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Giant tortoise habitats under increasing drought conditions on Aldabra Atoll—Ecological indicators to monitor rainfall anomalies and related vegetation activity

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Abstract: Aldabra Atoll has the largest population of giant tortoises (Aldabrachelys gigantea) in the world. As such an important biological resource, it is necessary to understand how the effects of climate change will impact this keystone species; in particular the frequency of drought, which is likely to affect tortoise habitat. To assess whether drought frequency has changed over the last 50 years on Aldabra, we calculated the standardized, precipitation index (SPI) to identify drought periods using monthly rainfall data collected during 1969–2013. We found that drought frequency has increased to more than six drought months per year today compared with about two months per year in the 1970s ($t = 2.884$, $p = 0.006$). We used MODIS normalized difference vegetation index (NDVI) as a proxy for vegetation activity, to determine how vegetation has responded to the changing drought frequency between 2000 and 2013. We found that Aldabra's vegetation is highly responsive to changes in rainfall: anomalies in long-term mean monthly NDVI across Aldabra were found to decrease below the mean during most drought periods and increase above the mean during most non-drought periods. To investigate the response of tortoise habitat to rainfall, we extracted mean NDVI anomalies for three key habitat types. Open mixed scrub and grasslands, the preferred habitat of tortoises, showed the greatest decrease in vegetation activity during drought periods, and the greatest increase in average greenness during non-drought periods. Recent analysis has shown vegetation changes on Aldabra in recent decades. If these changes are caused by decreased precipitation, then the increased frequency of drought could impact the tortoise population, in both the short and long term, by limiting the quality and quantity of forage and/or shade availability within favoured habitats, and by changing the habitat composition across the atoll.

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Research Paper

Giant tortoise habitats under increasing drought conditions on Aldabra Atoll—Ecological indicators to monitor rainfall anomalies and related vegetation activity

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ABSTRACT

Aldabra Atoll has the largest population of giant tortoises (*Aldabrachelys gigantea*) in the world. As such an important biological resource, it is necessary to understand how the effects of climate change will impact this keystone species; in particular the frequency of drought, which is likely to affect tortoise habitat. To assess whether drought frequency has changed over the last 50 years on Aldabra, we calculated the standardized precipitation index (SPI) to identify drought periods using monthly rainfall data collected during 1969–2013. We found that drought frequency has increased to more than six drought months per year today compared with about two months per year in the 1970s ($t = 2.884$, $p = 0.006$). We used MODIS normalized difference vegetation index (NDVI) as a proxy for vegetation activity, to determine how vegetation has responded to the changing drought frequency between 2000 and 2013. We found that Aldabra's vegetation is highly responsive to changes in rainfall: anomalies in long-term mean monthly NDVI across Aldabra were found to decrease below the mean during most drought periods and increase above the mean during most non-drought periods. To investigate the response of tortoise habitat to rainfall, we extracted mean NDVI anomalies for three key habitat types. Open mixed scrub and grasslands, the preferred habitat of tortoises, showed the greatest decrease in vegetation activity during drought periods, and the greatest increase in average greenness during non-drought periods. Recent analysis has shown vegetation changes on Aldabra in recent decades. If these changes are caused by decreased precipitation, then the increased frequency of drought could impact the tortoise population, in both the short and long term, by limiting the quality and quantity of forage and/or shade availability within favoured habitats, and by changing the habitat composition across the atoll.

1. Introduction

Semi-arid oceanic islands are one of the most vulnerable ecosystems to the effects of climate change (Nurse et al., 2014). While most islands have been severely degraded after the arrival of humans (Brooks et al., 2002) a few islands have been largely protected from human influence due to their geographical isolation. Today, however, the resilience of these relatively intact endemic ecosystems are now challenged by new environmental drivers due to climate change (Whittaker and Fernández-Palacios, 2007). On Aldabra Atoll in the Indian Ocean, climate change has the potential to threaten the many endemic and indigenous species. A recent management assessment by the International Union for Conservation of Nature (IUCN) highlighted an urgent need to investigate climate-driven threats to the atoll and its biodiversity, including sea level rise and ocean acidification, as well as changes in vegetation that can affect plant-animal interactions through bottom-up dynamics (Osipova et al., 2014).

The terrestrial food web on Aldabra is unique as it is dominated by a reptilian herbivore, the Aldabra giant tortoise *Aldabrachelys gigantea*. The largest vertebrate on the atoll, the tortoises act as ecosystem

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engineers: manipulating the ecosystem and influencing the distributions of plant species through seed dispersal, nutrient cycling, and controlling plant distributions through grazing (Hansen et al., 2010). For example, the intensive grazing of the tortoises create areas of "tortoise turf", a collection of low-growing herbaceous species, grasses, and sedges (Gibson and Phillipson, 1983a; Merton et al., 1976). They were also likely the first colonizers on Aldabra, spreading plant species from Madagascar (Hnatiuk, 1978), and their distribution, movements, and foraging behavior are important in shaping the current landscape and vegetation distribution (Merton et al., 1976). Aldabra giant tortoises are considered vulnerable (IUCN Red List) to extinction so it is important from ecological and conservation perspectives to investigate how potential vegetation changes due to drought could impact their habitats. A deeper understanding of the ecosystem role of Aldabra giant tortoises under global change will also be important for conservation and restoration projects on similar islands that harboured giant tortoises until recently (Hansen et al., 2010).

