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Fragmentation, forest structure, and topography modulate impacts of drought in a tropical forest landscape

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Abstract. Climate models predict increases in drought conditions in many parts of the tropics. Yet the response of tropical forests to drought remains highly uncertain, especially with regards to the factors that generate spatial heterogeneity in drought response across landscapes. In this study, we used Landsat imagery to assess the impacts of a severe drought in 2015 across an ~80,000-ha landscape in Puerto Rico. Specifically, we asked whether drought effects varied systematically with topography and with forest age, height, and fragmentation. We quantified drought impacts using anomalies of two vegetation indices, the enhanced vegetation index (EVI) and normalized difference water index (NDWI), and fit random forest models of these metrics including slope, aspect, forest age, canopy height, and two indices of fragmentation as predictors. Drought effects were more severe on drier topographic positions, that is, steeper slopes and southwest-facing aspects, and in second-growth forests. Shorter and more fragmented forests were also more strongly affected by drought. We also assessed which factors were associated with stronger recovery from drought. Factors associated with more negative drought anomalies were also associated with more positive postdrought anomalies, suggesting that increased light availability as a result of drought led to high rates of recovery in forests more severely affected by drought. In general, recovery from drought was rapid across the landscape, with postdrought anomalies at or above average across the study area. This suggests that forests in Puerto Rico might be resilient to a single-year drought, though vulnerability to drought varies depending on forest characteristics and landscape position.

Key words: drought; landscape fragmentation; light detection and ranging (LiDAR); Puerto Rico; random forest; remote sensing; second growth; tropical forest.

Introduction

Climate change is expected to cause shifts in precipitation patterns across the tropics, with some regions facing a reduction in annual rainfall as high as 50% along with changes in rainfall seasonality (Neelin et al. 2006, Feng et al. 2013, Knapp et al. 2015, Khalyani et al. 2016). Results from experimental studies in the Amazon have found that tropical forests are highly vulnerable to multiyear drought (Nepstad et al. 2002, 2007, da Costa et al. 2010), and observational studies have shown that even a single-year drought can have a prolonged effect on forest productivity and structure in the Amazon (Asner and Alencar 2010, Saatchi et al. 2013, Doughty et al. 2015). However, some evidence suggests tropical forests are surprisingly resilient to short-term drought and recover biomass quickly (Zuleta et al. 2017). Drought effects in tropical forests are thus highly uncertain—and variable—across individuals, species, and sites. Part of this uncertainty stems from a limited understanding of the factors that mediate spatial heterogeneity in forest responses to drought at the landscape scale (Anderegg et al. 2015, Uriarte et al. 2016*b*).

Topography can generate significant heterogeneity in forest drought response (Daws et al. 2002, Potts 2003, Silva et al. 2013). Moisture varies across slope position (ridges vs. slopes vs. valleys) because of differences in drainage and runoff (Burt and Butcher 1985, Western et al. 1998, Daws et al. 2002) and with slope aspect because of solar radiation (Stephenson 1990). Accordingly, drought-induced mortality is often higher in drier landscape positions (Fekedulegn et al. 2003, Guarín and Taylor 2005), and these differences are also linked to variation in the rate and degree of recovery from drought (Zuleta et al. 2017). Most evidence for the importance of topography in mediating drought response comes from temperate regions (Stephenson

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1990, Fekedulegn et al. 2003, Guarín and Taylor 2005, Paz-Kagan et al. 2017). A small number of studies in tropical forests have found more severe drought impacts in drier topographic positions (Nishimua et al. 2007, Silva et al. 2013, Zuleta et al. 2017), but this finding has not been consistent across studies (Nakagawa et al. 2000). Furthermore, these studies were conducted across relatively small areas (between 1 and 18 plots, spanning 1–9 hectares total area), limiting inference about how topography influences drought effects across landscapes. Assessing drought effects across landscapes with a wide range of topographic variation could help elucidate the relationship between topography and drought effects in tropical forests.

The spatial configuration of forests across many tropical landscapes is patchy, potentially adding further complexity to drought responses of tropical forests. Specifically, forest fragmentation can change environmental conditions and species composition in ways that could influence forests' susceptibility to drought. Forest edges tend to be drier than interiors (Camargo and Kapos 1995, Laurance and Bruce Williamson 2001, Laurance 2004), which could mean that water deficits during drought are more severe, or alternatively, that trees close to forest edges may be better acclimated to dry conditions. However, forest fragmentation also tends to increase the proportion of early-successional species (Laurance et al. 2006), which tend to be more vulnerable to drought. Nineteen percent of tropical forests lie within 100 m from a forest edge (Brinck et al. 2017), so fragmentation could be an important driver of spatial variation in drought response across tropical forests. However, few studies have considered how drought effects vary with fragmentation (but see Laurance et al. 2001).

Drought effects likely vary between second-growth and old-growth forests as well. Over 70% of all remaining tropical forests in the world are second-growth forests growing on former agricultural or logged lands (Food and Agriculture Organization of the United Nations [FAO] 2010). These regenerating forests differ from old growth in composition, size structure, and spatial configuration in the landscape and thus are expected to respond differently to climate extremes (FAO 2010, Anderson-Teixeira et al. 2013, Uriarte et al. 2016*a*, Schwartz et al. 2017). Differences in species composition between old- and second-growth forests suggest that second-growth forests are likely to suffer stronger drought impacts. Early- and mid-successional species that dominate young stands have characteristics that may make them physiologically vulnerable to drought (Phillips et al. 2010, Uriarte et al. 2016*a,b*). For example, low wood density, common in early successional species, has been associated with vulnerability to cavitation under drought conditions (Van Nieuwstadt and Sheil 2005). Several studies have observed an increase in mortality in second-growth forests following reduced rainfall, particularly for early successional species (Slik 2004, Chazdon et al. 2005, Uriarte et al. 2016*b*). However, these early successional species tend to have faster growth rates under high-resource conditions (Grime 1979, Bazzaz and Pickett 1980), meaning they might be better able to take advantage of increased understory light following drought (Slik 2004), and thus recover more quickly.

