# Tropical dry forest resilience and water use efficiency: an analysis of productivity under climate change

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# ENVIRONMENTAL RESEARCH
## LETTERS

# Tropical dry forest resilience and water use efficiency: an analysis of productivity under climate change

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## Abstract

Tropical dry forests (TDFs) worldwide have an environment-sensitive phenological signal, which easily marks their response to the changing climatic conditions, especially precipitation and temperature. Using TDF phenological characteristics as a proxy, this study aims to evaluate their current continental response to climate change across the Americas. Here, we show that TDFs are resilient to water stress and droughts by increasing their rain use efficiency (RUE) in drier years and recovering to average RUE in the year following the drought. Additionally, we find that TDF productivity trends over the past 18 years are spatially clustered, with sites in the northern hemisphere experiencing increased productivity, while equatorial regions have no change, and the southern hemisphere exhibiting decreased productivity. The results indicate that the TDF will be resilient under future climatic conditions, particularly if there are increasing drought conditions.

## 1. Introduction

The productivity of a given forest is inherently linked with biomass accrual and can be measured using leaf growth or woody mass (Skovsgaard and Vanclay 2008, Reich 2012). In both cases, this measure of biomass is linked to the ability of the forest to sequester carbon, a fundamental ecosystem service, as well as to the ecosystem resilience, thereby indicating forest health (Albrecht and Kandji 2003, Spasojevic et al 2016). Resilience, in this case, is defined as the ability of an ecosystem to recover to a similar functionality after a disturbance and the time of return to this functionality (Holling 1996, Spasojevic et al 2016). The mechanisms of resilience are typically assessed in the a pre and post disturbance return time (Bhaskar et al 2018). It has been found by recent research that species diversity with different response strategies increases the resilience of an ecosystem (Alvarez-Yepiz et al 2018, Bhaskar et al 2018). Other research finds that this are tradeoffs between being resistant to

distubances and increasing the resilience, with a particular trade-offs between wood density and resprouting (Paz et al 2018).

One of the components of resilience and the recovery times in the tropical dry forests (TDFs) is based on the water availability in the region (Paz et al 2018). Water availability is directly related to the productivity and biomass of an ecosystem and thereby the resilience of an ecosystem (Hatfield et al 2001). Water use efficiency (WUE) is ratio of the productivity, biomass, or yield against the available moisture, typically in the form of evpaotranspiration (Hatfield et al 2001, Xue et al 2015). Increased WUE improves drought tolerance, and there has been increasing interest in ways to improve the WUE of crops (Ruggiero et al 2017). Water limited ecosystems, such as the TDF, are of particular interest, because there is concern that increasing drought will reduce the resilience in these areas, particularly if the WUE does not increase accordingly (Zhang et al 2019).

With severe threats to TDFs already coming from anthropogenic sources from high deforestation rates and forest protection under 10% for most countries, this already strained ecosystem is located in an area that is projected to experience severe climatic changes (Portillo-Quintero and Sanchez-Azofeifa 2010). The different regions of the TDF, though, are projected to different types of climate change based on where they are located, and not all models project the same changes to occur (Magrin *et al* 2014). Some research suggests that TDF will not have the capability to adapt to changes in timing and distribution of rainfall leading to reduced carbon sequestration potential (Allen *et al* 2017); however, this has not been tested in long-term cross-continental assessments. Given the uncertainty of future climate regimes and projections of decreased rainfall (Magrin *et al* 2014), the resilience of TDFs is unclear, especially when assessing biodiversity, productivity, and carbon sequestration potential (Allen *et al* 2017).

While there have been studies correlating TDF development and growth to climatic variables, these have typically focused on local assessments and short timeframes (Saynes *et al* 2005, Navar-Chaidez 2011, Ito and Inatomi 2012). There has not, however, been a holistic and cohesive analysis of the response of the whole Meso and South American TDFs to climatic variables, nor has there been a recent long-term analysis (since 2000) studying how these forests are responding to the ongoing changes in climate.

In this study, we analyze the continental-scale response of Meso and South American TDF productivity to site variables, including both climatic and biophysical characteristics. Additionally, we analyze the variability of productivity in response to water stress using a combination of *in situ* and remote sensing data, assess the forest productivity trends since 2000, and assess the impact of El Niño Southern Oscillation (ENSO) cycles on TDF productivity.