Aldabra, like many isolated islands, is home to other unique species threatened by limited distribution ranges and small numbers, and thus also threatened by drought and habitat change. The Aldabra drongo *Dicrurus aldabranus* is only found on the atoll and is considered near threatened (IUCN Red List), while the Aldabra rail *Dryolimnus cuvieri aldabranus* is the last remaining flightless bird in the western Indian Ocean. Introduced predators such as cats and rats are a direct threat to most bird species on Aldabra (Stoddart, 1971; Van De Crommenacker et al., 2015), and changes in habitat could affect cover and nest protection for all bird species.

Aldabra is experiencing reduced rainfall patterns similar to trends seen in East Africa (Shekeine et al., 2015) which are driven by Indian Ocean sea surface temperatures (Tierney et al., 2013). While the frequency and severity of droughts across Africa are predicted to increase due to climate change (Dai, 2011; Hoerling et al., 2006), water stress has already increased in sub-tropical Africa (Dai et al., 2004; Mu et al., 2013) resulting in decreased vegetation activity (Potter et al., 2012; Zhao and Running, 2010). As tortoise turf productivity on Aldabra is highly reliant on rainfall (Gibson and Phillipson, 1983b), increasing drought could lead to habitat changes that could impact tortoise health and distribution.

Here, we examine whether Aldabra is already experiencing more frequent drought periods, and whether there are detectable impacts on the atoll's vegetation. While this study focuses on resource availability for the Aldabra giant tortoise, a key species of conservation, the developed methods are equally relevant for monitoring fluctuations of vegetation activity for any plant communities that rely on seasonal rainfall. We combine meteorological data and satellite-derived normalized difference vegetation index (NDVI) data to examine trends in occurrence of drought periods and how they may affect Aldabra's vegetation. Specifically, we aim to: 1) detect drought periods on Aldabra based on its long-term rainfall record over the period 1969–2013, and 2) assess the response of atoll-wide mean vegetation activity and habitat-specific vegetation activity to drought and non-drought periods from 2000 to 2013.

2. Materials and methods

2.1. Study site

Aldabra Atoll, a UNESCO World Heritage Site managed by the Seychelles Islands Foundation, is approximately 1100 km southwest of Mahé, the principal island of the Seychelles (9°25′0.05″ S, 46°24′59.94″ E). The raised coral atoll has a mean altitude of 8 m a.s.l. (maximum 19 m a.s.l.) and is comprised of four main islands: Grande Terre, Malabar, Picard and Polymnie (Fig. 1). The atoll is ca. 34 km long and 14 km wide. Aldabra giant tortoises are found on all islands, except Polymnie. Vegetation on Aldabra includes large continuous patches of shrubs of varying height, and areas with a mosaic of shrubs with open rocky ground and grasses and sedges of different cover (Hnatiuk, 1979). Plants on Aldabra are highly distinctive with 20% being endemic and 80% indigenous (Renvoize, 1971).

Aldabra's climate is determined by two distinct seasons: the wet season during the north-west monsoon (November–April) (Stoddart and Mole, 1977); and the dry season during the south-east monsoon (May–October). The mean annual temperature on Aldabra is 24–28 °C (Shekeine et al., 2015) and mean yearly rainfall is 975 mm.

A recent study using data collected over two years from 31 GPS-tagged tortoises found that open mixed scrub and grasslands are the preferred habitat for Aldabra giant tortoises (Walton, 2015). These habitats are comprised of tortoise turf interspersed with mixed shrubs and are limited in distribution, covering only 16.3% and 2.89%, respectively, of the total area of the atoll (Walton, 2015). Open mixed scrub is frequently surrounded by or interspersed with small trees, which together with shrubs provide needed shade resources to the tortoises during the midday sun (Bourn and Coe, 1978). Much of Aldabra is dominated by the evergreen shrub *Pemphis acidula* (hereafter "*Pemphis*") (Hnatiuk, 1979). In our study, we investigate the response of open mixed scrub and grasslands (here after "open mixed scrub"), *Pemphis*, and mangrove forests (hereafter "mangroves") to rainfall anomalies. While tortoises were found to avoid *Pemphis* and mangroves (Walton, 2015), they still use these habitats to provide shade during the hottest part of the day.

2.2. Rainfall data

Monthly instrumental rainfall data, available for 1969–2013 (Shekeine et al., 2015), was converted into the standardized precipitation index (SPI) to identify drought periods on Aldabra. SPI transforms long-term precipitation time series to a rainfall probability by fitting the Gamma function, and measures actual compared to predicted precipitation, in units of standard deviations, for specific time periods (Mckee et al., 1993). Rainfall deficits are then used to quantify rainfall anomalies, including drought (Mckee et al., 1993). SPI quantifies departures of observed precipitation from the long-term climatological mean rainfall for a given period of time (Mckee et al., 1993). We chose SPI over raw rainfall data because: 1) drought is pre-defined (Mckee et al., 1993); 2) it can be applied over multiple time periods (Mishra and Singh, 2010); 3) it can be correlated to vegetation changes observed in the field (Lotsch, 2003); and 4) it provides consistent analyses at all spatial locations (Hayes et al., 1999).