On the other hand, differences in size structure in old- vs. second-growth forests suggest second-growth forests could be more resilient to drought. In tropical forests, plot-based analyses have shown that bigger trees are generally more susceptible to drought-induced mortality, presumably due to larger trees having greater evaporative demand (Phillips et al. 2010, Silva et al. 2013, Bennet et al. 2015, Uriarte et al. 2016*b*). However, recent work based on remote sensing analyses of large areas has shown that taller forests may exhibit lower sensitivity in their photosynthetic responses to precipitation variability (F. Giardina, A. G. Konings, M. Uriarte, R. S. Oliveira, and P. Gentine, *unpublished manuscript*). Larger trees may also have deeper roots and access deeper water, thus only experiencing moisture shortages when subsurface water dries under more severe drought conditions (Dawson 1996). These studies underscore our limited understanding of how variation in tree height and its effect on drought susceptibility scale up from trees to landscapes, and how differences in species composition and tree canopy height influence drought response in second-growth vs. old-growth forests.

Most studies on drought responses in tropical forests have focused on individual trees or on quantifying overall drought impacts on carbon or biomass at landscape scales (e.g., Asner and Alencar 2010, Phillips et al. 2010). As a result, the environmental factors associated with landscape heterogeneity in drought impacts in the tropics are not well understood (Allen et al. 2010). This limited knowledge illustrates the logistical challenges associated with collecting sufficient field data across patchy, heterogeneous landscapes (Loehle 1991). Remote sensing, with its broad spatial extent and high temporal resolution, can be used to detect patterns that may be unfeasible or impossible in field studies (Chambers et al. 2007). Remote sensing approaches have been used to characterize impacts of drought in forests across large spatial extents in many studies (Chambers et al. 2007, Asner and Alencar 2010, Asner et al. 2011, Anderson et al. 2010, Brouwers et al. 2013, Saatchi et al. 2013, Varhola and Coops 2013, Morton et al. 2014, AghaKouchak et al. 2015, Byer and Jin 2017). Light detection and ranging (LiDAR) –derived data on canopy height are newly available for a small but growing number of tropical forest landscapes. These data—in combination with maps of drought impacts, land-use history, and forest age from satellite remote sensing—could help tease apart how variation in tree height, species composition, and land-use history affect tropical forest responses to drought.

In this study, we use satellite remote sensing to assess how landscape variation in topography and forest characteristics modulate forest response to drought in the

Luquillo Mountains of eastern Puerto Rico. In 2015, the island experienced one of the most severe droughts on record (Fig. 1), providing a unique opportunity to examine drought effects in a tropical forest landscape. We address the following questions:

1) Did drought affect leaf water content and productivity in Puerto Rican forests, as measured from satellite remote sensing indices? Do leaf water content and productivity recover 1 yr after drought, or are there lag effects of drought?
2) What environmental factors and forest characteristics modulate landscape heterogeneity in forest drought response and recovery from drought?

METHODS

Study area

This study was conducted in and around El Yunque National Forest (EYNF) in the Luquillo Mountains of Puerto Rico (Fig. 2). EYNF is a 113-km^2 forest preserve administered by the U.S. Forest Service. Topography in EYNF is variable and slopes can be steep, with elevation ranging from ~100 m above sea level, to the highest peak at 1,065 m above sea level. Mean annual rainfall is 3,500 mm. In 2015, Puerto Rico experienced the second driest year on record: rainfall in El Yunque was only 2,035 mm. However, the drought was short-lived, and in 2016 total rainfall was 3,506 mm (Fig. 1). At lower elevations in EYNF and outside the national forest, there was previously extensive land use, including farming, logging, and charcoal production; today, many of these areas have regenerated and represent a mosaic of forest fragments ranging in age from 20 to 60 yr, interspersed with some pasture lands (García-Montiel and Scatena 1994, Thompson et al. 2002).

Data

Forest cover and characteristics.—Distribution of forest types within EYNF was obtained from the PR-GAP Project (Gould et al. 2007; Fig. 2). Forests are all evergreen and are classified into four main types along increasing elevation: Tabonuco forest up to about 600 m (dominated by *Dacryodes excelsa*), Palo Colorado forest from about 600 to 900 m (dominated by *Cyrilla racemosa*), Sierra palm forest found above 500 m (dominated by *Prestoea acuminata* var. *montana*), and elfin woodland above 900 m (Weaver 1983). Due to high cloud cover at high elevations, and to avoid confounding effects of landscape factors with major differences in vegetation type along the elevation gradient, we limited our study to Tabonuco forest, found between elevations of 150–600 m above sea level. We included all Tabonuco forest within EYNF and a 5-km buffer area around it. Forest cover and age maps were obtained from Kennaway and Helmer (2007). We classified forests under 66 yr old (the maximum known age of second-growth forests) as second-growth forest, and over 66 yr as old-growth forest. We also used these forest maps to characterize fragmentation, namely, patch size and distance from forest edge, using the R package SDMTools (VanDerWal et al. 2014). Mean forest patch size was 14,225 ha (SD = 9,767 ha), and mean distance from edge was 105 m (SD = 113).

Canopy-height data were derived from a high-accuracy LiDAR flyover of Puerto Rico (Fig. 3). LiDAR

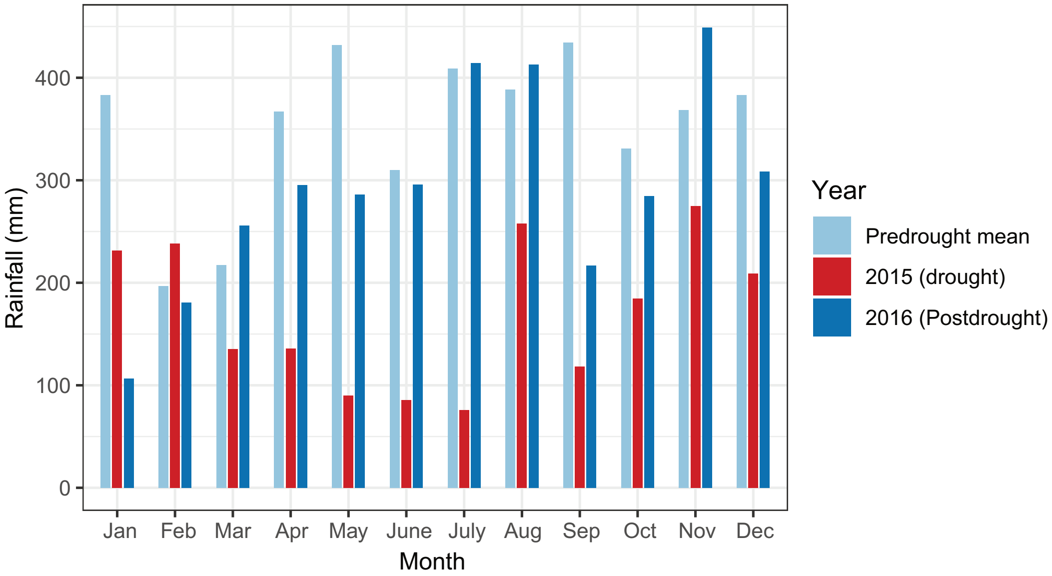

FIG. 1. Monthly rainfall at the El Verde field station. Predrought mean includes data from 2004 to 2014.