## 2. Methods

### 2.1. Literature search and site selection
A literature search using the keywords TDF, tropical semi-deciduous forests, litterfall, annual net primary productivity (ANPP), biomass, and leaf litter was used to collect data regarding litterfall sites for this analysis. These sites were vetted against the Sánchez-Azofeifa *et al* (2005) definition of TDFs, which includes restrictions on temperature, precipitation, elevation, and deciduousness, for site consistency. The deciduousness was restricted for by a combination of the *in-situ* assessments and the dry season productivity. Only sites with a unimodal, highly deciduous productivity pattern were included because the integrated enhanced vegetation index (EVI) that is used in this site is highly sensitive to this measure, and has been previously shown to perform poorly in evergreen forests (Shi *et al* 2017).

Futhermore, only sites that included *in-situ* measures of biomass and litterfall and adhered to the above definition were included in the subsequent analysis. The sites were then compared against both the TDF map (Portillo-Quintero and Sanchez-Azofeifa 2010), as well as Google Earth images, to ensure there is continuous forest within a 1 km buffer of each point. Highly fragmented sites were moved to the nearest patch of continuous forests with a 1 km buffer; however, if there were no nearby sites with intact forests, the point was removed.

Of the original 50 TDF points collected from the literature survey, 32 sites remained for the analysis. The 32 sites span Mexico, Costa Rica, Venezuela, Brazil, Argentina, and Bolivia are predominantly classified as late-stage forest, although there are three early stage sites and one intermediate stage site (SI 1; SI 2 (available online at stacks.iop.org/ERL/16/054027/mmedia)). Climate variables (including precipitation and temperature) elevation, litterfall data from ground traps, successional stage, and forest type from each site were gathered from each site. These *in situ* data were used to develop relationships with remote sensing products with the goal of analyzing productivity trends, and their relationship to site variables.

### 2.2. Data collection
The remote sensing datasets used in this analysis included the moderate resolution imaging spectroradiometer (MODIS) MOD13Q1 EVI and VI Quality Version 6 products for determining proxy productivity (Didan 2015). The MODIS product was used because of its longevity, resolution, and frequent observations. These data were filtered based on the quality flags and any anomolous data was removed. The EVI products were downloaded from February 2000 to February 2018 for each of the litterfall sites and integrated annually at a 1 km resolution. This data was also assessed in TIMESAT for seasonality parameters, including the start, end, and length of season (Jönsson and Eklundh 2004). EVI was used as a measure of proxy productivity because other studies have found it to be robust as a empirical measure of vegetation dynamics, as well as its relationship to productivity through the fraction of photosynthetically active radiation (Pettorelli *et al* 2005, Eckert *et al* 2015, Kath *et al* 2019).

Relevant site parameters including climatic variables, such as mean annual temperature (MAT), climatic moisture deficit (CMD), evapotranspiration (*E*ref), and the atmospheric heat-moisture index (AHM) were pulled from the ClimateSA model. The model has historical data derived from 1901 to 2009 Climatic Research Unit Time Series (CRU-TS) 3.1, with updated data until 2013 by the CRU-TS 3.22 until 2013. The ClimateSA model has also been previously related to sites in Mesoamerica and used to assess productivity changes and resilience

(Stan *et al* 2020). These climatic variables were collected at a 1 km resolution between February 2000 and February 2013.

Precipitation was taken from the Tropical Rainfall Measuring Mission 3B43 product, given the product's longevity and the compiled satellite data's return time. *In situ* litterfall data from the plots were correlated against satellite data from the corresponding years. Despite the TRMM satellite decommissioning in 2015, the 3B43 product combines information from eight earth observation sensors from a variety of different programs, so it continues to produce rainfall data. Given this, the $0.25° \times 0.25°$ resolution satellite data was compiled from February 2000 to February 2018.

Soil moisture for the litterfall sites came from the European Space Agency Climate Change Initiative (ESA-CCI) product. This daily soil moisture product is a compilation of multi-frequency radiometers including SMMR, SSM/I, TMI, AMSR-E, and Windsat, C-band scatterometers (ERS-1/2 scatterometer, METOP Advanced Scatterometer), and other microwave sensors including Soil Moisture and Ocean Salinity and Soil Moisture Active Passive (SMAP) Mission and ran 1978–2016. The data we used was taken from 2000 to 2016 at a resolution of $0.25° \times 0.25°$.

