LETTER

Effects of long-term rainfall decline on the structure and functioning of Hawaiian forests

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Abstract
Climate change is altering the dynamics of terrestrial vegetation, with consequences for the functioning of Earth’s biomes and the provisioning of ecosystem services. Changes in forest dynamics due to drought events or short-term drying trends have been described at different ecological scales, but few observational studies have determined the relative effects of short- and long-term precipitation trends (e.g. decade and century, respectively) on forest canopy structure and functioning. Using gridded annual precipitation maps from 1920 to 2012, and temporal data from airborne light detection and ranging (LiDAR) and MODIS Enhanced Vegetation Index (EVI), we present evidence for a large-scale decline in forest canopy volume (area vs. height) and greenness (a metric of photosynthetic function) driven by a long-term drying trend on Hawaii island. Decreases in canopy greenness were observed in step with shorter-term (10 y) precipitation declines, but decreases in greenness were two-fold greater where longer-term (∼100 y) precipitation declines had occurred. Canopy volume mainly reduced where long-term precipitation declines occurred. We conclude that long-term precipitation trends critically impact forest canopy structure and functioning, which likely has cascading consequences for numerous ecological processes such as subcanopy light availability, species interactions, carbon storage, and animal habitat.

Introduction
Record-breaking warming and drought events have been documented at local to continental scales (e.g. Frazier and Giambelluca 2017, Jiménez-Muñoz et al 2016). These climatic anomalies are expected to increase in frequency and spatial extent (Cai et al 2015), with consequences for the condition of major biomes (Malhi et al 2008, Allen et al 2010). A single drought event or short-term (e.g. decadal) drying trend can undermine the photosynthetic activity of forest canopies (Zhou et al 2014, Hilker et al 2014) because water deficits generate plant stress, such as loss of leaf turgidity, negative carbon balance, hydraulic failure, and leaf abscission (Kozloewski and Pallardy 2002, Chaves et al 2003, Farooq et al 2009). If the stress remains over time, the trees may show partial crown dieback or mortality (Anderegg et al 2013, Allen et al 2015), ultimately increasing stand-level vulnerability to widespread mortality and reduced carbon stock (Phillips et al 2009, Lewis et al 2011). Although our knowledge of these climate-vegetation interactions has improved over time, few studies have considered the impacts of changes in climate on vegetation structure relative to function.

Episodic drought events show immediate and sometimes persistent effects on forest vegetation (Saatchi et al 2013), illustrating time-lag responses between the climate anomalies and vegetation properties and processes (Wu et al 2015). The persistent effects of a single drought event on forests suggest that, on long timescales (e.g. centuries), numerous drought events may cause cumulative changes in structure, function, and composition of vegetation. That is, we expect that repeat climate disturbances can cause cumulative negative effects on canopy structure and functioning over time. Satellite observations (e.g. Enhanced Vegetation Index or EVI)...
have indeed uncovered pervasive and large-scale impacts of drought events on primary productivity, water content, and the structure of tropical forests (Saleska et al. 2007, Samanta et al. 2010). However, few studies have focused on the effects of precipitation anomalies or drying trends on large-scale changes in forest structure (partial and complete crown dieback). Although the tools needed to monitor changes in vegetation structure at the landscape-scale have been limited, new approaches have become available to achieve such a goal (e.g. Light Detection and Ranging or LiDAR).

The importance of vegetation responses to long-term climatic trends is widely recognized. However, the trends remain somewhat controversial (Allen et al. 2015, Hartmann et al. 2015). For example, Zhu et al. (2016) have reported a greening of tropical vegetation, via increases in leaf area, suggesting large-scale CO2 fertilization as a potentially important driver. Others have reported widespread vegetation browning and tree mortality trends in equatorial regions, driven by droughts, long-term rainfall decline, and/or heat stress (Feeley et al. 2007, Allen et al. 2010, Zhou et al. 2014). Yet, others have shown absence of change in vegetation due precipitation anomaly (Zhang et al. 2017). Such variable findings indicate that climatic trends may be site- or region-specific. Indeed, complex variation in environmental factors and vegetation composition has limited our ability to more generally assess whether long-term climate trends have a strong, directional effect on vegetation properties or composition (e.g. via species migration). The Hawaiian islands have long provided a model system to study environmental drivers of vegetation structure and functioning, while simultaneously controlling for forest canopy composition and environmental factors (Vitousek 2004). Recently, gridded precipitation maps were published for Hawaii for the years 1920 to 2012 (Frazier et al. 2016, Frazier and Giambelluca 2017), providing an opportunity to assess forest responses to near-century climate trends without the confounding effect of changes in species composition. Analysis of the climate data indicates large regions of long-term precipitation decline on the western side of Hawaii island (figure 1 and figures S1, S2, S3 and S4 in the supplementary material available at stacks.iop.org/ERL/12/094002/mmedia).