The SPI was computed at multiple time scales (one month to twelve months) using the Aldabra monthly rainfall data, where an SPI time series computed at a time-scale t represents the cumulative deficit (SPI $<$ 0) or excess (SPI $>$ 0) over t months. All calculations were carried out using the 'spi' function from the 'SPEI' package in R (Beguería and Vicente-Serrano, 2013). All analysis was performed in R version 3.2.4 (R Core Team, 2016). No rainfall data were collected in October 1976 and between December 1991 and March 1993; and these periods were therefore removed from the analysis. The output of the spi function was the SPI value calculated for each month of the study, based on the previous one to twelve months. McKee (1993) defines monthly drought intensity categories based on monthly SPI values: between 0 to -0.99 is defined as mild drought, -1.00 to -1.49 as moderate drought, -1.50 to -1.99 as severe drought, and ≤ -2.00 as extreme drought. We used these definitions to count how many months per decade (1970s through 2000s) were in each of these drought intensity categories.

2.3. Vegetation activity data

NDVI anomalies, in the form of Z-scores, were used to assess changes in vegetation during times of drought and non-drought. NDVI is used as a proxy for vegetation activity (Tucker, 1979) and is considered to be a reliable indicator of how ecosystems respond to

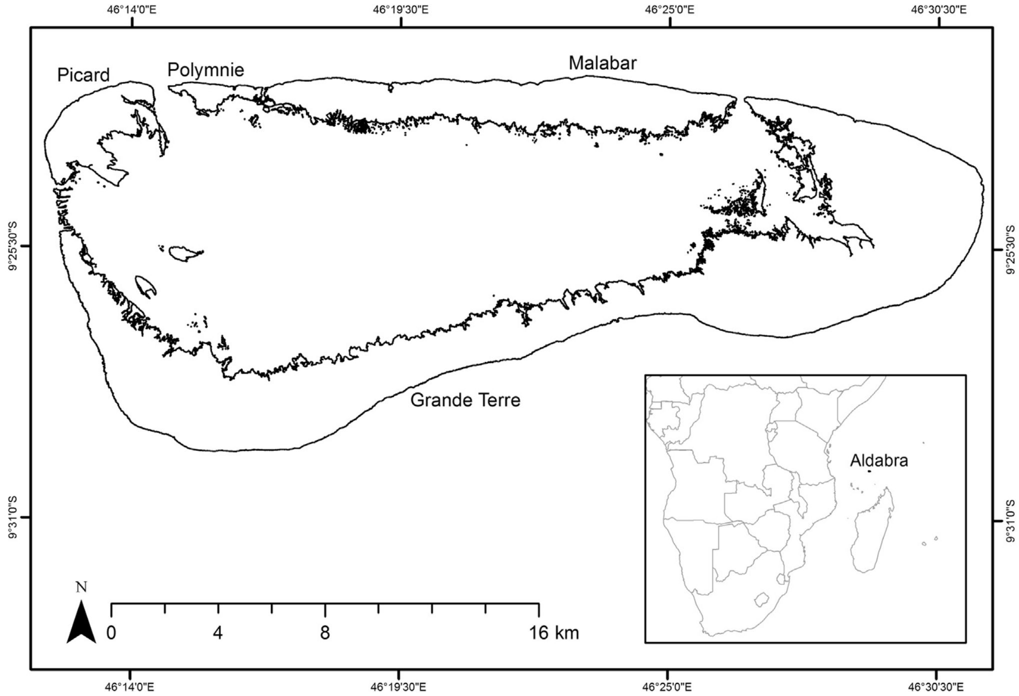

Fig. 1. The four main islands of Aldabra Atoll: Picard, Polymnie, Malabar, and Grande Terre. Inset shows Aldabra's location with respect to Africa and Madagascar.

climate variability over many time scales (Anyamba et al., 2001). The NDVI data products used to derive vegetation response were obtained from the MODIS sensors aboard the Terra and Aqua satellites (Solano et al., 2010). The products, MOD13Q1 and MYD13Q1, consist of vegetation indices for 16-day periods, eight days apart (phased products), with a spatial resolution of 250 m (Solano et al., 2010). All NDVI data covering Aldabra were downloaded for 2000–2013 (Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC, 2011)). Using the 'raster' package in R (Hijmans, 2016), the NDVI layer from both products was extracted such that each pixel comprised two NDVI time series (one for each product) along with the corresponding acquisition dates. The intermediate 2005 MCD12Q1 land cover product was used to mask out the water for all NDVI images, and we used the products' quality layers to filter and retain only the two highest quality levels (i.e., 0 = "Good Data" and 1 = "Marginal Data") (Solano et al., 2010). Next, we calculated the monthly mean NDVI time series for each pixel by averaging all NDVI observations (MOD13Q1 and MYD13Q1) for each pixel for every month over the 2000–2013 period. Each pixel's monthly NDVI time series was then converted into Z-scores defined as:

$$z_{ijk} = \frac{NDVI_{ijk} - \overline{NDVI}_{ij}}{\sigma_{ij}}$$

where z_{ijk} is the Z-score for pixel i for month j for year k (Liu and Negron-Juarez, 2001; Peters et al., 2002), with the monthly mean and standard deviation being taken from the entire study period, in this case 14 years. The Z-scores determine NDVI anomalies relative to the long-term mean, normalized by the standard deviation of the multiannual values for a given month and is widely used to assess responses of vegetation activity to drought (Bayarjargal et al., 2006; Pennington and Collins, 2007). A Z-score of zero represents the baseline condition at which the NDVI score for a given pixel can be regarded as 'normal' for that particular month. Positive Z-score values indicate greener than average conditions while negative Z-score values may reflect stressed vegetation conditions e.g. due to drought. In this study, the Z-score represents the monthly NDVI anomaly from its long-term mean over the 2000–2013 period. This dataset of per-pixel monthly Z-scores (hereafter "NDVI anomaly") was then used as the measure of vegetation response to assess the response of the vegetation activity to rainfall anomalies.

