






Increased mortality of tropical tree seedlings during the extreme 2015–16 El Niño

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Abstract

As extreme climate events are predicted to become more frequent because of global climate change, understanding their impacts on natural systems is crucial. Tropical forests are vulnerable to droughts associated with extreme El Niño events. However, little is known about how tropical seedling communities respond to El Niño-related droughts, even though patterns of seedling survival shape future forest structure and diversity. Using long-term data from eight tropical moist forests spanning a rainfall gradient in central Panama, we show that community-wide seedling mortality increased by 11% during the extreme 2015–16 El Niño, with mortality increasing most in drought-sensitive species and in wetter forests. These results indicate that severe El Niño-related droughts influence understory dynamics in tropical forests, with effects varying both within and across sites. Our findings suggest that predicted increases in the frequency of extreme El Niño events will alter tropical plant communities through their effects on early life stages.

KEYWORDS

climate change, drought, forest dynamics, Panama, rainfall gradient, tropics

1 | INTRODUCTION

Extreme climatic events, such as droughts associated with the El Niño–Southern Oscillation cycle, are predicted to become more frequent over the next century (Cai et al., 2014; Wang et al., 2019). Because the El Niño–Southern Oscillation is the largest source of interannual variation in global climate, there is a critical need to understand the impacts on both human (Iizumi et al., 2014) and

natural systems (McPhaden et al., 2006). The 2015–16 El Niño was the “first extreme El Niño of the 21st century” (Santoso et al., 2017) and one of the strongest in recorded history (Figure 1a). During the 2015–16 El Niño, many tropical regions experienced unprecedented climate conditions with severe droughts, which were intensified by anthropogenic warming trends (Jiménez-Muñoz et al., 2016; Rifai et al., 2019; Santoso et al., 2017; Spinoni et al., 2019). Tropical forests are among the most important