Here, we combine multi-temporal remote sensing data with annual gridded precipitation maps to answer two questions: (1) have long-term declines in precipitation affected forest structure and function in Hawaii? (2) What are the relative effects of short- and long-term drying trends in forest canopy structure and function? To answer these questions, we utilized a

![Figure 1. Mean precipitation anomaly from 1920 to 2012 throughout the island of Hawaii. The precipitation anomaly (hereafter, centennial precipitation anomaly) is the average change in annual precipitation for all years between 1920 and 2012 relative to baseline precipitation (see Frazier et al. (2016) and the 'Precipitation anomaly' section in our methods for details). The black squares indicate the location and extent of analyses of changes in forest canopy function (greenness) using NASA MODIS EVI data. Asterisks indicate the location of the airborne LiDAR data used to assess changes in forest canopy structure. For complete details on the spatial distribution of weather stations and spatial interpolation methods of the rainfall dataset, see Frazier and Giambelluca (2017) and Frazier et al. (2016).]
combination of spatially explicit precipitation data (from 1920 to 2012), multi-temporal satellite green-ness (NASA MODIS EVI) data (2002–2016), and airborne LiDAR data acquired in 2007 and 2016 to measure changes in canopy structure and functioning over time.

**Methods**

**Study sites**

Our study was conducted on two forested landscapes of the island of Hawaii: (1) the upper leeward side of the island containing mesic-to-wet tropical forest, and (2) the upper windward side containing wet tropical forest (see landscape locations in figure 1). These areas were chosen because of their similarity in forest canopy species composition (Gon et al. 2006, State of Hawaii 2016), but dissimilarity in the rate of precipitation decline during the last century (Frazier and Giambelluca 2017, also see figure 1). The flora in both landscapes exhibit low species diversity and canopy structural complexity when compared to continental lowland rainforests (Zimmerman et al. 2008), and a few species dominate a broad range of successional stages and environmental conditions (Wagner et al. 1990). The wet forest canopies located in the windward study landscape are hyper-dominated by endemic Metrosideros polymorpha and Acacia koa trees, with an understory mostly comprised of Cibotium glaucum and Dicranopteris linearis ferns. In the mesic-to-wet montane forest in the leeward study landscapes, the canopy is also dominated by M. polymorpha and A. koa, but understory vegetation includes more shrubs (e.g. Sophora chrysophylla; Myoporum sandwicense) and introduced grasses (such as Pennisetum clandestinum and P. setaceum) (Blackmore and Vitousek 2000).

Elevation on the leeward study landscape ranges from 10 to 2400 m a.s.l., annual precipitation from 550 to 1400 mm (figure S5 in supplementary material), and annual temperature ranging from 9 to 23°C (Giambelluca et al. 2014). On the windward side, elevation ranges from 600 to 1600 m a.s.l., annual precipitation ranges from 2000 to 6000 mm, and annual temperature varies from 12 to 20°C (Giambelluca et al. 2014). While in the eastern, windward part of the island, increases in precipitation in the last century were not statistically significant, the western, leeward half of the island has undergone large and significant precipitation decreases (figure 1, and see Frazier and Giambelluca 2017 for a complete statistical analysis on the temporal changes in rainfall).

**Precipitation anomaly**

We used rainfall maps of Hawaii island at 250 m spatial resolution, covering the period 1920 to 2012 (available at http://rainfall.geography.hawaii.edu/). To provide these maps, Frazier et al. (2016) spatially interpolated monthly rainfall data for the years 1920 to 2012 from over 1000 rain gauge stations distributed throughout the State of Hawaii. For complete details on the spatial distribution of weather stations, interpolation methods of these rainfall dataset, and accuracy of the maps see Frazier and Giambelluca (2017) and Frazier et al. (2016).