2.4. Rainfall-vegetation activity time lag analysis

The SPI can be calculated at multiple time scales to measure how rainfall changes over several months. To establish the most appropriate SPI time-scale for this study, we analysed the correlation between the SPI time series, computed at time-scales from one to twelve months, and the monthly NDVI anomaly time series (Lotsch, 2003). We used the 'cor.test' function in R (R Core Team, 2016) to measure correlation between monthly NDVI anomalies from $2000-2013$ and the corresponding monthly (one to twelve month) SPI value for each month. The Pearson r values were plotted for each SPI time-scale, with correlation increasing to a plateau at five months, (Fig. 2). This pattern suggests that Aldabra's vegetation lags behind precipitation variation by about five months, leading us to use a monthly SPI-5 value (i.e., the SPI value over the last five months) for each month during 1970–2013. This dataset is hereafter referred to as "SPI-5".

2.5. Analysis of drought dynamics

McKee (1993) defined drought as any period along the SPI series when the SPI is continuously less than or equal to zero and reaches -1 at least once. The drought period begins the month when SPI is first less than or equal to -1, and ends when the SPI goes above zero. We used this definition to identify drought periods in the SPI-5 time-series. We defined non-drought periods as months that were not in drought each year (not within a period where SPI-5 values reached -1). Non-drought periods include times with little change from normal rainfall (high or low), as well as those with greater than average rainfall.

To understand how drought dynamics have changed on Aldabra over the last four decades, we plotted a binary representation of drought periods based on SPI-5 (drought or non-drought) for each month from 1970 to 2009, based on the above definition. Long-term cumulative values of SPI should be near zero since the SPI represents

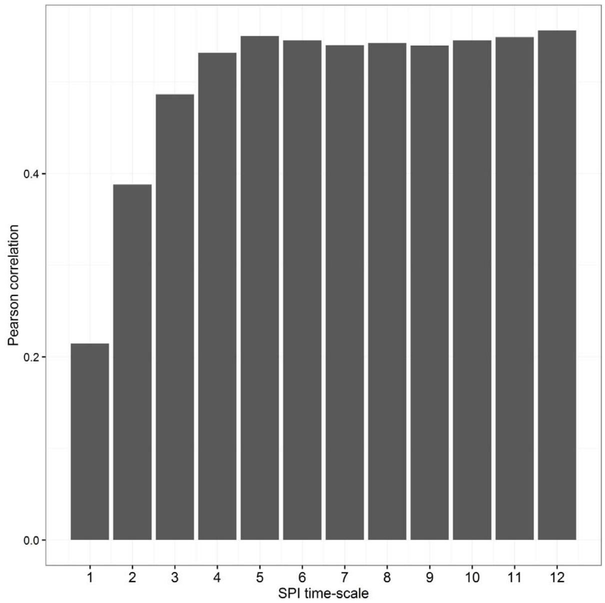

Fig. 2. SPI correlation with NDVI anomalies across Aldabra Atoll. X-axis represents SPI time-scale in months. The atoll reached the peak correlation values at about five months.

variation from the mean precipitation for the same time period over the entire length of the study. We plotted monthly SPI-5 values from January 1970 (calculated using data from September 1969 through January 1970) to December 2013, and calculated the cumulative SPI-5 (sum of all monthly positive and negative SPI-5 values) and decadal SPI-5 values over the study period. When data were not available between December 1991 and March 1993, we excluded the entire rain year in the analysis and began calculating SPI-5 again in December 1993 (using data from August through December 1993).

After identifying drought periods, we counted the number of months each year falling within each drought or non-drought period, and divided by 12 to calculate the proportion of months per year that were considered 'drought months' (hereafter "drought frequency") during 1970–2013. We began this analysis in 1970 since this was the first full year with data. To investigate how the proportion of drought months per year has changed over the study, we used a generalized linear model with a quasibinomial distribution and a logit link function (because there was significant overdispersion) using the 'glm' function in R (R Core Team, 2016). We also calculated the length of each drought period and ran a linear regression analysis to determine if the length of drought periods has changed.

2.6. Analysis of vegetation response to SPI-derived drought periods

We assessed the vegetation response at pixel level by averaging the monthly NDVI anomaly values of each pixel for each drought and non-drought period identified in the drought dynamics analysis. Resulting averages represent the aggregate response in vegetation activity over each period for all of Aldabra. Averages were then compared to the SPI-5 from 2000 to 2013. We calculated the Pearson product-moment correlation coefficient, using the 'cor.test' function in R (R Core Team, 2016), to assess the relationship between mean NDVI anomalies and mean SPI-5 values for drought and non-drought periods.