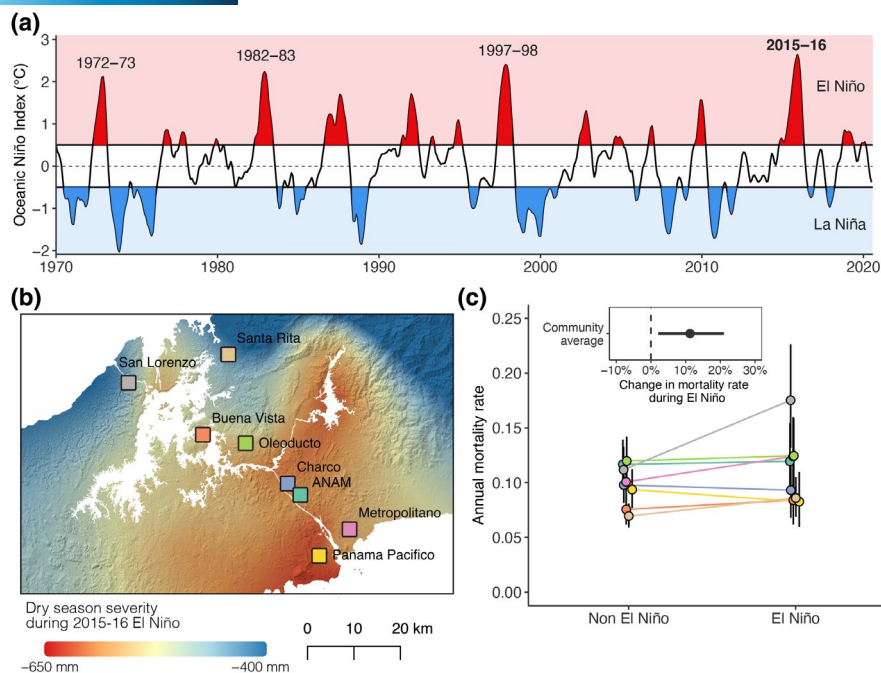


FIGURE 1 Impact of the extreme 2015–16 El Niño across the Isthmus of Panama. (a) Oceanic Niño Index (ONI) from 1970–2020 showing that the 2015–16 El Niño was among the strongest in modern history. El Niño events (red) occur when ONI $\geq 0.5^{\circ}\text{C}$, La Niña events (blue) when ONI $\leq -0.5^{\circ}\text{C}$, and neutral phases occur at values in between. (b) Dry season severity (mm, cumulative rainfall deficit) during the 2015–16 El Niño across the Isthmus of Panama. Rectangles indicate the eight 1 ha forest plots used in this study spanning a strong rainfall gradient. (c) Community-wide annual seedling mortality rates in each forest plot for an average non-El Niño year and in the census interval covering the 2015–16 El Niño. Forests are labeled with the same colors as in panel b. The inset shows the overall community-wide change in mortality rate during the El Niño census interval averaged across all seedlings and all sites. Circles indicate median values along with 95% credible intervals

ecosystems for primary productivity, carbon cycling, and biodiversity (Beer et al., 2010; Bonan, 2008; Fine et al., 2009), yet the impacts of extreme El Niño events on tropical forest dynamics remain uncertain (Bonal et al., 2016).

El Niño-induced droughts generally lead to increased tree mortality in tropical forests (Bonal et al., 2016; Condit et al., 1995; Nakagawa et al., 2000; Slik, 2004; Williamson et al., 2000). When combined with other consequences, such as reduced growth and photosynthesis, extreme El Niño events can dramatically alter ecosystem function and carbon cycling (Brodribb et al., 2020; Liu et al., 2017; Rifai et al., 2018; Wigneron et al., 2020). Increased frequency of severe El Niño-related droughts may also lead to shifts in taxonomic and functional composition of tropical tree communities, as has been documented in response to long-term drying trends in some tropical regions (Aguirre-Gutiérrez et al., 2020; Fauset et al., 2012). Uncertainty surrounding the drivers of variation in mortality among species and forests following drought is a key obstacle to predicting the impacts of future extreme climates on tropical forests (Corlett, 2016; McDowell et al., 2018). In particular, relatively little is known about how communities of tropical forest seedlings respond to extreme drought (Bunker & Carson, 2005; Comita & Engelbrecht, 2014; Engelbrecht et al., 2002; Gilbert et al., 2001). Although drought-related mortality typically increases with tree size in larger trees (Bennett et al., 2015), understanding how drought

events affect seedlings and saplings in the understory is critical because dynamics at juvenile life stages shape the future diversity and structure of tropical forests.

Species vary widely in functional traits and life history strategies that allow them to avoid or tolerate the negative consequences of drought (Comita & Engelbrecht, 2014; O'Brien et al., 2017; Santiago et al., 2016). Many tropical forests experience a strong annual dry season that selects for traits related to drought resistance and filters drought-sensitive species from the community, which can then impact the distribution of species across moisture gradients at regional scales (Condit et al., 2013; Engelbrecht et al., 2007). Three hypotheses have been proposed to explain how species may respond to extreme drought such as those associated with El Niño events. First, species affiliated with dry forests may be able to withstand the potential negative impacts of extreme drought due to their higher drought resistance, whereas species affiliated with wetter forests are more likely to be drought-sensitive and thus especially vulnerable (Pulla et al., 2015). Alternatively, species affiliated with drier forests may already be near their climatic limits, where an extreme drought would push them beyond the range of conditions they can tolerate and lead to higher mortality (Anderegg et al., 2019; Carnicer et al., 2011). A third possibility is that all species extend to their climatic limits and show similar increases in mortality in response to extreme drought (Choat et al., 2012).

The high diversity of species in tropical forests has made it challenging to assess these hypotheses of responses to extreme droughts for many species.