To assess the impact of the ENSO periods on productivity, the data from 2000 was further subsetted into El Niño, neutral, and La Niña years as determined by the National Oceanic and Atmospheric Association (NOAA). ENSO years were identified following the NOAA definition of a minimum of 15 consecutive months where the sea surface temperature (SST) in the equatorial Pacific Ocean is more than a $+0.5$ °C difference from the 40 year average SST.

### 2.3. Relationship between climate variables and productivity

The 32 litterfall sites were used to pull the MOD13Q1 data for 2000–2018. Of those sites, there were six with *in-situ* data collected during the 2000–2018 period. These six sites included three sites with two plots that were used, leading to nine overall plots used to determine the relationship between the annually integrated EVI (iEVI) and the ground measure of ANPP found at each site. This data was added to the global measure of this relationship, as originally developed by Ponce Campos *et al* (2013) in order to verify if they fit along their proposed curve.

Once this relationship was established, the remaining years and sites were analyzed in TIMESAT. TIMESAT is a program designed to analyze the seasonality trends in satellite-based time series data (Jönsson and Eklundh 2004). The iEVI at each site in every year was transformed through this relationship to determine the measure of annual proxy productivity in each site (Jönsson and Eklundh 2004).

This productivity data is used as the ANPP in all subsequent analyses. The EVI time series data was smoothed using the Savitsky–Golay method (Jönsson and Eklundh 2004), and subsequently, the start, end, and length of the season are calculated based on 0.25 of the annual EVI amplitude.

The soil moisture, from the ESA-CCI, was averaged from the daily product into monthly products from 2000 to 2016. The TRMM precipitation data was compiled for the growing season (period of sustained precipitation), not for the calendar year. To calculate the evapotranspiration, a combination of the TRMM precipitation data and % forest cover was used in the Zhang *et al* (2001) equation:

$$\mathrm{ET} = \left( f \frac{1 + 2\frac{1410}{P}}{1 + 2\frac{1410}{P} + \frac{P}{1410}} \right.$$
$$\left. + (1 - f) \frac{1 + 0.5\frac{1100}{P}}{1 + 0.5\frac{1100}{P} + \frac{P}{1100}} \right) P \quad (1)$$

where

ET = evapotranspiration (mm)
$f$ = percent forest cover within 1 km (%)
$P$ = mean annual precipitation (mm)

To assess the relative importance of the site characteristics in explaining the variations in the ANPP at each plot, the ANPP, climate variables (precipitation, $E_{ref}$, temperature, AHM, CMD) and site specific characteristics (elevation, latitude, longitude) over the most recent decade (2007–2017) were ordinated using a principal component analysis (PCA). Soil moisture was not included in the PCA because not all sites had data available.

All factors, productivity and site variables, were tested for normality using the Shapiro–Wilks test. The sites' ANPP were then correlated against all site variables, including the soil moisture if available, using the Pearson correlation. The relationships were assessed for significance using the correlation coefficient ($\alpha < 0.05$). These variables were also run through multi-variate linear regression models to find the model and site variables which fit best and are best able to assess the cross-continental variability in site net primary productivity. A full linear model (LM), and optimized variable selection LM (LEAPS), the least angle regression (LARS), and the elastic net regression (ENET) were all tested and assessed for the $R^2$ in the R stats program (R Core Team 2020).

### 2.4. Rain use efficiency under wet and dry conditions

The relationship between ANPP and precipitation is the rain use efficiency (RUE; Huxman *et al* 2004) and was calculated for the average precipitation in the most recent decade, between 2008 and 2018, as well as for the driest and wettest years. This decadal correlation calculated between proxy productivity and evapotranspiration for each site as the WUE

(Monson *et al* 2010). Both the RUE and WUE are the slope found between precipitation and evapo-transpiration, respectively, and are metrics assessing the productivity response of ecosystems to annual changes in available water (Bai *et al* 2008).

Using the average, driest, and wettest years, the efficiency of the forest's use of water under differing conditions can be determined based on the slope of the relationship (Monson *et al* 2010). The TDF sites were further subset into the severest droughts where precipitation >2 SD below the decadal average. The RUE for the droughts and the year following, when the rainfall returns to average, is also calculated. The WUE was used also investigated in the wettest and driest years for comparison against other biomes, globally.