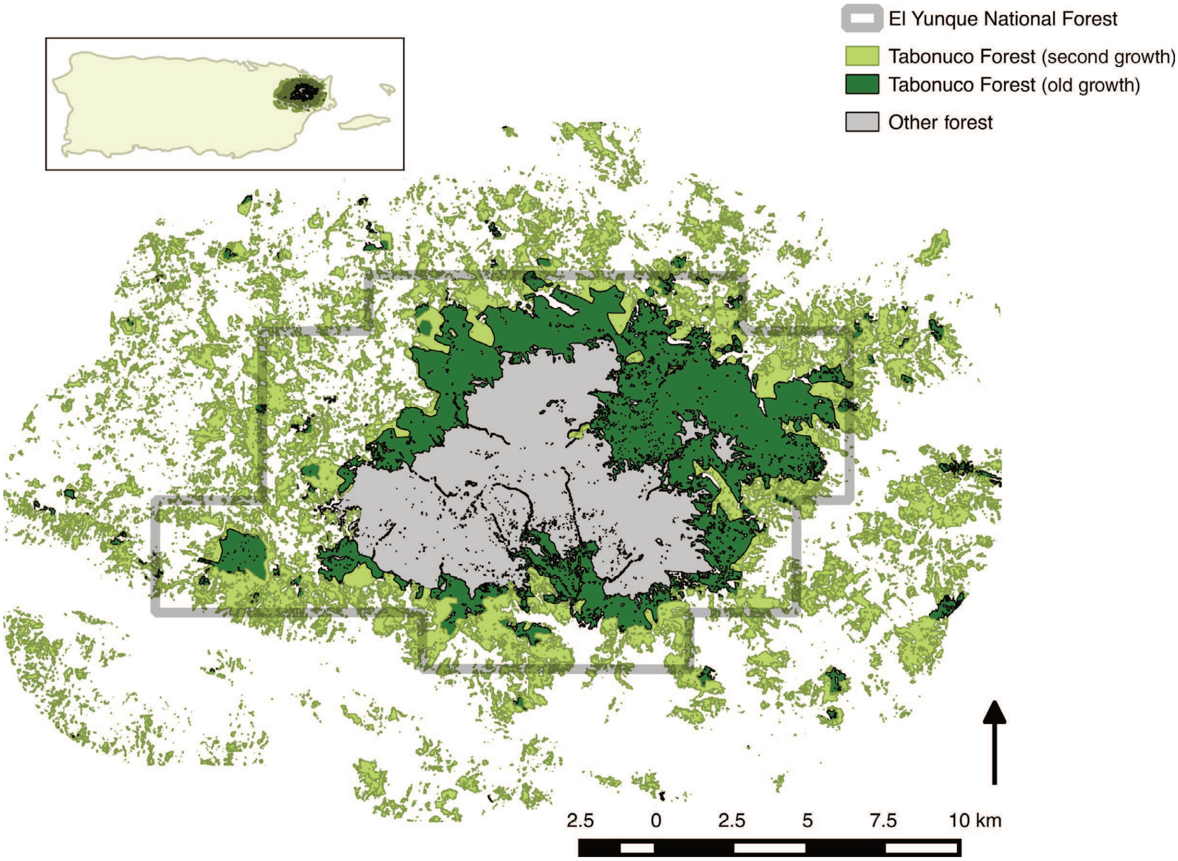

FIG. 2. Study area and its location in Puerto Rico (top left inset). Analyses were restricted to old-growth and second-growth Tabonuco forest.

data were acquired between Jan 2016 and March 2017, and were processed according to USGS 3D Elevation Program (3DEP) specifications (https://nationalmap.gov/3DEP/3dep_about.html). The vertical accuracy of these data based on independent ground control points acquired over vegetated areas is 12.7 cm. Canopy height was resampled to 30 m to match the resolution of the other remotely sensed data sets.

Topography.—Topographic variables were derived from a 30-m digital elevation model (DEM) obtained from the Shuttle Radar Topography Mission (SRTM; Farr et al. 2007). Slope and aspect were derived from the DEM using ArcGIS. Aspect was transformed using the following equation:

$$A_{\mathrm{T}} = -\cos(45 - A) \qquad (1)$$

where A is aspect measured in degrees and A_{T} is transformed aspect. Transformed aspect ranges from -1 to 1, where 1 represents southwest-facing slopes and -1 represents northeast-facing slopes (Pierce et al. 2005). In our study area, transformed aspect is positively correlated with solar radiation (calculated with the Area Solar Radiation tool in ArcGIS; $r = 0.42$, $P < 0.0001$), meaning that southwest-facing slopes have greater solar radiation.

Remote sensing of drought impacts.—We used Landsat 7 ETM+ imagery to assess drought impacts. Many studies of landscape-scale drought impacts use the MODIS satellite, but we chose Landsat imagery because of its comparatively fine (30 m) spatial resolution, which allowed us to assess landscape heterogeneity in drought impacts and matched the scale of the elevation and forest-cover data sets. Furthermore, Landsat data are not subject to large subpixel atmospheric effects, which can influence reflectance and confound detection of drought effects in coarser-resolution data, such as MODIS (Asner and Alencar 2010). All scenes were acquired as surface reflectance with atmospheric corrections precomputed with the LEDAPS algorithm (Schmidt et al. 2013). Clouds and cloud shadows were masked using the Fmask band included in the surface reflectance product (Zhu and Woodcock 2012, Zhu et al. 2015). Images were acquired and processed in Google Earth Engine (Gorelick et al. 2017).