At the community level (i.e., assemblages of multiple species of a similar size class), the response of entire forests to extreme drought depends in part on species composition and long-term climatic factors (Allen et al., 2015; Phillips et al., 2010; Sousa et al., 2020). Because of selection and environmental filtering during the annual dry season, dry forest communities may be dominated by drought-resistant species that could buffer or amplify the response of dry forests to extreme droughts, depending on if species are near their climatic limits (see above). The impacts of an extreme drought may also depend on the strength of its anomaly compared with the long-term mean conditions experienced by a forest (Phillips et al., 2010). A strong drought anomaly in either a wet or dry forest may increase the probability that species are pushed past their climatic limits, leading to higher mortality. Resolving how both species and communities distributed across environmental gradients respond to severe drought is critical for understanding the regional impacts of climate change and identifying species and forests that are particularly vulnerable to extreme drought.

In this study, we analyzed a multiyear demographic data set of tropical seedling plots that span a rainfall gradient across the Isthmus of Panama and include measurements made during the 2015–16 El Niño (Figure 1b), which was associated with the most severe drought in Panama's recent history (Spinoni et al., 2019). We addressed the following questions: (1) Overall, what was the impact of the extreme 2015–16 El Niño on seedling mortality in this region? (2) At the species level, are differences in mortality response to the 2015–16 El Niño explained by indices of species' drought resistance? (3) At the community level, did the 2015–16 El Niño have differential impacts on seedling mortality at drier versus wetter sites along the rainfall gradient?

2 | MATERIALS AND METHODS

2.1 | Study area and seedling censuses

We censused seedling communities in eight 1-ha plots across the Isthmus of Panama, spanning a 65-km rainfall gradient with mean annual precipitation ranging from approximately 3200 mm on the northern Atlantic side to 1600 mm on the southern Pacific side (Condit et al., 2013; Figure 1b; Table S1). Despite this wide variation in rainfall and differences in tree species composition, all forests along this gradient are classified as seasonal moist tropical forest. Within each 1-ha plot, we established 400 1 m² seedling plots in October 2013, where all seedlings ≥200 mm in height and <1 cm DBH (diameter at 1.3 m above ground) were individually tagged and measured following the protocols of Comita et al. (2007). We re-censused seedling plots annually between November and February, that is, toward the beginning of the annual dry season, and new seedlings that met the size criteria were entered into the census.

Because of limited site access, Panamá Pacífico was not censused in 2018, and Oleoducto was not censused in either 2019 or 2020.

2.2 | Overall mortality response to El Niño

We quantified the El Niño mortality response as the difference between mortality rates in the census interval including the 2015–16 El Niño compared with the average mortality rates of the remaining non-El Niño census intervals. To that end, we analyzed all seedling observations that met the following criteria: (1) known survival status; (2) known height in the prior census ≥200 and ≤1300 mm; (3) identified to species level ($n = 428$ individuals removed for lack of species identification); and (4) <2-year interval between census observations ($n = 53$ observations removed). Our full data set consisted of 28,972 observations of 9966 individuals from 457 species.

To model overall and site-specific mortality response to the 2015–16 El Niño, we used a hierarchical logistic regression model, fit using Bayesian methods in Stan (Carpenter et al., 2017) using the “rstan” package v.2.21.2 (Stan Development Team, 2020). The model took the following form:

$$\text{Mortality} \sim \text{Bernoulli}(\hat{y}_i^{\text{time}}),$$

$$\text{logit}(\hat{y}_i) \sim \alpha_{\text{overall}} + \alpha_{\text{species}_{\text{spp}}} + \alpha_{\text{census.site}_{\text{c,s}}} + \alpha_{\text{plot}_p} + \beta_1 \cdot \text{InitialHeight}_i,$$

$$\alpha_{\text{species}_{\text{spp}}} \sim \text{Normal}(0, \sigma^2),$$

$$\alpha_{\text{census.site}_{\text{c,s}}} \sim \text{Normal}(0, \sigma^2),$$

$$\alpha_{\text{plot}_p} \sim \text{Normal}(0, \sigma^2),$$

where α_{overall} represented the overall estimated mean mortality across all individuals, α_{species} was a species level random intercept for species spp, $\alpha_{\text{census.site}_{\text{c,s}}}$ was a random intercept estimated separately for each census, c, and site, s, combination, α_{plot_p} was a plot level random intercept for each 1 m² seedling plot p, and β_1 estimated the effect of seedling height on mortality for census observation i . The probability of mortality was scaled to an annual rate based on the time since last census, time. From this model, we estimated community-wide impacts of the 2015–16 El Niño on mortality as a derived parameter where for each site, s, the El Niño mortality response was the difference between the mortality estimate in the census interval including the El Niño compared with the average mortality estimates of the remaining non-El Niño census intervals:

$$\text{NinoMortResponse}_s = \alpha_{\text{census.site}_{\text{NinoYear}_s}} - \text{mean}(\alpha_{\text{census.site}_{\text{NonNinoYear}_s}}).$$

We estimated the overall community-wide mortality response as the average of the site-level mortality responses:

$$\text{NinoMortResponse}_{\text{overall}} = \text{mean}(\text{NinoMortResponse}_s).$$

2.3 | El Niño and dry season severity

We used dry season severity, defined as the most extreme cumulative rainfall deficit reached in the dry season, as our primary metric to quantify the intensity of each dry season at each site. Following the methods of Condit et al. (2013), the most extreme cumulative deficit (referred to as dry season moisture availability in Condit et al., 2013) was determined based on the lowest value resulting from rainfall minus potential evapotranspiration (PET) between all potential pairs of days between September 1 and July 1 the following year, which encompasses the December-to-May dry season, following the formula:

$$D_{ij} = \sum_{t=i}^j (P_t - PET_t),$$

where P_t is the rainfall and PET_t is the potential evapotranspiration on day t . Because PET typically exceeds rainfall during the dry season, dry season severity is a negative number, with lower (i.e., more negative) values indicating more severe dry seasons.

To approximate the dry season severity at each plot from the weather station data, we used spatial interpolation using the “spatialProcess” function in the “fields” R package (Nychka et al., 2017) with default values. This produced kriged surfaces (Figure 1b), where we extracted estimated dry season severity estimates for the study plots.

We excluded rainfall data from calculations for a given weather station if more than 5% of daily rainfall data was missing for a given dry season. For estimates of PET, we used daily data from a weather station located on Barro Colorado Island, which is near our Buena Vista study site (Paton, 2019). We adjusted PET so that there was a 0.1 mm decrease in daily PET per 100 m increase in elevation following Condit et al. (2013) and Thornthwaite (1948).

To predict site-by-site variation in El Niño response, we estimated three separate metrics of dry season severity: (1) long-term dry season severity; (2) dry season severity during the 2015–16 El Niño; and (3) the dry season severity anomaly of the 2015–16 El Niño. First, we estimated long-term yearly average dry season severity based on available data from 1961 to 1990 from 27 weather stations (data sets provided by the Meteorological and Hydrological Branch of the Panama Canal Authority and by the Physical Monitoring Program of the Smithsonian Tropical Research Institute; Figure S1). We chose 1961–1990 as the baseline for estimating long-term averages as this time frame maximizes the availability of data from the weather stations while avoiding recent changes in rainfall due to contemporary changes in climate. Because daily PET was not available prior to 1994, to calculate long-term yearly dry season severity, we calculated the average PET for each day of the year using available data from 1994 to 2018 and then calculated a 7-day rolling average of these daily PET values to minimize measurement noise (Figure S2). Second, we estimated dry season severity during the 2015–16 El Niño dry season using rainfall data from 51 weather stations (Figure S1). The dry season severity estimates were strongly correlated with

field measurements of gravimetric soil water content at our plots during the 2015–16 El Niño (Figure S3). Finally, we estimated the anomaly of the dry season severity during the 2015–16 El Niño dry season as the absolute difference between the dry season severity during the 2015–16 El Niño and the 1961–1990 long-term average. Across sites, the dry season severity metrics were moderately to strongly correlated with each other (Figure S1), with the long-term dry season severity estimate being most strongly correlated with dry season severity during the 2015–16 El Niño (Pearson's $R = 0.98$, $p < 0.001$). Data on the Oceanic Niño Index used in Figure 1 was obtained from NOAA (2020).