**Centennial precipitation pattern**

We used the gridded precipitation maps to assess the centennial precipitation anomaly (CA) and the centennial cumulative precipitation anomaly (CCA) for each year between 1920 and 2012. We used CA and CCA to evaluate the effects of long-term drying trends on the forest canopy. CA and CCA for a particular year ‘i’ were calculated as:

\[
CA_i = \frac{\text{Rainfall}_i - \text{Rainfall}_{1920-1940}}{\text{Rainfall}_{1920-1940}} \times 100
\]

\[
CCA_i = CA_i + CA_{i-1}.
\]

CA is the precipitation change in the year ‘i’ relative to the baseline precipitation (1920–1940); rainfall, is the total precipitation in the year ‘i’ and rainfall_{1920-1940} is the mean precipitation in the baseline period (1920–1940). We used the average precipitation that occurred in the first 20 year segment (1920–1940) of the centennial period as the reference baseline. We also calculated the average of CA for all years between 1920 and 2012 for each pixel in the gridded precipitation map (figure 1), indicating the spatial distribution of positive and negative precipitation trends during the study period. The CCA is the sum between the CA in the time ‘i’ and ‘i–1,’ showing how the relative change in precipitation accumulates throughout the centennial time series (i.e. sum of percentage values).

**Decadal precipitation pattern**

We trimmed the centennial precipitation data (Frazier and Giambelluca 2017) to the last decadal range (2002 to 2012) to evaluate the effects of a short-term drying trend on forest canopy structure and function. In this case, the gridded precipitation maps were also used to calculate the decadal precipitation anomaly (DA) and the decadal cumulative precipitation anomaly (DCA). Because of the restricted time-range in the decadal analysis, we used the first three years of precipitation data as the baseline period (figures S1, S2, S3, and S4 in the supplementary material show absolute and relative precipitation values of the entire time series). DA and DCA were calculated as:

\[
DA_i = \frac{\text{Rainfall}_i - \text{Rainfall}_{2002-2004}}{\text{Rainfall}_{2002-2004}} \times 100
\]

\[
DCA_i = DA_i + DA_{i-1}.
\]

DA is the degree of precipitation change in the year ‘i’ relative to a baseline precipitation (2002 to 2004); rainfall, is the total precipitation in the year ‘i’ (mm)
and rainfall 2002–2004 is the mean precipitation of the baseline period (2002 to 2004). Finally, the DCA_t is the sum of DA (relative change in precipitation) in the time ‘t’ and ‘t–1’, showing how the relative change in precipitation accumulates throughout the decadal time series (i.e. sum of percentage values).

**Canopy photosynthetic activity**

We used the Enhanced Vegetation Index (EVI), a metric of forest canopy function and greenness provided by the MODIS MYD13A1 product (16 day) to infer photosynthetic activity. EVI data were obtained from the NASA Moderate Resolution Imaging Spectroradiometer (MODIS) for our two study regions on Hawaii island (locations are shown in figure 1). EVI has been used in studies of canopy functioning over a diverse range of ecosystems (e.g. Saleska et al. 2007, Zhou et al. 2014, Zhu et al. 2016). The MODIS 16 day EVI product has a spatial resolution of 500 m and low cloud contamination due to daily acquisition interval and compositing procedures (Huete et al. 2002). Per-pixel Quality Assessment metadata (Huete et al. 2002) were used to check the product performance to measure the EVI among study sites and throughout the years. In our study landscapes, we obtained 327 EVI images between 2002 and 2016. Because of the restricted time-range of the EVI dataset, we used the first years of data as the baseline period (see below). Using this MODIS dataset, we calculated both the photosynthetic anomaly (PA) and the cumulative photosynthetic anomaly (CPA):

\[
PA_t = \frac{EVI_t - EVI_{2002-2004}}{EVI_{2002-2004}} \times 100
\]

\[
CPA_t = PA_t + PA_{t-1}
\]