We used a tortoise habitat map derived from GeoEye-1satellite imagery (Walton, 2015) to understand how different habitat types throughout Aldabra respond to the drought dynamics. Because this habitat map was originally developed at 2 m resolution, we rescaled it to the 250 m spatial resolution of the MODIS NDVI data. We reclassified the map using majority rules to set all pixels within 250 m × 250 m to the majority of the smaller pixels, and used nearest neighbour approximation to upscale. This rescaled habitat map was cropped to the same outline as was analysed for the MODIS NDVI, and merged with the NDVI anomaly time series. Pixels of mangroves, *Pemphis*, open mixed scrub, and grasslands habitat types were then extracted. Because there were only 24 pixels dominated by grassland, and because they were typically within the open mixed scrub, these two classes were

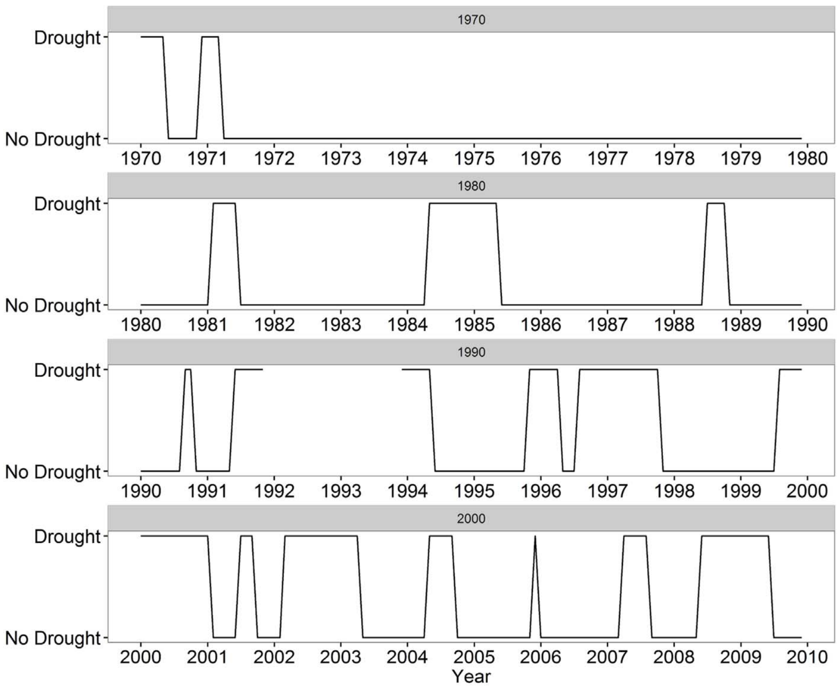

Fig. 3. Timing of drought periods on Aldabra over the past four decades. The frequency of drought has visibly increased since the early 1990s. No data were available for October 1976 and for the period December 1991–March 1993.

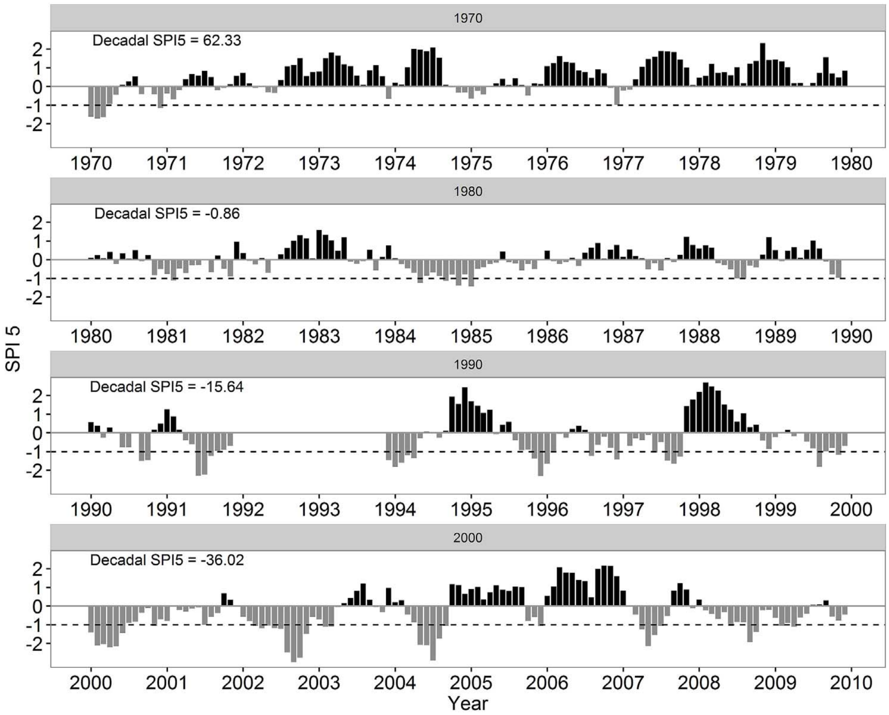

Fig. 4. Monthly SPI-5 values from 1970–2010, where positive SPI-5 values are in black and negative are in grey. Dashed line shows SPI-5 = −1. When monthly values drop below this value, the drought period begins. Cumulative decadal SPI-5 shows decreasing rainfall during this period.

combined for the remaining analysis (hereafter "open mixed scrub"). We then calculated the mean NDVI anomaly for each drought and non-drought period determined in the drought dynamics analysis for each habitat type to observe the different vegetation responses.

3. Results

3.1. Drought dynamics

We found that drought frequency increased in each decade of the study (Fig. 3). The long-term cumulative SPI-5, the sum of all monthly SPI-5 values indicating the overall rainfall excess or deficit, over all four decades was 9.81 (Fig. 4). During the 1970s the decadal cumulative SPI-5 value was large and positive (62.33, i.e., cumulative rainfall above the mean), but this value decreased, and was the lowest during 2000–2009 (−36.02, i.e., cumulative rainfall below the mean; Fig. 4).