### 2.5. Productivity changes over the last two decades

The ANPP trends from each site were assessed over the past 18 years using a linear regression and tested for directionality and significance ($\alpha < 0.05$). Changes to the site-specific variables were assessed over the same period using linear regressions and tested for significance ($\alpha < 0.05$). Both the productivity and site variables were assessed spatially for latitudinal patterns. Correlations between the direction and significance of productivity and the site characteristics were also assessed.

### 2.6. El-Niño southern oscillation impact on productivity

Based on the NOAA years, El Niño years were 2003, 2007, 2010, and 2015–2016. Neutral years were 2001–2002, 2004–2006, 2009, 2013–2014, and La Niña are found to be 2000, 2008, 2011–2012, and 2017–2018. The difference in the productivity of sites between ENSO cycles were tested for significance using *t*-tests. Additionally, the difference between productivity in each phase of the ENSO cycle was compared against the 18 year ANPP average. The difference between years was interpolated across the remaining TDF in Meso and South America to assess the spatial patterns.

## 3. Results

### 3.1. Relationship between climate variables and productivity

To assess the relationship between productivity and climate variables, we first tested the reliability of the iEVI from MODIS against *in situ* litterfall data. Litterfall was collected after 2000 in 6 of 32 sites across Meso and South America which had litterfall traps, with three of those sites having two plots that were sufficiently far from each other to be compared against separate MODIS data (SI 1/2). This litterfall–iEVI relationship for each of these nine plots was integrated into the linear relationship between *in-situ* litterfall and satellite data developed by Ponce Campos *et al* (2013). The relationship follows the
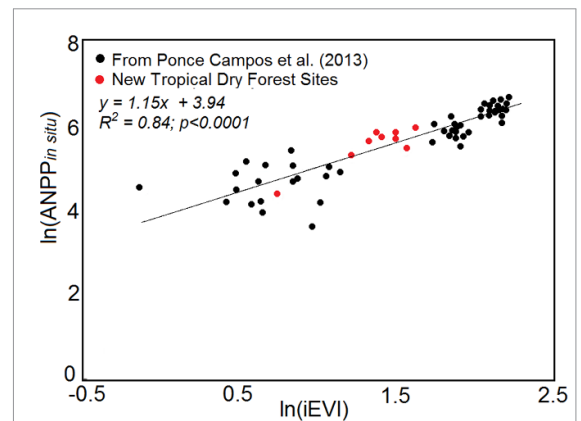


**Figure 1.** Relationship between annually collected *in situ* litterfall, from ten Forest and Grassland sites (modified after Ponce Campos *et al* 2013) and six TDF sites, and the corresponding annual iEVI from the same year. The TDF sites fall between the grassland and forest data within the relationship found by Ponce Campos *et al* (2013; $p < 0.0001$; $R^2 = 0.84$). Reprinted by permission from Springer Nature Customer Service Centre GmbH: Springer Nature. Nature. Ecosystem resilience despite large-scale altered hydroclimatic conditions. Ponce Campos *et al* Copyright © 2013, Nature Publishing Group, a division of Macmillan Publishers Limited. All Rights Reserved. (2013).

Ponce Campos regression closely, with sites falling in a gap between the Mesic Grasslands and temperate american forest classes (figure 1). As using raw EVI data at various latitudes has been shown to have anisotropy issues, we determine ANPP$_{in\text{-}situ}$ from the iEVI of all 32 sites for all subsequent analyses (Fensholt *et al* 2010, Breunig *et al* 2015). The precipitation data from the Tropical Rainfall Measuring Mission was also correlated against the *in-situ* rainfall data and found to be both linear and significant ($p < 0.05$).

PCA and Pearson correlations were used to assess the relationship between the TDF ANPP and site variables, both climatic and biophysical. In the PCA, points in Mexico, Bolivia, and Brazil cluster by country, respectively, with Mexico clustering in higher ANPP and MAP, Bolivia in the centre, and Brazil as the lowest ANPP and highest moisture deficits (figure 2). The first three components of the PCA explain 90% of the variance in the study sites. The first component is most highly associated with the CMD, AHM, evapotranspiration, and longitude. The second component is highly influenced by the temperature variables: MAT, mean coldest month temperature (MCMT), mean warmest month temperature (MWMT) and elevation, and the third component is mostly influenced by the latitude. The precipitation variance is predominantly split between components 1 and 2.