2.4 | Site-level mortality response to El Niño related to dry season severity

To test how seedling mortality response across forests was related to the three metrics of dry season severity, we added a hierarchical component to the mortality model described above where the site-level mortality response to El Niño was a linear function of either (1) long-term dry season severity; (2) dry season severity during the 2015–16 El Niño; or (3) dry season severity anomaly of the 2015–16 El Niño. The three dry season severity metrics were fit independently from each other but simultaneously with the mortality model. Thus, variation across iterations in the estimation of the derived parameter of site-level mortality response to El Niño ($\text{NinoMortResponse}_s$) was propagated into the estimation of the relationship between the dry season severity metrics and El Niño response. The models took the form:

$$\text{NinoMortResponse}_s \sim \alpha_{\text{longterm}} + \beta_2 \cdot \text{LongtermDSS}_s,$$

$$\text{NinoMortResponse}_s \sim \alpha_{\text{nino}} + \beta_3 \cdot \text{NinoDSS}_s,$$

$$\text{NinoMortResponse}_s \sim \alpha_{\text{anomaly}} + \beta_4 \cdot \text{AnomalyDSS}_s.$$

We then compared the ability of each of these three models to predict forest-level mortality response using the widely applicable information criterion (WAIC) in the “loo” R package (Vehtari et al., 2017; Watanabe & Opper, 2010). WAIC is a generalized version of AIC that is useful for comparing Bayesian models. We found that using field measurements of gravimetric soil water content during the 2015–16 El Niño to predict site-level mortality response produced similar patterns as our estimated metrics of dry season severity (Figure S4).

Unless otherwise stated, we used weakly informative priors of Normal (0, 1) for variance parameters and Student_t (5, 0, 2.5) for coefficients following the Stan prior choice recommendations (Stan Development Team, 2017). We placed a stronger prior of Normal (0.2, 0.05) on the variance parameter for the hierarchical component linking the different metrics of dry season severity to site-level mortality response to ensure that the model converged without divergences because any divergence indicates an issue with

model estimation (Stan Development Team, 2020). Qualitative results when using a weakly informative prior were not different than when using a stronger prior (Table S2). To sample the posterior, we ran four independent chains for a total of 10,000 iterations, with 5000 iterations used as warmup (aka “burn-in”). We assessed chain convergence by ensuring that the potential scale reduction factor statistic (“rhat”) was <1.1 for all model runs (Kéry, 2010). We also ensured that there were no divergent transitions for any model run (Stan Development Team, 2020). For each model, seedling height was log-transformed and normalized within-species to mean = 0, SD = 1 to aid in model convergence (Bolker et al., 2013) and account for differences in average seedling heights across species. We considered the effects of covariates on mortality to be significant if their 95% posterior credible intervals (CI) did not overlap zero. Full model code, data, and instructions to reproduce all statistical analyses in this study are available on figshare: <https://doi.org/10.6084/m9.figshare.14204258>

2.5 | Species mortality response to El Niño related to moisture affinity and drought sensitivity

We used two different drought resistance indices to predict mortality response to the 2015–16 El Niño: (1) species' affinity to moisture and (2) species' experimentally assessed drought sensitivity. These indices are independent and complimentary: the first is based on correlations of species occurrences with dry season severity and included the majority of species in our seedling data set (291 species), whereas the second provides a more direct, mechanistic assessment of drought impact but was available for fewer species (34 species). We obtained moisture affinity estimates for species in our study from Condit et al. (2013), which used a hierarchical model to estimate the relationship between dry season severity and occurrence across 72 sites for 550 species across the Isthmus of Panama, while controlling for other factors such as soil nutrients. This moisture affinity metric was the best predictor of species distributions, with soil phosphorus a close second (Condit et al., 2013). Our metric of moisture affinity is the first-order parameter from the logistic model linking species occurrence with dry season severity. Species with higher, positive moisture affinity estimates are more likely to be found in areas with mild dry seasons compared with species with lower, negative moisture affinity scores, which are more likely to be found in areas with severe dry seasons. After filtering species with corresponding moisture affinity data, the seedling census data set included 20,391 observations from 7,196 individuals of 291 species.