The number of drought months per year increased from 1970 to 2013 ($t = 2.884$, $p = 0.006$; Fig. 5), while drought length did not change ($t = 0.614$, $p = 0.547$, Adj. $R^2 = -0.034$). The SPI-5 analysis showed that today roughly six months of the year can be classified as drought months, while in the 1970s it was only two months. Moderate and extreme drought months showed the greatest increase over the course of the study (Table 1).

3.2. Vegetation response to SPI-derived drought periods

Of the 20 drought periods identified between 1970 and 2013, ten occurred during the time range in which MODIS NDVI data were available (2000–2013), allowing us to investigate how vegetation activity responded to drought and non-drought periods. We compared the mean NDVI anomaly value for each drought or non-drought period to the SPI-5 and found that the vegetation activity response across Aldabra was coupled to the drought dynamics: during most droughts (eight of ten), there were negative deviations from the mean NDVI, while during non-drought periods, there were positive deviations from

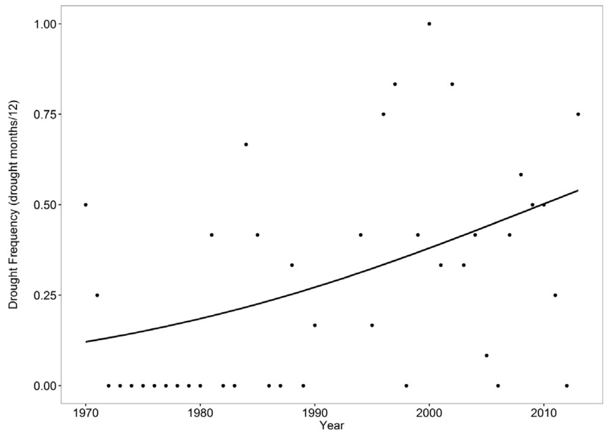

Fig. 5. Yearly drought frequency on Aldabra in each year during 1970–2013. The fitted line is from a logistic regression model.

Table 1
Number of months in each drought magnitude category based on monthly SPI-5 value, for each decade of the study.

Decade	Drought magnitude (SPI-5 range)			
	Mild (0 to −0.99)	Moderate (−1.00 to −1.49)	Severe (−1.50 to −1.99)	Extreme (≤ −2.00)
1970s	5	1	3	0
1980s	15	7	0	0
1990s	19	13	5	3
2000s	20	20	3	11

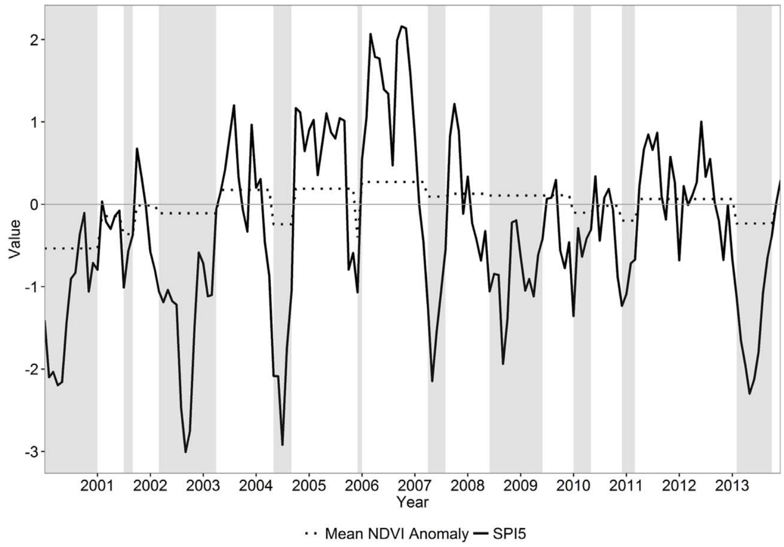

Fig. 6. Mean NDVI anomalies (dotted lines) track SPI-5-defined drought periods (solid lines). Grey vertical bars indicate a drought period, which typically correspond with negative mean NDVI anomalies. White vertical bars indicate non-drought periods, which typically correspond with positive mean NDVI anomalies.

the mean NDVI (Fig. 6). There was also a significant correlation between mean NDVI anomalies and the mean SPI-5 during drought and non-drought periods ($r = 0.749$, $p < 0.001$). Overall, there was a strong, positive correlation between the trends, indicating that vegetation activity is dependent on drought conditions on Aldabra.

Our analysis of habitat-specific responses found that open mixed scrub was the most sensitive habitat to rainfall anomalies (Fig. 7). Open mixed scrub had the lowest, or very close to the lowest mean NDVI anomaly during six drought periods, while during six of ten non-drought periods it had the highest NDVI anomaly. The *Pemphis* NDVI anomaly also strongly tracked the response of open mixed scrub, while mangroves varied less than the other habitats.

4. Discussion

Our study found that drought frequency on Aldabra increased from 1970 to 2013. Similarly, previous research showed that rainfall on Aldabra has decreased by an average of 5.8 mm per year from 1969 to 2012 (see Shekeine et al., 2015 for discussion of changes in overall rainfall). We found that rainfall since the 1970s has steadily decreased in each subsequent decade, with a substantial decrease in the 2000s. Aldabra currently spends more than half the year in drought, double the amount of time in the early 1970s, and the number of drought months spent in moderate or severe drought categories has increased. While individual drought periods are not getting longer, the amount of time between drought periods is, however, decreasing with increasing drought frequency. This limits the time during which vegetation can recover between drought periods.