There were individual significant linear relationships observed between ANPP and precipitation ($p < 0.001$; $R^2 = 0.84$), evapotranspiration ($p < 0.001$; $R^2 = 0.85$), elevation ($p = 0.02$; $R^2 = 0.24$) and soil moisture ($p < 0.001$; $R^2 = 0.95$), but not between ANPP and temperature-related metrics
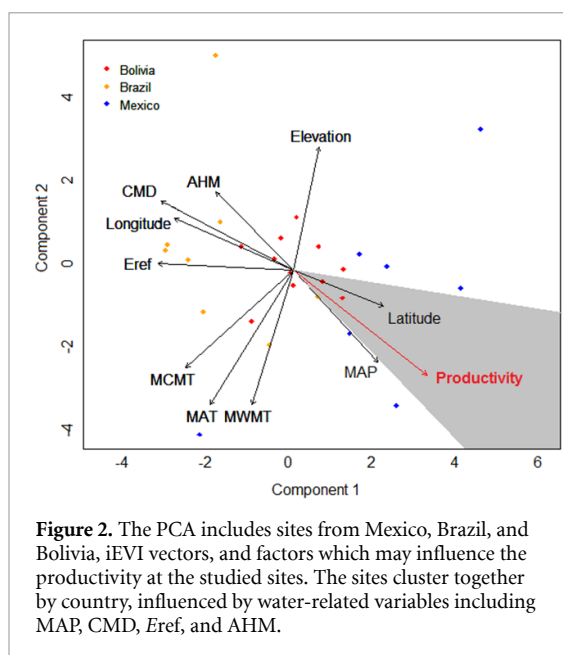
**Figure 2.** The PCA includes sites from Mexico, Brazil, and Bolivia, iEVI vectors, and factors which may influence the productivity at the studied sites. The sites cluster together by country, influenced by water-related variables including MAP, CMD, *E*ref, and AHM.



**Figure 3.** RUE (the ANPP as a function of the incoming precipitation at a site) for comparing the wettest to driest years, the average RUE and the years following droughts.

**Table 1.** Comparison of different multi-variate LMs including the LARS, linear regressions without variable selection (LM), and with optimized variable selection (LEAPS), and the ENET.

| Model | $R^2$ |
| --- | --- |
| ENET | 0.37 |
| LARS | 0.59 ($p < 0.01$) |
| LM | 0.52 ($p = 0.045$) |
| LEAPS | 0.62 |

(MAT, MCMT, MWMT; $p > 0.10$) or the length of the season ($p = 0.32$). When combined into multivariate LMs, the LEAPS model (linear regression with optimized variable selection) performed the best with the highest $R^2$ ($p < 0.01$; $R^2 = 0.62$) when using the CMD, latitude, elevation, mean annual precipitation (MAP), and length of the season (table 1; SI 3/4).