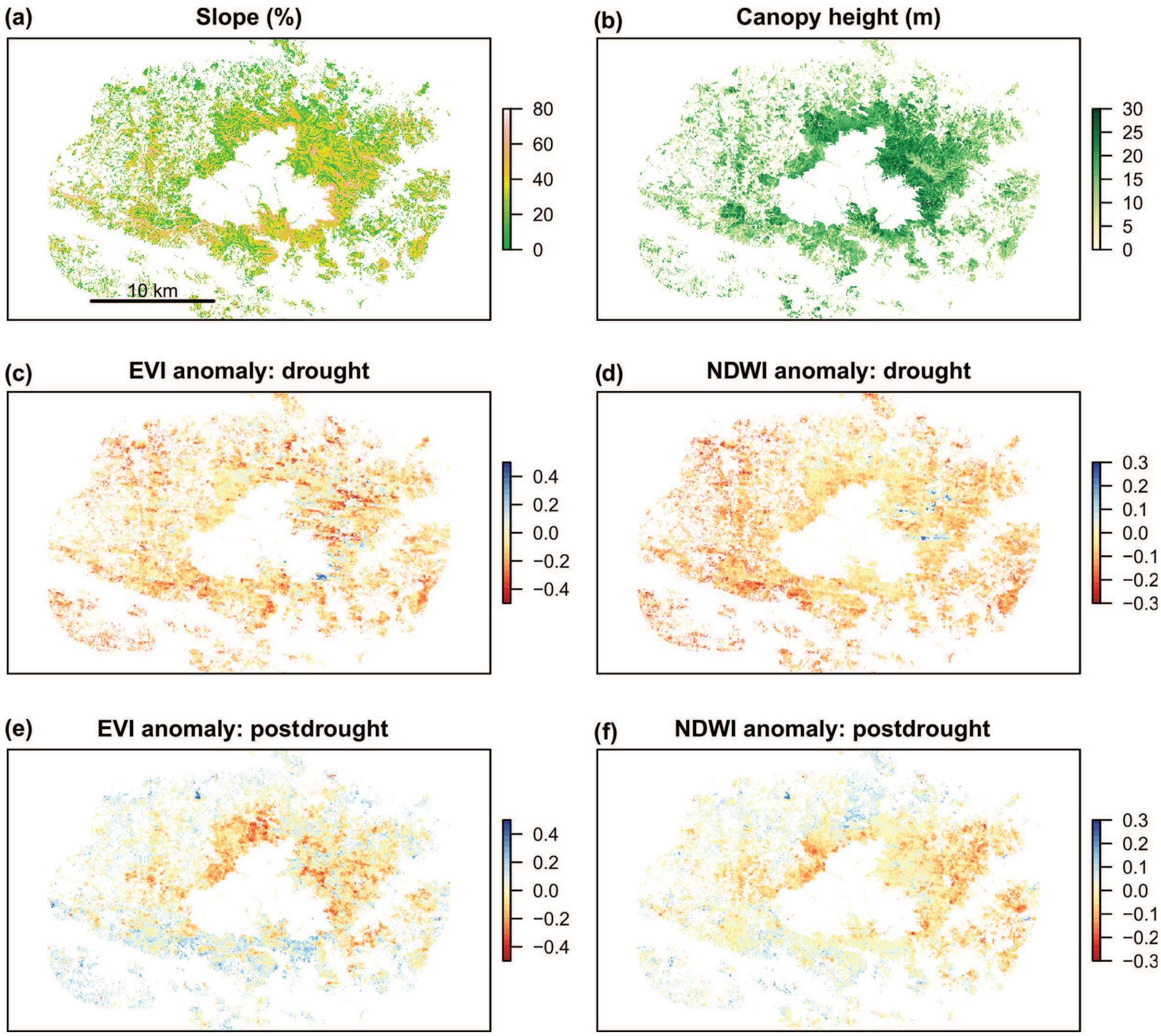

Fig. 3. Maps of (a) slope, (b) canopy height, (c) enhanced vegetation index (EVI) anomalies during drought, (d) normalized difference water index (NDWI) anomalies during drought, (e) EVI anomalies after drought, and (f) NDWI anomalies after drought. White space represents non-Tabonuco forest areas not included in analyses.

To assess the impacts of drought on forests around EYNF, we compared vegetation status during the drought (2015) and the year after the drought (2016) to a reference period (2004–2014). This reference period was selected to be sufficiently long to characterize typical non-drought conditions. Average rainfall during this period was 4,131 mm and ranged from 3,194 to 5,632 mm. Only images collected between April and November were considered to minimize effects of varying sun-sensor geometry (Morton et al. 2014) and because the severity of the drought was highest during these months (Fig. 1). We considered two indices indicative of vegetation status: the enhanced vegetation index (EVI) and the normalized difference water index (NDWI).

Enhanced vegetation index is an index of vegetation condition and is sensitive to canopy chlorophyll content, leaf area index, architecture, and morphology (Huete et al. 2002). EVI was developed as an extension of the normalized difference vegetation index (NDVI), which saturates in high-biomass regions and can be subject to atmospheric influences and soil background effects (Huete et al. 2002). Because of this improved sensitivity in high-biomass areas (Huete et al. 2002, Caccamo et al. 2011), we chose to use EVI rather than NDVI to assess drought effects on vegetation condition. EVI is calculated as

$$\mathrm{EVI} = 2.5 \times ((\mathrm{NIR} - \mathrm{RED})/(\mathrm{NIR} + 6 \times \mathrm{RED} - 7.5 \times \mathrm{BLUE} + 1) \qquad (2)$$

where the NIR is the near-infrared band (band 4, 0.77–0.9 μm), RED is the red band (band 3, 0.63–0.69 μm), and BLUE is the blue band (band 1, 0.45–0.52 μm).

Higher values of EVI indicate higher biomass, photosynthetic rates, and greenness (Huete et al. 2002), and reduced EVI values during drought compared to average are indicative of a reduction in greenness, photosynthesis, or productivity (Caccamo et al. 2011).

Normalized difference water index is indicative of the volume of liquid water in vegetation canopies (Ceccato et al. 2001). Liquid water is more absorptive in the 1.5–2.5 μm and more reflective in the 0.9–1.3 μm range; NDWI is calculated as a normalized difference between reflectance in these wavelengths (Gao 1996). With Landsat 7, NDWI is calculated as

$$\mathrm{NDWI} = (\mathrm{NIR} - \mathrm{SWIR})/(\mathrm{NIR} + \mathrm{SWIR}) \qquad (3)$$

where NIR is the near-infrared band (band 4, 0.77–0.9 μm) and SWIR is the shortwave infrared band (band 5, 1.55–1.75 μm). NDWI values range from −1.0 to 1.0, with more negative values indicating lower leaf water content. NDWI tends to decline during drought (Gao 1996). Furthermore, NDWI is less sensitive than other metrics to atmospheric effects and uses the short-wave infrared band to improve sensitivity to leaf water content (AghaKouchak et al. 2015).