Recent analysis (Duhec et al., 2010) suggests that Aldabra's rainfall pattern follows Indian Ocean Dipole (IOD) events. Five of the wettest eight years during 1968–2009 coincided with positive IOD events, and three highly dry years were related to negative IOD events. Positive IOD

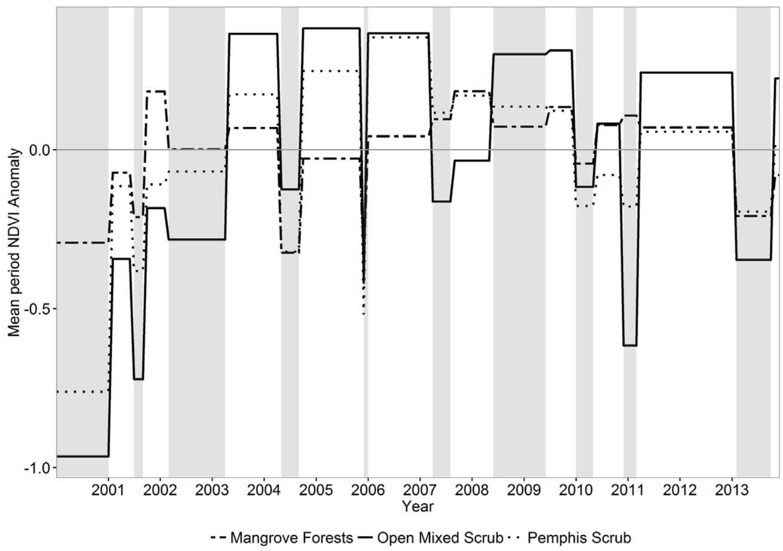

Fig. 7. Mean NDVI anomalies of three vegetation types track SPI-5-defined drought periods. Grey vertical bars indicate a drought period, with negative mean NDVI anomalies and white vertical bars indicate non-drought periods, with positive NDVI anomalies. Open mixed scrub tends to show the strongest response to drought with the lowest anomalies during drought periods, and the highest during non-drought periods.

is related to higher than normal sea surface temperatures and increased rainfall in the western Indian Ocean, while the opposite conditions prevail during negative IOD events (Saji et al., 1999). Global climate change models predict the Seychelles to have wetter wet periods, and drier dry periods, along with an overall warming trend (Payet and Agricole, 2006). The recent rainfall pattern of Aldabra has closely matched the increased drought and dry periods found in Africa, while rainfall models for Africa predict increased drying throughout the next century (Dai, 2011; Hoerling et al., 2006; Lyon and DeWitt, 2012). If Aldabra continues to follow this pattern, we can expect further increases in drought frequency, which is likely to affect the vegetation and potentially the entire terrestrial ecosystem of the atoll.

Our analysis revealed a strong relationship between SPI and NDVI anomalies across Aldabra Atoll with a lag of five months, suggesting that the vegetation is most responsive to the previous five months of rainfall. Other arid and semi-arid ecosystems show similar responses with vegetation activity lagging rainfall anomalies by 4–6 months (Lotsch, 2003). The lag is most likely due to a combination of the water storage properties of the vegetation and soil on Aldabra. While no studies have been done to measure soil moisture content, Trudgill (1979) described the soils on Aldabra as typically shallow and underdeveloped, consisting mostly of vegetation litter and carbonate, with up to 50% of an area covered by bare rock, suggesting that water storage capacity is low.

We found that the mean NDVI anomaly for the entire system follows a similar track to drought; during drought periods, the vegetation is less green. Conversely, when rainfall is above average, the vegetation is greener than average. Pennington and Collins (2007) found a similar response in the New Mexico desert where arid grasslands quickly increased NDVI after the drought ended and rainfall returned to normal, and Vicente-Serrano (2007) found that droughts increased active vegetation variability in arid Mediterranean landscapes with low vegetation cover. During the last four years of the study, the NDVI anomalies during non-drought periods were consistently lower than in the previous ten years, which could indicate that the increasing drought frequency is having longer-term effects on Aldabra's vegetation health by reducing recovery time following droughts. While our study found the NDVI anomalies to correlate with drought, recent research in New Mexico highlights how changes in NDVI trends can be related to biomass changes seen in arid systems (Browning et al., 2017). Our study shows the importance of (experimental) research into the impacts of declining rainfall and extreme droughts on Aldabra's vegetation and how these propagate through the terrestrial food web.

The methods developed in this study are important for identifying drought and vegetation change on Aldabra, and for identifying situations to increase monitoring of the important species found on the atoll. Drought has a direct influence on vegetation succession on island systems (Hnatiuk and Merton, 1979; Lohse et al., 1995; Loope and Giambelluca, 1998), and these methods could help identify shifts in vegetation in other ecosystems due to large-scale mortality of woody species, and associated shifts to herbaceous species (Lohse et al., 1995). On Aldabra, the largest negative NDVI anomaly was identified at the beginning of the study in 2000. Remote sensing of satellite imagery could be used to investigate habitat distributions before and after this drought to understand if there were any large-scale changes in vegetation dynamics or succession.

Our results suggest that some of Aldabra's habitats, especially the open mixed scrub, are more strongly affected by increasing drought frequency than others. Since the mid-1990s, satellite image analysis has revealed changes in vegetation distribution on Aldabra (Constance, 2016). The link between these changes and increasing drought frequency needs to be investigated further, but the timing of the change is consistent with when droughts became more common on Aldabra. If this pattern continues, habitats that are more rainfall-dependent (such as the tortoise turf) may change to more drought-tolerant scrub species, which may support fewer tortoises.