### 3.2. Rain use efficiency under wet and dry conditions

For the TDF areas the average RUE is 0.56 ($p < 0.001$; $R^2 = 0.97$), while the driest year of each site has a RUE of 0.78 ($p < 0.01$; $R^2 = 0.91$) and of 0.44 ($p < 0.001$; $R^2 = 0.96$) in the wettest year at each site (figure 3). These values indicate the TDF sites can be equally or more productive in drier years. Additionally, we find that interannual RUE variability does not significantly vary between the TDF sites across the precipitation regime, indicating that the increase in RUE is a function of the reduction of precipitation in each site, not a function of the total precipitation it receives (SI 5). The WUE, a measure of ANPP under different evapotranspiration conditions, follows the same trend as the RUE, with the driest years having a WUE of 0.93 ($p < 0.001$) and the wettest years having a lower
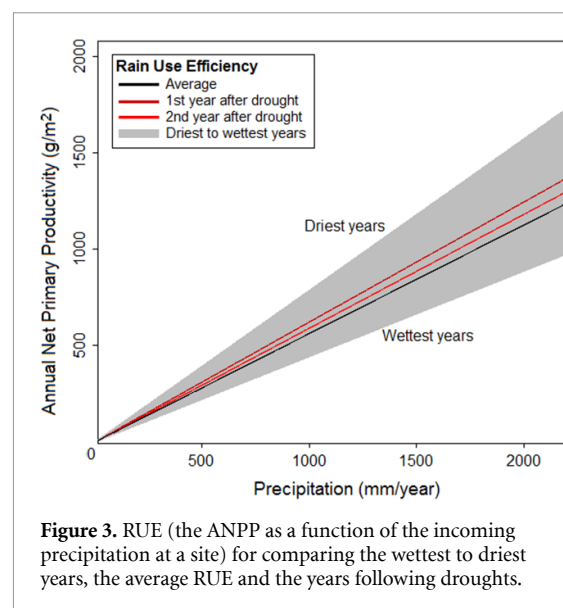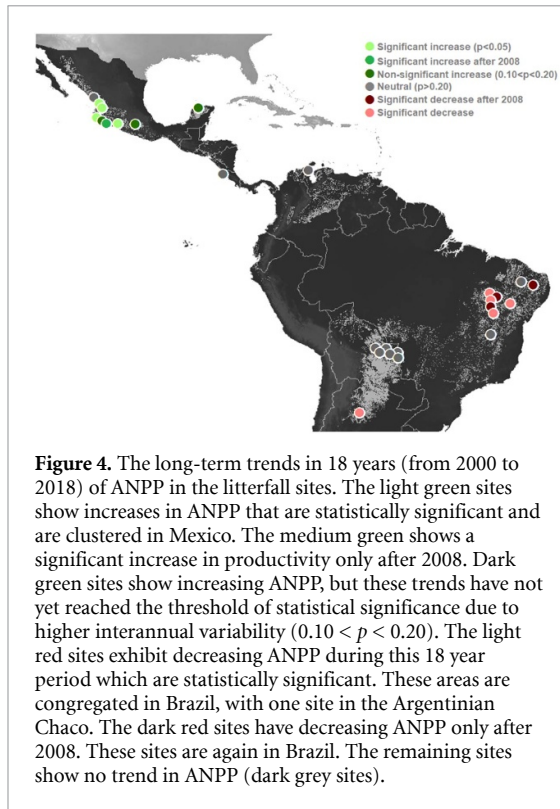
WUE of 0.63 ($p < 0.001$). The average WUE for all sites was 0.72 ($p < 0.001$).

The RUE in the year following the driest year recovers to the decadal average (0.56). In sites with severe droughts, >2 standard deviations lower than the decadal average rainfall, the RUE is higher than the driest year of all sites at 1.10 ($p < 0.01$), and it does not recover back to normal despite average precipitation in the following year (RUE = 0.623; $p < 0.01$). The second year following the drought has a RUE which returns to average.

### 3.3. Productivity changes over the last two decades

When considering the resilience of the TDF under climatic changes, it is important to determine the direction, magnitude and spatial patterns of changes that are already occurring. It should be noted that there is no significant spatial autocorrelation in the ANPP trends ($p > 0.3$). For the long-term analysis, nine sites (four in Brazil, four in Mexico, and one in Argentina) had significant changes in their ANPP between 2000–2018 ($p < 0.05$). Of these significant changes, the Mexican sites (in Nayarit/Jalisco/Guerrero) experienced a significant increase in productivity, while the Brazilian (in Piauí/Bahia) and Argentinan (Chaco) sites experienced a decrease in productivity. There are sites that have experienced significant trends in their productivity in the past decade alone. There are four sites with significant changes to the their productivity, with one increase in Mexico, and three with decreased productivity in Brazil. Additionally, there are an additional three sites with with increases to their productivity, but their interannual variability is sufficiently high that they have not reached the required $p < 0.05$ level for significance. These sites are experiencing an overall increase in their productivity, and if trends continue will likely hit that threshold within the next decade; however, they currently have

**Figure 4.** The long-term trends in 18 years (from 2000 to 2018) of ANPP in the litterfall sites. The light green sites show increases in ANPP that are statistically significant and are clustered in Mexico. The medium green shows a significant increase in productivity only after 2008. Dark green sites show increasing ANPP, but these trends have not yet reached the threshold of statistical significance due to higher interannual variability ($0.10 < p < 0.20$). The light red sites exhibit decreasing ANPP during this 18 year period which are statistically significant. These areas are congregated in Brazil, with one site in the Argentinian Chaco. The dark red sites have decreasing ANPP only after 2008. These sites are again in Brazil. The remaining sites show no trend in ANPP (dark grey sites).