We calculated a long-term mean EVI and NDWI (2000–2014) for each pixel to establish a baseline against which to compare drought effects. There were no severe droughts over this period, nor were there any major hurricanes. When establishing the baseline, we removed any observations >2 standard deviations from the mean observed values for each pixel to minimize the effect of random noise. We calculated anomalies for the drought (2015) and postdrought (2016) years by subtracting the baseline from the pixel mean EVI and NDWI values during those years. These anomalies represent the deviation in the vegetation indices observed during and after the drought compared to reference years in which there were no severe droughts. More negative anomalies indicated reductions in productivity (EVI anomaly) and vegetation water content (NDWI anomaly). A total of 58 images were available from the predrought baseline period (2000–2014), 13 from the drought year (2015), and 14 from the postdrought year (2016). We restricted analyses to pixels for which there were at least 10 cloud-free observations during the baseline period and at least two observations during the both the drought and recovery period; 145,484 pixels met these criteria.

Statistical analysis

Statistical analyses were conducted on a subsample of 15,000 randomly selected pixels. We subsampled in order to facilitate computation and avoid spatial autocorrelation. To assess whether drought effects were observable with EVI and NDWI, we compared mean values of the vegetation indices during the baseline period, the drought year, and the postdrought year using ANOVA and post hoc Tukey tests. To understand the drivers of spatial variability in drought impacts and recovery, we fit random forest models of drought and postdrought anomalies in EVI and NDWI as a function of landscape factors. Random forest is a nonparametric regression tree approach that fits many regression trees from randomized subsets of data and then averages across trees (Breiman 2001). Random forests allow for complex, nonlinear relationships between variables, and in preliminary analyses they explained more variance in our response variables than parametric regression. Random forest also allows calculation of the relative importance of variables as the degree to which predictions are degraded when randomly permuting values for that variable (Breiman 2001). Partial dependence plots show the relationship between each predictor and the response variable, assuming that other predictors are held at their average values (Cutler et al. 2007). Predictors included in random forests were as follows: topography (slope and aspect), a binary variable for old growth (0) vs. second growth (1), canopy height, fragmentation (pixel distance to edge and patch size), and baseline EVI/NDWI. We included baseline EVI/NDWI to assess whether forests that were more productive (higher EVI) or had higher leaf water content (higher NDWI) during average years were more susceptible to drought.

RESULTS

Did drought affect leaf water content and productivity in Puerto Rican forests, and did they recover 1 yr after drought?

Effects of drought were evident in both vegetation indices (Fig. 3; Appendix S1: Fig. S1). EVI during the drought year (mean = 0.72, SD = 0.11) was significantly lower than the baseline (mean = 0.81, SD = 0.08, ANOVA $F = 3{,}360$, $P < 0.00001$), indicating that photosynthetic activity and forest structure were significantly affected by drought (11% mean reduction in EVI). Most pixels had negative EVI anomalies during the drought year (mean anomaly = 0.09, SD = 0.10, Fig. 4). Mean EVI during the postdrought year was equal to the baseline (0.81, SD = 0.14; Appendix S1: Fig. S1), and the average anomaly was 0.001 (SD = 0.11, Fig. 4), indicating a strong recovery after the drought. NDWI was also reduced during the drought year (mean = 0.35, SD = 0.07, compared to baseline mean = 0.42, SD = 0.04, ANOVA $F = 6{,}678$, $P < 0.00001$; Appendix S1: Fig. S1), and most pixels had negative NDWI anomalies during the drought year (mean anomaly = 0.07, SD = 0.05, equal to 17% reduction in NDWI, on average; Fig. 4). NDWI recovered to just below baseline (mean = 0.41, SD = 0.06, mean anomaly = −0.01, SD = 0.06) in the year following the drought.

What environmental factors and forest properties modulate landscape heterogeneity in forest drought response and recovery?

Drought response.—Models of EVI and NDWI drought anomalies explained 20.42% and 19.17% of the variation in drought anomalies, respectively. Though the magnitude and relative importance of the various predictors differed between the model of EVI anomaly and NDWI anomaly (Fig. 5), the directions of the relationships between the predictors and response variables were consistent across models (Fig. 6). EVI and NDWI anomalies were weakly correlated with each other ($r = 0.27$, $P < 0.0001$).

Relative variable importance differed across the EVI and NDWI models. The most important predictor in the model of EVI drought anomalies was reference EVI, and the most important predictor in the model of NDWI drought anomaly was patch size. In both models, canopy height was the second most important predictor, and fragmentation variables (patch size and distance from edge) were more important than topographic predictors and whether the pixel was dominated by second-growth forest. In general, the directions of the relationships between the predictors and response variables were similar in both models of drought anomalies, though the partial dependence plots reveal nonlinear relationships in many cases (Fig. 6). Pixels that had higher baseline EVI or NDWI during the predrought period were more negatively affected by drought, indicating stronger drought effects in areas with high average leaf water content and high average greenness. Canopy height had a positive effect on drought anomalies, indicating that taller forests were less susceptible to drought than shorter stands (Fig. 6). Second-growth forests were more negatively affected by drought in terms of both their EVI and NDWI anomalies (Fig. 4). Landscape configuration influenced drought response, with pixels in bigger patches and further from forest edges having less negative anomalies. Topography influenced the severity of drought effects in both models as well, with pixels on steeper and more southwest-facing slopes having more negative EVI and NDWI anomalies, though these effects were relatively weak.

Recovery.—Models of postdrought anomalies explained 24.14% and 24.51% of the observed variation in EVI and NDWI anomalies, respectively. Relative variable importance differed across models, though the top three predictors—baseline EVI/NDWI, patch size, and distance from edge—were consistent across both models of postdrought anomalies (Fig. 5). Partial dependence plots again revealed nonlinear relationships between the predictors and response variables (Fig. 6). Pixels with higher reference EVI had more positive anomalies after drought, indicated a stronger recovery in areas with higher average productivity. Conversely, pixels with lower average NDWI had lower postdrought anomalies, meaning that areas with higher average leaf water content were slower to recover from drought. The effects of landscape and forest characteristics on drought recovery were opposite their effects in the models of drought response in many cases, indicating that many locations that responded strongly to drought also recovered quickly. Canopy height was negatively associated with postdrought anomaly, indicating that shorter forests, which were more negatively affected by drought, exhibited a stronger recovery, though these responses were not linear. Similarly, second-growth forests also had more positive anomalies after drought than old-growth forests, and most second-growth forest pixels had overall positive anomalies after drought (Fig. 4), meaning second-growth forests were more productive and had higher vegetation water content during the year after the drought than during the baseline period. The partial dependence plots of patch size and distance to edge