where \(PA_t\) is the EVI anomaly in the time ‘t’ (relative departure from the mean EVI between 2002 and 2004), EVI_t is the EVI value of each pixel in the time ‘t’, EVI_{2002-2004} is the average EVI within the baseline (2002–2004, see figure S6 in supplementary material) for the same pixel location. CPA in the time ‘t’ is the sum between the EVI relative anomaly (PA_t) in the time ‘t’ and the time ‘t–1’. We also calculated the average of PA_t of all years for each pixel in the gridded map. To exclude from the analysis variation in EVI related to land use, we only used MODIS pixels identified as native vegetation in the Hawaiian GAP land cover data (Gon et al. 2006, figure S7 in supplementary material). We assumed that deforestation and forest regrowth were minimal from 2006 to 2016 because of conservation laws and slow patterns of natural forest regrowth. Nevertheless, we excluded from the analysis well-known areas with natural deforestation due lava flow, management of invasive species, and native species outplanting.

**Canopy structure**

In January 2007 and again in January 2016, airborne LiDAR data were collected over our study landscapes (figure 1) using the Carnegie Airborne Observatory (Asner et al. 2007, Asner et al. 2012). The LiDAR sensor was operated at 2000 m above ground level, with a pulse repetition frequency of 50 kHz, and a scan angle of 36°. Laser-spot spacing was maintained at approximately 4 laser shots m^{-2}. See Asner et al. (2007) and Asner et al. (2012) for additional details on the LiDAR instrumentation.

We developed maps of top-of-canopy height (TCH) at 1.5 m × 1.5 m resolution for the LiDAR datasets from 2007 and 2016 using the LASTools software suite (Rapidlasso GmbH; Gilching, Germany). TCH provides an estimate of the maximum vegetation height in each pixel. We co-located the TCH data from the two datasets (2007 and 2016) or measurement periods (see Kellner et al. 2011 and Kellner and Asner 2014), and calculated the change in canopy height by subtracting the pixel values of 2007 and 2016.

We partitioned the available LiDAR data for each study landscape (figure 1) into contiguous hexagon-shaped units of 1 ha, totaling 7612 and 6096 ha in the leeward and windward landscapes, respectively (figure S8 in supplementary material). We defined hexagon-shaped areas to reduce the number of landscape units to cover each geographic area and, consequently, to minimize spatial biases in the analysis. Within each of these 1 ha units, we calculated the total forest canopy volume (m³) in 2007 and 2016 (i.e. Canopy Volume_{2007} and Canopy Volume_{2016}, respectively). Canopy volume (m³) was estimated as the sum of all TCH pixel values (m) multiplied by the canopy area (m²) within each 1 ha unit. In this calculation, we only included pixels with TCH values higher than 0.5 m, aiming to select all woody plants ranging from shrub to tree growth forms, while excluding grasses or other very small plants. To evaluate change from 2007 to 2016 in canopy volume within all the hexagon-shaped units, we calculated the percentage of canopy volume change (CVC) as:

\[
CVC = \frac{\text{Canopy Volume}_{2016} - \text{Canopy Volume}_{2007}}{\text{Canopy Volume}_{2007}} \times 100.
\]

**Statistical analyses**

After assessing the average and standard deviation (SD) of PA and CVC for windward and leeward landscapes, we tested for statistical differences in these variables between landscapes using t-test. We also evaluated the relative effects of short- and long-term drying trends in both forest canopy structure and canopy function, using a generalized linear model in R. In this analysis, we compared the relative importance of the decadal and centennial precipitation
patterns to predict PA and the CVC (figure S9 in the supplementary material shows maps of all dependent and independent variables). We included mean annual precipitation (average rainfall between 1978 and 2007, available at http://rainfall.geography.hawaii.edu/) as a fixed covariate (fixed effect) in the PA and CVC models. In doing so, we controlled the model results for rainfall conditions, assuming that usual differences in water supply may determine how plants respond to droughts and drying trends. We also created a null model that includes mean annual precipitation as independent variable. We compared the model performances using the Akaike information criterion (AIC) and R squared ($R^2$). We considered two models that differed in AIC ($\Delta$AIC) by less than two to be equally probable.