$0.10 < p < 0.20$. The remaining sites exhibited no long-term change in the past 18 years ($p > 0.50$) (figure 4).

Of the sites with increased ANPP in the long-term analysis, one site in Nayarit, Mexico had a corresponding increase in soil moisture ($p < 0.05$) and the second site in the same region had an increased growing season between 2000 and 2018 ($p < 0.05$; SI 4). Of the sites with decreased ANPP, one of the Brazilian sites in Bahia State had a corresponding drop in both precipitation and soil moisture ($p < 0.05$), while three other locations, two in Brazil and one in Argentina also saw a decline in soil moisture, without a significant change in precipitation (SI 6). The remainder sites with significant differences in Jalisco, Mexico ($p = 0.015$), Michoacán, Mexico ($p = 0.015$), and Piaui, Brazil ($p = 0.05$; two increased; one decreased ANPP) had no corresponding changes in any geo-climatic variables.

### 3.4. El-Niño southern oscillation impact on productivity

When the TDF sites were subset into their ENSO periods, the neutral years were found to be within 5%–10% of the 18 year average ANPP, with no significant variation based on the latitude of the TDF. During ENSO years, Mexico has a significant increase in ANPP compared to neutral years ($p = 0.0003$) and La Niña years ($p = 0.012$), with TDF showing up to 30% higher ANPP. In Brazil, there is a significant decrease in ANPP in ENSO years compared to La Niña years, with up to 20% drop in ANPP ($p = 0.04$). Bolivia has the highest reduction in ANPP in ENSO years with up

to a 30% decrease in ANPP, and a significant decrease compared to both neutral ($p = 0.004$) and La Niña years (p = 0.0029; figure 5). Argentinean sites have a significant increase in ANPP compared to La Niña years ($p = 0.03$; figure 5).
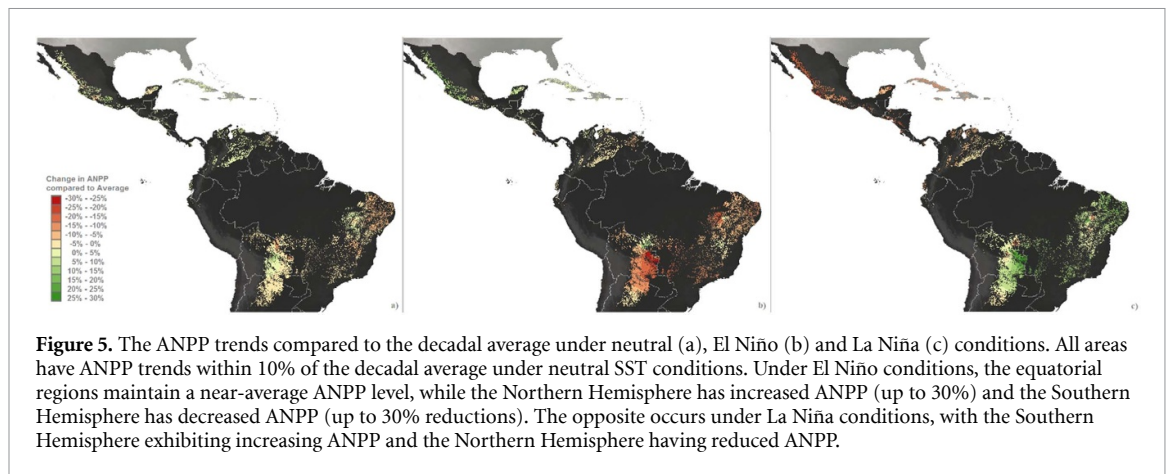
## 4. Discussion

Overall, the results of this study indicate a measure of resilience to drought conditions in Meso and South American TDFs. Higher RUE physiologically means that the ecosystem can produce the same or more leaves and woody biomass (assimilate more carbon) with less water (Keenan *et al* 2013). It also provides a measure of resilience, as this is a drought mitigation strategy which is stressful for the plants to maintain. Biomes which maintain a higher efficiency long after a drought ends are more heavily taxing their resources than those that return to their average efficiency quickly when normal water conditions return (Huang *et al* 2017).

