureand/or agriculture, wood exploitation and abandoned some time in the past. Although not addressed in our analyses, our results remain valid, since even without measuring or quantifying successional status or human impact, our results are coherent and significant.

From the coefficients of determination of the linear models that we presented here, we observe that one third of the productivity in Caatinga ecosystems are positively correlated to species richness. Since we only accounted for woody species richness, one can expect this relation to be higher if other life forms were included in the analyses. Grasses and other herbs are rarely included in plant structure studies in woody vegetation, but still play an important role in the diversity of Caatinga ecosystems (Moro *et al.,* 2016).

Despite the debate about the relationship between biodiversity and productivity (Fraser *et al.*, 2014; Fraser *et al.*, 2015; Gross *et al.*, 2000; Mittelbach *et al.*, 2001; Waide *et al.*, 1999), and its role on ecosystem functioning (Isbell *et al.,* 2018), being because diversity stabilizes the ecosystem, providing resistance or resilience (Hossain *et al.,* 2022), our data show this relationship clearly and positively for the 49 semiarid stands included in our analysesand also in other studies such as Araújo *et al*. (2022); Mazzochini *et al.* (2019) and Medeiros *et. al*. (2019).

Some studies have shown that more complex landscapes have higher biodiversity and are more resistant to climate change and/or extreme events (Duffy *et al.*, 2017; Oliveira *et al.*, 2022; Seddon *et al.,* 2016). In natural forest regions, in addition to biodiversity, heterogeneity is also identified as an important factor for stabilizing ecosystem productivity at multiple spatial scales (Qiao *et al.,* 2023). Although the Caatinga shows low productivity compared to other dry forests, it maintains a relative stability and resistance (as demonstrated in this time series). It also shows a high plant heterogeneity (Moro *et al.,* 2016), which is associated with the stabilization and functioning of the ecosystem.

Brazilian semiarid ecosystems are complex landscapes and can return to their original productivity after severe climatic events, such as droughts. But different to other complex landscapes, Caatinga requires a long time for the recovery of its original structure and composition, with a suggested period of at least 35 years (De Oliveira *et al.,* 2023).

When we correlated EVI2 and precipitation anomalies, we observed that the decrease in productivity is only one third of precipitation´s decrease (slope= 0.36, $p < 0.001$; $n = 588$; Graph 2). Such resistance to interannual variability of rainfall is the product of natural selection and is crucial for the maintenance ofbiodiversity and also the livelihood of millions of people living in this semiarid region.

Even with this vegetation´s resistance to climate severity, uninterrupted human use and exploitation may lead to an impoverished landscape, which might not return to previous original complexity, due to synergistic effects of both severe droughts and anthropogenic impact (such as deforestation and/or degradation).

In the year 2012 there was a severe and intense drought, caused by an almost total lack of rain, especially in the rainy season (Leivas *et al.,* 2014; Marengo *et al.*, 2016, 2017 and 2019; Martins e Magalhães, 2016). Because of this event, this was also the year with the lowest precipitation andEVI2. After this extremely dry year, in the following years, productivity levels rose to within average values for the whole period studied, even with some other dry (but not so dry) years, such as2015 and 2016. This also corroborates with the previous arguments on how the vegetation is resistant and resilient to interannual variability.

The relatively low correlation between precipitation and productivity at the regional scalemay seem unexpected, but since many other factors also drive productivity in the landscape level (and vary temporally and spatially) it plays a lesser role as a productivity driver regionally.

At the local scale, on the other hand, precipitation plays a much larger role, since most of the other factors do not vary locally (such as soil type, biodiversity, topography, among others),when there is no major human alteration taking place.

The region-wide low correlation between rainfall and productivity shows also that other factors, such as soil type and depth, play a more important role, even in the region´s hydrological budget. More important than how much rain falls in a year, is the amount of water that gets stored inthe basin and for how long. According to SUDENE (2017), the majority of semiarid Brazil is located in the crystalline geological basement, with a prevalence of shallow sandy and clay-sandy soils, which hinders water drainage and storage. Therefore, soils have a very fundamental role in water regulation (Antonino *et al.*, 2000). And for some plants, water availability in the soil is important (Wright *et al.,* 2021), more than rainfall per se, which ultimately might be the reason for the low correlation at the region-wide scale between precipitation and productivity.

As for the lag time between local rainfall and productivity, plant productivity seems to peak one month after rainfall. Such a response time has been reported elsewhere (*e.g.:* Costa, 2017; Salimon & Anderson, 2018; Schucknecht *et al.,* 2012).

In general, this vegetational mosaic called Caatinga (even with its high spatial physical and biological heterogeneity), might be able to withstand future climatic extremes, since it is adapted to such variations, as we have shown here in the anomaly analysis, where productivity showsonly one third of rainfall´s decrease - which is a very resistant response to severe droughts. Nevertheless, such droughts associated with human disturbances - which are intense and will increase in the near future - could lead to irreversible damage to ecosystems functioning specially in plant communities under soils with low water availability and high anthropogenic impact

(Ramos *et al.*, 2023).

It is important then, more than ever, that new studies elucidate the relationships between biodiversity and productivity and other determinant factors such as soils and temperature, since they have key role in primary productivity as controllers of basin water storage and drainage, and also in the opening and closure of stomata andleaf abscission in Caatinga species.

Finally, we emphasize that although deforestation in semiarid Brazil is not widely reported as in Amazonia, NorthEastern Brazil has lost more than 10% of its natural vegetation in the last 30 years, and 36% of the total semiarid regionis already deforested (MAPBIOMAS, 2023). Therefore, the impact of productivity reductiondue to biodiversity loss can and probably will affect in the decades to come the livelihood of more than 27 million people who inhabit the Northeastern Semiarid Brazil.

Conclusions

In this paper we showed how macroecological research conducted with secondary data is useful to elucidate ecosystem processes in semiarid vegetation such as the Caatinga, in face of climate variability and severity.

We conclude that the woody species richness and precipitation are directly and positively correlated to Caatinga's primary productivity. At a landscape scale, woody species richness drives primary productivity nearly three times more than precipitation, demonstrating its significant role as a productivity driver and, consequently, an important factor in maintaining the stability and functionality of the ecosystem. We have confirmed that woody species richness can and should be taken into account in future studies evaluating Caatinga productivity.

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