**Results**

Mean annual precipitation has declined from approximately 1156 mm (between 1920 and 1932) to approximately 765 mm (between 2000 and 2012) in the leeward study landscape (figure S1 in supplementary material). Leeward landscapes showed a high frequency and magnitude of negative CA values (figure S2 in supplementary material), resulting in a very high CCA (i.e. cumulative or summed precipitation anomaly) at the end of the time series (figure 2(a)). The rate of cumulative decline in precipitation (i.e. CCA) in leeward landscapes exponentially increased since the 1950s (figure 2(a)). In contrast, precipitation was stable over the last 90 years in the windward study landscape, where CCA was mostly positive or close to zero throughout this period (figure 2(a) and figure S2 in the supplementary material). Both study regions showed a noticeable decline in precipitation during the last decade (figure 2(b)). The temporal change in decadal cumulative rainfall anomaly (DCA) was three times higher in the leeward than in the windward region (figure 2(b)).

Tropical forests in both study areas also exhibited a decline in EVI over the past 14 years, suggesting a parallel trend between canopy photosynthetic activity and short-term precipitation decline (figure 2(b)). While the photosynthetic anomaly (PA) analysis also indicated a widespread EVI decrease in many forested regions of Hawaii island (figure 2(c)), this decline was two-fold larger in our leeward than in our windward study landscapes (figure 3(a), $p < 0.01$). Specifically, PA was $-11.2\%$ (SD = 3.8%) in leeward and $-6.1\%$ (SD = 3.0%) in windward regions (figure 3(a)).

Mean forest canopy volume change (CVC) was negative throughout the leeward landscape (CVC = $-14.9\%;$ SD = 18.9%), suggesting overall forest canopy structural decline (figure 3(b)). On the windward landscape, CVC was marginally positive (CVC = 4.4%; SD = 12.5%), indicating stable temporal pattern of canopy structure (figure 3(b)). Although losses and gains in CVC occurred within the portions of both landscapes (figure 3(b)), partial or complete canopy dieback was more common in leeward than windward forests (see examples in figure 4 and figure S8).

Using the AIC criterion (table 1; $\Delta$AIC < 2), we found that the long-term drying trend (1920–2012) better explained the photosynthetic anomaly (PA) and canopy volume change (CVC) than did the short-term
drying trend (2002–2012). Using mean annual precipitation as a covariate factor (i.e. fixed effect), models that included centennial precipitation anomaly explained nearly 50% of the variance in canopy structure change and 36% of the variance of photosynthetic anomaly (table 1).

**Discussion**

We found evidence for landscape-scale declines in both forest canopy volume (area × height) and greenness (EVI) correlated with precipitation declines. While moderate decreases in canopy greenness were
observed with shorter-term (10 y) precipitation declines, greenness losses were two-fold greater where longer-term (100 y) precipitation declines had occurred (figure 1 and table 1). In contrast, canopy volume decreased in step with centennial-timescale precipitation trends. These findings support the hypothesis that long-term decreases in precipitation generate cumulative physiological and structural damage in tropical forest canopies, which may weaken the capacity of forests to overcome climatic trends or shifts in the future (Anderegg et al. 2013).

We found substantial differences in canopy functional compared with structural responses to the observed moderate, but continuous, drying trend over time. Although reductions in canopy greenness were widespread in the study landscapes in step with both short- and long-term drying trends, these declines did not always generate corresponding changes in canopy structure. Specifically, canopy volume only decreased in the leeward landscape, where the precipitation anomaly and photosynthetic activity showed a stronger negative trend over time. Differences in the landscape-scale responses of canopy function and structure to precipitation changes suggest intricate patterns in the relationship between stand-level physiological stress and tree mortality or structural damage, following precipitation declines (e.g. Allen et al. 2015). Expanding our knowledge of landscape-scale relationships between climate, canopy function and structure may help us to better understand mortality risk thresholds that can be used to forecast climate-related threats to forest health (Maslin 2004, Sperry and Love 2015).