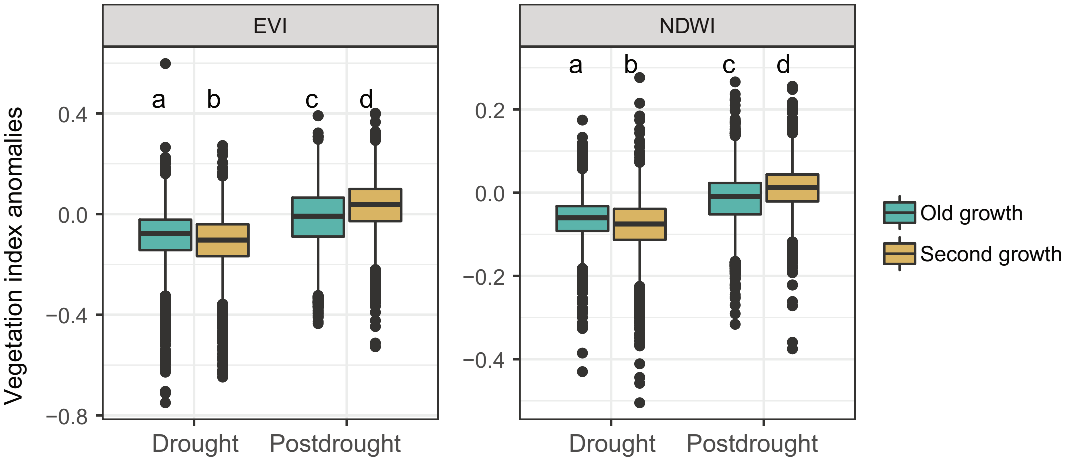

Fig. 4. Distribution of enhanced vegetation index (EVI) and normalized difference water index (NDWI) anomalies in old-growth vs. second-growth Tabonuco forest during the predrought baseline, the drought year, and the postdrought year.

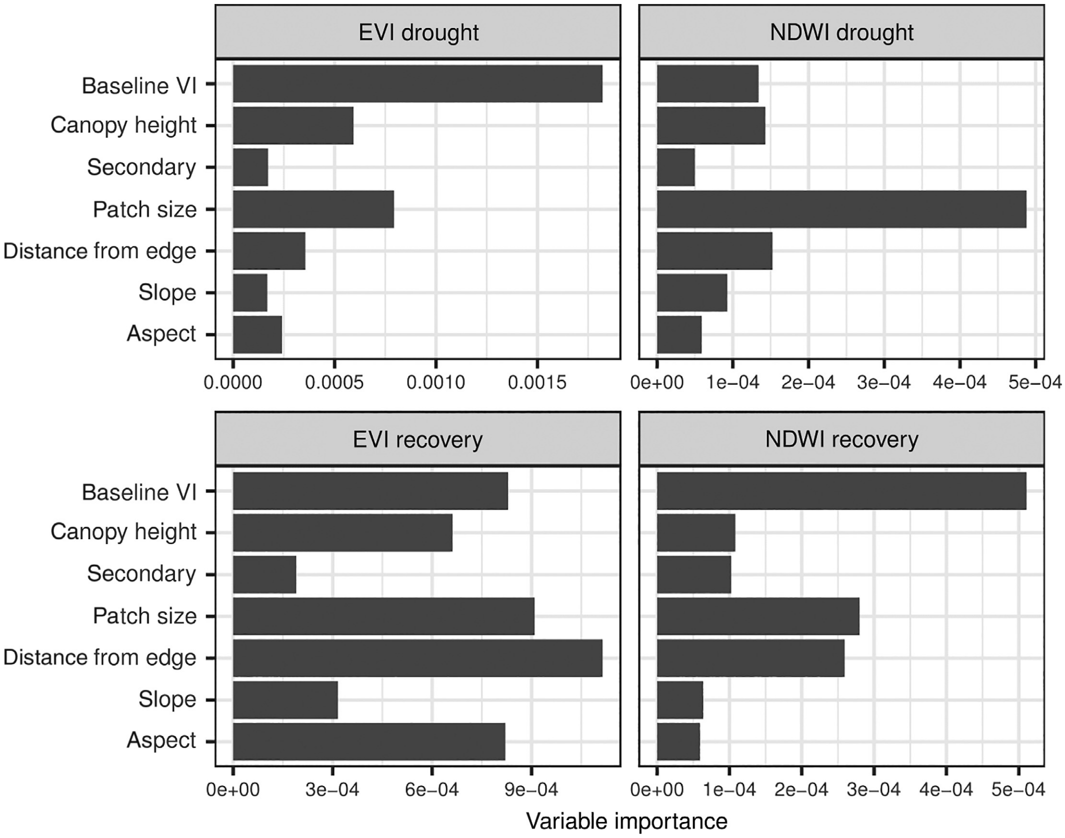

FIG. 5. Variable importance of predictors from random forest models of enhanced vegetation index (EVI) and normalized difference water index (NDWI) anomalies during drought and during the postdrought recovery period.

indicate that more fragmented pixels (in smaller patches and closer to edges) had more positive postdrought anomalies, with the exception of the effect of patch size on NDWI anomaly. Slope had a weak, negative effect on drought recovery. In the model of EVI, aspect was an important predictor of recovery, and the partial dependence plots indicate that pixels on more southwest-oriented slopes had more positive postdrought anomalies, indicating stronger recovery in terms of EVI.

DISCUSSION

Despite model agreement that the Caribbean region will get drier (Neelin et al. 2006, Khalyani et al. 2016, Herrera and Ault 2017), few studies have considered how drought affects Caribbean forests (but see Burrowes et al. 2004, Reyer et al. 2017, Yu et al. 2017). Furthermore, most studies of drought in tropical forest have not considered how drought effects vary across heterogeneous landscapes, though most tropical forests are fragmented (Brinck et al. 2017) and regenerating from anthropogenic disturbance (FAO 2010). In this study, we used satellite remote sensing to address these gaps, quantifying drought impacts on Puerto Rican forests, and assessing how these impacts varied with forest age, topography, and fragmentation. We found that (1) productivity and leaf water content (EVI and NDWI) in Puerto Rican forests are sensitive to drought, (2) these indices quickly recovered to predrought values within a year after drought, and (3) forests that are fragmented, young, and on dry topographic positions were more sensitive to drought, but also exhibited higher EVI and NDWI after the drought, suggesting stronger recovery.