The quick recovery time following droughts is replicated in other equatorial regions and globally in TDFs, while forests at higher latitudes recover slower (Yu *et al* 2017, Tng *et al* 2018). These areas of increased WUE in times of drought include the Amazon, Central Africa, Indonesia, and southern India (Yu *et al* 2017), while the Australian TDFs have been found to have multiple drought adaptive strategies in its species to ensure resistance to drought conditions, and quick recovery in post-drought periods (Tng *et al* 2018).

When looking at the long term trends in productivity, it is interesting to note that there is a break point in some of the sites, after which their trends become significant. One such driver of this may be the change in fires in the TDF. There has been a 9% drop in fires across the drylands since 2008, the timing of which corresponds to these shifts in productivity (Yin *et al* 2020). It is also of interest to note that with the exception of one site, all other sites that have changes to their productivity are found in the the desert or arid climate zones, as determined by the Lang Aridity Index (Traore *et al* 2020). This includes both the positive and negative changes to productivity, and indicates that productivity is changing only in the most arid areas of the TDF (Traore *et al* 2020; SI 7). This pattern does fit in with more global research that suggests that increasing droughts in semi-arid and sub-humid ecosystems will in fact experience a decrease in their WUE over a longer time period (Yang *et al* 2016).

One caveat to this study is that it does not take into account the transition of species that could occur due to changing climatic conditions. The significant changes to the RUE due to drought indicate that the species present have a high level of isohydricity (Yi *et al* 2019); however, if there are increased droughts

**Figure 5.** The ANPP trends compared to the decadal average under neutral (a), El Niño (b) and La Niña (c) conditions. All areas have ANPP trends within 10% of the decadal average under neutral SST conditions. Under El Niño conditions, the equatorial regions maintain a near-average ANPP level, while the Northern Hemisphere has increased ANPP (up to 30%) and the Southern Hemisphere has decreased ANPP (up to 30% reductions). The opposite occurs under La Niña conditions, with the Southern Hemisphere exhibiting increasing ANPP and the Northern Hemisphere having reduced ANPP.

found due to climate change, the forests could recruit further isohydritic species to adapt to this new regime. This is also echoed by eco-evolutionary research which suggests that sites with highly deciduous species, as was controlled for in this site, are not as stable as more evergreen sites in terms of species composition, allowing for higher turnover or the invasion of better adapted species (Vico *et al* 2017).

Unfortunately, there has been very little research into the relationship between hydro-climatic shifts and the population dynamics, and what little information there is results in highly varied results. Some research indicates that there is little shift in the overall forest population dynamics due to changes in hydro-climate (Swenson *et al* 2012), other research indicates that there is a shift in the composition towards more drought tolerant species (Feeley *et al* 2011), and some research indicates that both are true with the collapse of a few species, while the remainder are unchange (Katabuchi *et al* 2017). There has also been some research to suggest that ENSO events increase mortality rates but there is rapid species recruitment and a return to normal mortality rates in the years following these extreme events (Calvo-Rodriguez *et al* 2021). This most recent research indicates that there may be changes to the species composition in the longer-term and the functional shift found may be largely due to the environmental changes, as opposed to being random in nature (Swenson *et al* 2020, Calvo-Rodriguez *et al* 2021). This indicates that this area must be brought into further analysis about the resilience of the TDF and what resilience in an ecosystem truly means.

## 5. Conclusion

Overall, the WUE found for the wettest and driest years, and the return time to average rain use efficency, indicates that TDFs resilient under drought conditions. When there are severe droughts, TDFs require more than two years to return to pre-event conditions, and the efficiency is higher in the year following the drought, indicating a higher level of stress. Long-term trends show that significant increases in productivity are occurring exclusively in the Northern Hemisphere, and decreases are happening in the Southern Hemisphere, although there is wide variation among sites as to the timing of these changes. These changes correlate to alterations in soil moisture, precipitation, and length of the growing season. Finally, we find that while the productivity in forests in highly related to water-related climate variables, temperature variables have not had a significant relationship with productivity in the past decade. One essential aspect of resilience, however, that is not considered in this study is the combined impact of species variation across the TDFs. This aspect of resilience will be increasingly important as climate changes in the future.

## Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

## Acknowledgments

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