A growing number of studies show that very large-scale (e.g. continental) drying trends and drought events reduce forest canopy photosynthetic activity (Samanta et al. 2010, Zhou et al. 2014, Hilker et al. 2014) and, ultimately, can cause mortality in tropical vegetation (Allen et al. 2010). Particular to our study, we found that precipitation anomalies at landscape scales (that is, 10–100 km apart) are also very important in driving changes in forest structure and functioning, something that, so far, has been challenging to resolve due to the lack of high spatial and temporal resolution observation-based climate data. Furthermore, by utilizing the unique environmental controls offered by Hawaii island while controlling for species turnover (Vitousek 2004), we accounted for potential confounding variables in the analysis of the effects of climate change on vegetation, such as differences in forest canopy species composition.

The mechanisms by which decreasing precipitation results in partial or complete canopy dieback may include both disruption of plant physiology as well as changes in biotic agents (e.g. pathogens and insect populations). To avoid xylem cavitation or hydraulic failure, plants close stomata and reduce productivity when experiencing precipitation anomalies, which may lead to carbon starvation and disorder of cellular metabolism (Martinez-Vilalta et al. 2002). Although this physiological tradeoff helps plants to acclimate to drought events, it eventually results in branch mortality if precipitation decreases for long periods of time (Rood et al. 2000). Moreover, damage to canopy structure caused by insect attacks are also likely to increase with climatic anomalies. This trend is expected because the frequency of insect outbreaks often increases, and the resistance of plants to these attacks decreases, with hotter and drier climatic conditions (Mattson and Haack 1987, Logan et al. 2003).

We recognize some limitations to our study. First, we evaluated temporal changes in canopy structure using a very high spatial resolution data on canopy height from only two periods of time (January 2007, January 2016). There is thus a lack of information on the rate of change in canopy structure over the time, which leaves questions as to whether the decline in canopy volume throughout the study landscapes occurred gradually or episodically. Although we analyze canopy function using MODIS EVI with a very high temporal resolution, the limitation of this dataset rests on its low spatial resolution. The 500 m pixel size of MODIS EVI product makes these data better suited for larger geographic regions. Nonetheless, we contend that our sources of data were sufficient to resolve and quantify changes among contrasting study regions in not only canopy greenness (used as a metric of photosynthetic function), but also forest canopy structure. More subtle changes, should they occur in other parts of

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**Table 1.** Summary of generalized linear models showing the relationship between precipitation anomaly (centennial and decadal anomaly) and canopy properties (photosynthetic anomaly and canopy volumetric change). AIC = Akaike information criterion. $R^2 = \text{square root}.$

| Variable                     | Model                   | $\Delta$AIC | Weight | $R^2$ | Estimate |
|------------------------------|-------------------------|-------------|--------|-------|----------|
| Photosynthetic anomaly       | Centennial precip anomaly$^a$ | 0           | 1      | 0.36  | −0.07    |
|                              | Decadal precip anomaly$^a$    | 643         | 0      | —     | —        |
|                              | Null model$^a$              | 1338        | 0      | —     | —        |
|                              | Centennial precip anomaly$^b$ | 0           | 0.81   | 0.47  | −0.0005  |
|                              | Decadal precip anomaly$^b$    | 3           | 0.19   | —     | —        |
|                              | Null model$^b$              | 76.7        | 0      | —     | —        |

$^a$ We have included in all models mean annual precipitation (average precipitation between 1978–2007) as a covariate factor (fixed effect).
Hawaii island or elsewhere, may be investigated using datasets with higher temporal and spatial resolutions. We believe that caution should be taken when comparing areas with different forest types and precipitation. Although forests located in windward sites may be taller or greener than the ones located in leeward sites, we expected similar responses to temporal changes in precipitation because canopy species composition is similar in both sites. To minimize biases in the analysis, we have completed all comparisons using relative changes in vegetation function and rainfall.

Conclusion

Large-scale damage to forest canopy structure due to climate change remains poorly understood worldwide (Hartmann et al. 2015). We found that long-term precipitation trends are linked to changes in photosynthetic activity and structure of canopies, which likely has cascading effects on numerous ecological processes such as light availability, species interactions, carbon storage, and animal habitat. We also demonstrated the potential of combining active (LiDAR) and multi-temporal passive (MODIS) remote sensing with spatially explicit precipitation data to quantitatively assess the magnitude and rate of canopy structural and functional change in areas undergoing secular changes in climate such as long-term drying.

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