Drought effects and recovery

Reductions in EVI and NDWI reflect different dimensions of the effects of drought on vegetation (Gao 1996): EVI is linked to vegetation condition and photosynthetic activity (Huete et al. 2002), and NDWI is more strongly related to the liquid water content of canopies (Gao 1996). Although some studies have found that EVI and NDWI decline during drought (Xu et al. 2011), others have observed increases in EVI under dry conditions, presumably because of higher light availability or leaf flushing that occurs during drier periods (Anderson et al. 2010, Asner and Alencar 2010). The 2015 drought in Puerto Rico reduced both EVI and NDWI, but the reduction in NDWI was of greater relative magnitude. This finding, along with the relatively weak correlation

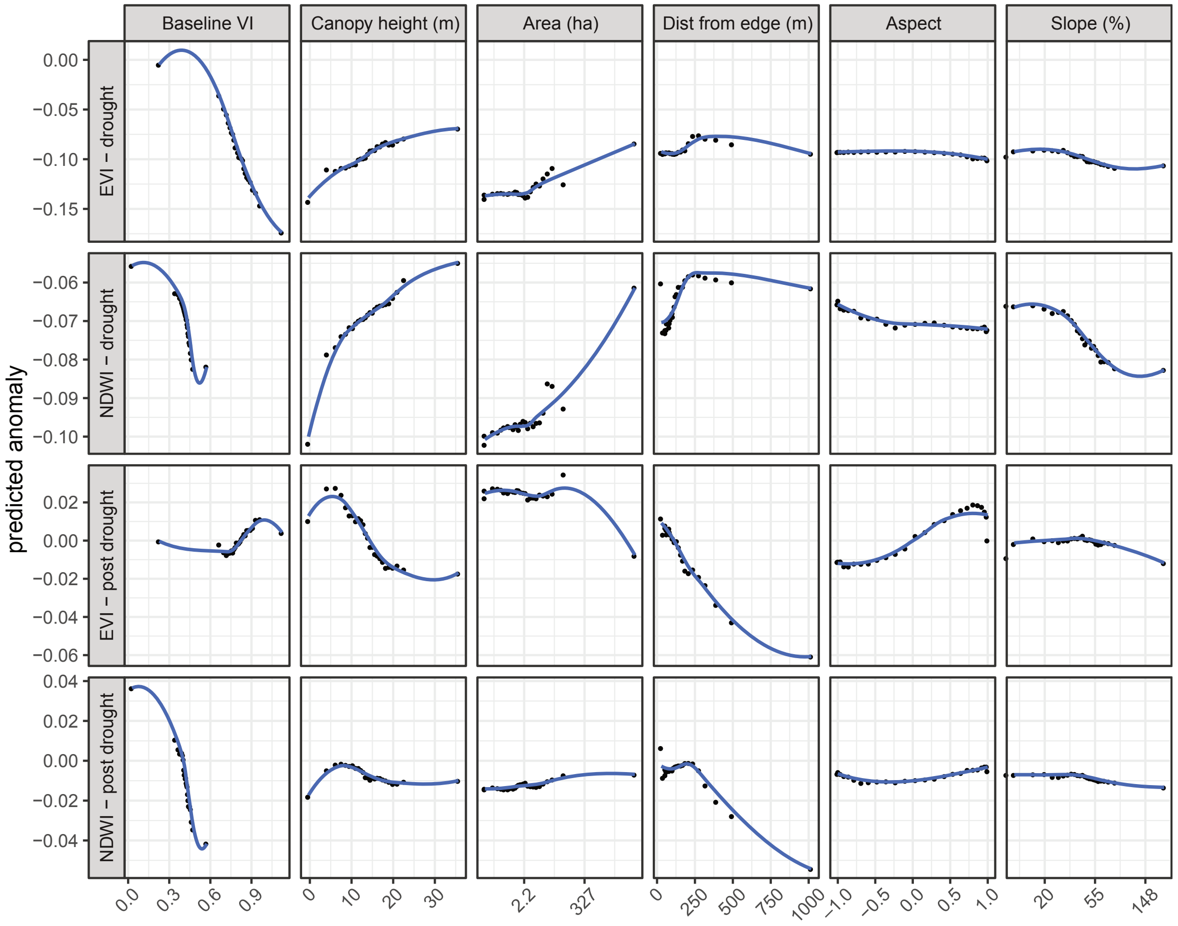

FIG. 6. Partial dependence plots for the continuous variables from each random forest model, identified as row titles. The *y* axis represents predicted values for vegetation index (enhanced vegetation index [EVI] and normalized difference water index [NDWI]) anomalies for each predictor, identified in column headers, assuming all other predictors are held at their mean values. Note that the *x* axes for area and slope are on log scales.

between EVI and NDWI anomaly (Appendix S1: Table S1) suggest that loss of canopy water and decline in photosynthesis are not necessarily coupled at the landscape scale. Species differ in their photosynthetic response to leaf water deficit depending on stomatal response and water-use efficiency (Hsiao and Acevedo 1974, Cornic and Massacci 1996). These disparities may scale up to the landscape level because of variation in species composition across sites, highlighting the need to consider multiple remote-sensing indices of drought effects on vegetation to get a comprehensive picture of how drought affects vegetation (AghaKouchak et al. 2015).

Because extensive ground data on mortality or other drought impacts are not available, we cannot conclude with any certainty whether the reductions in EVI and NDWI during the drought year translated into mortality, biomass loss, or major changes in canopy structure. However, we found that EVI and NDWI rapidly recovered to predrought levels, suggesting that at the landscape scale, drought effects were not long lasting. N. B. Schwartz, M. Uriarte, X. Feng, R. Muscarella, N. G. Swenson, M. N. Umaña, and J. Zimmerman (*unpublished data*) detected a strong effect of the 2015 drought on individual tree growth but no mortality effect in four forest plots in EYNF. In experimental and observational studies in other tropical forests, drought effects on mortality have varied. Some studies have observed significant increases in mortality after just 1 yr of drought (Slik 2004, Phillips et al. 2009, Lewis et al. 2011, Doughty et al. 2015, Uriarte et al. 2016*b*), whereas in others there was no increase in mortality in a single year of drought (Nepstad et al. 2007, da Costa et al. 2010). Our findings, along with the limited ground data available from EYNF, suggest that Puerto Rican forests may be resilient to a single-year drought, despite a nearly 50% reduction in rainfall. However, a stronger or more prolonged drought could have more detrimental effects. Observations under more severe drought conditions is necessary to understand Puerto Rican forests' responses to drought fully.