The distribution of shade trees may also influence tortoise habitat use. Tortoises seek shade during the heat of the day and important shade trees may also be affected by drought, as they frequently lose leaves even during normal dry seasons (Fryer, 1910; Hnatiuk and Merton, 1979; Merton et al., 1976). The lack of shade trees may also cause tortoises to relocate to other foraging areas that offer shade, which may in turn affect tortoise size- and sex distributions (Turnbull et al., 2015).

Under normal conditions in the dry season, Aldabra giant tortoises become less selective and their feeding shifts to shrub leaf litter (Gibson and Hamilton, 1983). Thus, a reduction in turf or shrub cover could affect tortoise health, reproduction, and growth as they could be forced to shift to non-preferred food sources. Although analysis of Aldabra giant tortoise monitoring data (1998–2012) has not revealed any downward population trend during this recent period of increased drought frequency (Turnbull et al., 2015), there is evidence of a population change prior to the start of the monitoring programme in 1998 (Bourn et al., 1999). Grande Terre, with its highest open mixed scrub and grassland cover and tortoise population density among the main Aldabra islands, showed a strong decrease in population size, while the population size on Malabar and Picard increased during the same period (Bourn et al., 1999). This indicates that highest population densities are related to abundant open mixed scrub and grassland cover, but at the same time may be highly vulnerable to drought periods affecting the productivity of these important habitats. Current tortoise monitoring on Aldabra focuses on the adult population, which are the most long-lived and resilient individuals, and thus it may be difficult to identify large-scale change in tortoise population dynamics or size unless there are more drought and vegetation effects with lethal consequences for adult tortoises. However, seasonal rainfall has been shown to affect survival of juvenile Hermann's tortoises (*Testudo hermanni*) in southern Europe (Fernández-Chacón et al., 2011), thus increased drought frequency on Aldabra may act more strongly on the recruitment of juvenile Aldabra giant tortoises, which should be monitored more closely in the future.

While no studies have investigated the direct effects of drought on Aldabra giant tortoises, drought in the Mojave desert has been linked to increased mortality in desert tortoises (*Gopherus agassizii*) due to dehydration, starvation, increased susceptibility to disease (Peterson, 1994), as well as decreased vegetation productivity (Longshore et al., 2003). Desert tortoises have also been found to reduce activity and home range use during drought periods, due to decreased forage quantity and quality, as well as decreased availability of drinking water (Duda et al., 1999; Peterson, 1996). These tortoises are believed to employ a strategy to minimize energy expenditure during drought times until resources improve, at which time they can use their energy reserves to seek out better conditions (Duda et al., 1999). Data retrieved from GPS tags on Aldabra giant tortoises during drought periods may reveal similar patterns and will be explored in future research.

Understanding the effects of increasing drought frequency on open mixed scrub is also important for the bird community on Aldabra. A recent study has shown that most birds are found in this habitat, with *Pemphis* also being important (Van De Crommenacker et al., 2015). Between 2002 and 2013, landbird populations increased (in general) or remained stable (Aldabra drongo), suggesting that the droughts experienced since 2002 have not negatively affected their population (Van De Crommenacker et al., 2015). However, this does not take into account the large changes in rainfall patterns developing from the 1980s to 1990s, and could represent the new baseline bird community structure resulting from any vegetation and water availability changes due to increasing drought.

5. Conclusions

As the global climate changes, we need to find ways to monitor its effects on ecologically important habitats, especially those home to rare endemic species. Our study found drought frequency to have increased at the UNESCO World Heritage Site of Aldabra Atoll since the 1970s, and that drought conditions now prevail for more than half of the year. Using MODIS NDVI, we were able to track how specific tortoise habitats respond to these drought periods. While open mixed scrub typically showed the greatest decrease in greenness during drought periods, it appeared to respond quickly when rains returned, showing the greatest increase above average greenness. Aldabra giant tortoises rely on this habitat for food and shade; thus we need to monitor vegetation response to drought, habitat change, and tortoise distribution and health during these drought periods to further understand both short- and long-term impacts of decreasing rainfall.

We found that SPI-5 can be used to identify and monitor drought on Aldabra. Because vegetation across the atoll, and specifically open mixed scrub NDVI anomalies follow SPI-5 patterns so closely, we can use SPI-5 as an indicator for monitoring vital tortoise habitat. However, if increasing drought frequency on Aldabra leads to habitat shifts, the link between SPI-5 and NDVI anomalies may also change as vegetation may move more towards drought-tolerant species.

This analysis also identified a potential decreasing vegetation recovery after more than a decade of increasing drought frequency. This situation should be closely monitored along with habitat change, as the system could be moving towards a critical transition from more productive habitats (open mixed scrub and grasslands) to less productive (D'Odorico et al., 2012; Scheffer and Carpenter, 2003). If climate change causes a shift to less preferred tortoise habitats, it will become import to understand how decreased habitat availability affects Aldabra giant tortoise (and other species) population and fitness, and how Aldabra's biodiversity responds to stressed and changing environments. Aldabra's iconic status, combined with the substantial quantity of data collected on the atoll gives it the potential to act as a model and 'sentinel' site for more detailed investigation into the impacts of climate change on low-lying islands.

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