Landscape heterogeneity in drought response and recovery

Consistent with studies in temperate landscapes (Fekedulegn et al. 2003, Guarín and Taylor 2005, Paz-Kagan et al. 2017), we found that landscape and forest characteristics contribute to spatial heterogeneity in drought response. Tree species with acquisitive strategies can take up water quickly and maintain high metabolic rates under wet conditions, but they may suffer more during drought compared to conservative species that maintain lower rates but have higher stress tolerance (Reich 2014). Although we limited our analysis to the zone where Tabonuco forest dominates, there are still significant differences in species composition across the landscape that reflect land-use history (Thompson et al. 2002). These differences may explain why higher baseline EVI and NDWI were associated with more severe drought anomalies: higher baseline EVI may be indicative of a higher abundance of species with more acquisitive strategies. The stronger recovery (i.e., more positive post-drought anomalies) in places with higher baseline EVI lends support to this hypothesis: surviving individuals of fast-growing species could more rapidly take up and use water once rainfall returned to normal. Differences in species composition likely also explain why second-growth forests were more strongly affected by drought than old-growth forests, and showed a stronger recovery. Second-growth forests are dominated by pioneer and secondary forest species, which grow quickly under favorable conditions, but tend to have characteristics that make them more vulnerable to drought (Nicotra et al. 1999, Hasselquist et al. 2010, Lebrija-Trejos et al. 2011, Uriarte et al. 2016*a,b*). Despite recent advances in mapping plant functional traits (Asner et al. 2014, 2015, 2017), we still lack information on how this variation scales up to differences in vegetation indices and response to disturbance, which are important avenues for future research.

A large body of evidence suggests that large trees in the tropics experience greater mortality during drought (Nepstad et al. 2007, da Costa et al. 2010, Phillips et al. 2010), and so, we expected that forests with taller canopies would have exhibited more negative anomalies during the 2015 drought. Instead, we found the opposite—that taller forests were less sensitive to drought. Larger trees appear to be more vulnerable to mortality due to hydraulic failure under extremely dry conditions, but this difference does not correspond to a stronger growth response to drought among large trees (Rowland et al. 2015). Instead, photosynthesis of taller forests in the tropics might be less sensitive to interannual variability in precipitation, perhaps because of deeper roots that buffer the effects of reduced precipitation (F. Giardina, A. G. Konings, M. Uriarte, R. S. Oliveira, and P. Gentine, *unpublished manuscript*). The drought we consider here does not appear to have caused extensive tree mortality and instead seems to have affected forests mostly through a reduction in productivity, growth, and leaf water content, thus explaining why tall forests were not more severely affected by drought.

Despite the ubiquity of fragmentation in the world’s forests (Haddad et al. 2015), few studies have considered if and how drought effects differ in fragmented forests. Laurance et al. (2001) compared drought-related mortality rates in Amazon forest edge vs. interior, but found no difference between the two habitats. In this study, we found that pixels closer to forest edges and in smaller patches had more negative drought anomalies. Edge effects on microclimate could explain these differences, though the relationship between forest edges and moisture conditions are highly variable across studies (Camargo and Kapos 1995, Murcia 1995). Alternatively, differences in species composition at edges and in small patches compared to interior forests could explain this result; early successional species tend to increase in abundance at forest edges (Laurance et al. 2006), and these species tend to be more susceptible to drought.

Surprisingly, the effect of topography on drought response was less important than the effects of the other variables considered. Moisture availability varies depending on insolation, runoff, and soil conditions, all of which are linked to topography (Stephenson 1990), and so, we expected strong relationships between slope and aspect and drought response. We found drought effects were more severe on steeper slopes and more southwest-facing aspects, corresponding with our expectations that drought effects would be more pronounced on topographic positions we generally expect to suffer more severe moisture deficits (Guarín and Taylor 2005, Gitlin et al. 2006, Nishimua et al. 2007). Our finding of more severe drought effects on more southwest-facing aspects is consistent with effects of aspect at higher latitudes (Guarín and Taylor 2005, Gitlin et al. 2006); few studies have tested for such effects in tropical forests. The differences in drought response we observed across aspects were likely due to differences in solar radiation, which is correlated with aspect, but could also be linked to differences in moisture-bearing trade winds that arrive from the northeast and release moisture on north-facing slopes in Puerto Rico (Daly et al. 2003); trees growing in these wetter areas may be more susceptible to drought. However, the relationships between drought effects and topography were not particularly strong, and slope and aspect were generally among the least important variables in our random forest models. This may be driven by differences in species composition across topography, such that species that tend to occur on steeper slopes are less sensitive to dry conditions. These results suggest that effects of fragmentation on species composition and microenvironmental conditions outweigh those of topography.

Nonlinear relationships observed in the partial dependence plots (Fig. 6) suggest thresholds in drought response to landscape factors. For example, drought response appears relatively constant on shallower slopes <20%, but anomalies quickly decline as slope increases beyond 20%. This effect may be due to nonlinear variation in soil properties, such as soil depth, along slopes. We also observe thresholds with patch size, in which drought effects are strong for very small patches, but begin to weaken after patch size increases beyond a threshold of about 2 ha. Threshold effects of forest fragmentation have been observed in many studies, though scales differ (Fahrig 2003). This effect may be driven in part by greater edge/interior ratios in smaller patches. Drought anomalies displayed strong responses to distance from edge at less than 250 m from the forest edge, but were less sensitive to edges beyond that distance. The scale of edge effects on ecological processes has been long debated, and ranges from <50 m to five or more kilometers (Laurance 2000, Ewers and Didham 2008). These edge effects may reflect abiotic conditions near edges or shifts in species composition with distance to edge.

Drought increases light availability to the understory (Delissio and Primack 2003, Slik 2004, Brando et al. 2008). This increase likely explains why, with a few exceptions, most predictors that were associated with more negative anomalies during drought were associated with more positive anomalies during the year after the drought. Higher light availability likely resulted in higher growth rates and recruitment, as has been observed after drought in other studies (Slik 2004). Many species in EYNF are light limited (Uriarte et al. 2018). Higher than average EVI and NDWI after drought does not necessarily indicate that all effects of drought disappeared after a year; drought can have long-lasting effects on forest structure that are not detectable with these vegetation indices alone (Saatchi et al. 2013). High understory photosynthetic rates can lead to observations of postdrought vegetation index values similar to predrought values, without being indicative of recovery of overstory vegetation (Breshears et al. 2005, McDowell et al. 2015). Further investigation with remote sensing techniques that shed more light on forest structure and species composition, including hyperspectral or microwave remote sensing, would provide more conclusive evidence about the effects of drought on vegetation structure.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2677/suppinfo