We obtained our second drought resistance index from estimates of experimentally assessed drought sensitivity from Engelbrecht et al. (2007). The drought sensitivity index represents the relative survival difference of first-year seedlings in drought versus irrigated treatments in the forest understory. Higher values of drought sensitivity indicate higher mortality when exposed to experimental drought conditions. The original study assessed drought sensitivity in 48 species found in the forests of Central Panama. After filtering

species with drought sensitivity data, the seedling census data set included 4129 observations from 1329 individuals of 34 species.

To model how mortality rates in the census interval covering the 2015–16 El Niño relative to other census years were associated with species moisture affinity or experimentally assessed drought sensitivity, we used a similar modeling framework as described above. In one model, we added a species moisture affinity term (β_5) as a predictor of mortality. In a separate model, we used a species experimentally assessed drought sensitivity term (β_6) as a predictor of mortality. In each model, the terms were estimated separately for each census:

$$\text{logit}(\hat{y}_i) \sim \alpha_{\text{overall}} + \alpha_{\text{species}_{\text{ spp}}} + \alpha_{\text{census}_{\text{ c}}} + \alpha_{\text{site}_{\text{ s}}} + \alpha_{\text{plot}_{\text{ p}}} + \beta_1 \cdot \text{InitialHeight}_i + \beta_{5,\text{ c}} \cdot \text{MoistureAffinity}_i,$$

$$\text{logit}(\hat{y}_i) \sim \alpha_{\text{overall}} + \alpha_{\text{species}_{\text{ spp}}} + \alpha_{\text{census}_{\text{ c}}} + \alpha_{\text{site}_{\text{ s}}} + \alpha_{\text{plot}_{\text{ p}}} + \beta_1 \cdot \text{InitialHeight}_i + \beta_{6,\text{ c}} \cdot \text{DroughtSensitivity}_i,$$

$$\beta_{5,\text{ c}} \sim \text{Normal}(0, \sigma^2),$$

$$\beta_{6,\text{ c}} \sim \text{Normal}(0, \sigma^2),$$

$$\alpha_{\text{species}_{\text{ spp}}} \sim \text{Normal}(0, \sigma^2),$$

$$\alpha_{\text{census}_{\text{ c}}} \sim \text{Normal}(0, \sigma^2),$$

$$\alpha_{\text{site}_{\text{ s}}} \sim \text{Normal}(0, \sigma^2),$$

$$\alpha_{\text{plot}_{\text{ p}}} \sim \text{Normal}(0, \sigma^2).$$

where $\beta_{5,\text{ c}}$ and $\beta_{6,\text{ c}}$ were random effects that estimated the relationship between mortality and moisture affinity or drought sensitivity separately for each census c . Census and site were treated as separate random effects in order for the model to converge without divergences. We scaled moisture affinity to range from -1 to 1 across all species in the data set, where moisture affinity = 1 represented the species across the entire study region with the strongest association to wetter habitats. We normalized drought sensitivity to mean = 0 , SD = 1 to aid in model convergence (Bolker et al., 2013) and back-transformed values for prediction.

3 | RESULTS

3.1 | Elevated seedling mortality during El Niño

Community-wide seedling mortality averaged across all eight forests increased 11.3% (2.1 to 21%, 95% CI) during the census interval including the 2015–16 El Niño compared with baseline mortality rates estimated from other census intervals (Figure 1c), controlling for plot, species, and seedling size effects. Mortality rates varied widely across forests both during the 2015–16 El Niño and in an average non-El Niño year (Figure 1c).

3.2 | Wet-affiliated and drought-sensitive species exhibited the strongest mortality response to El Niño

For both indices of drought resistance, our results indicate that the 2015–16 El Niño had a stronger impact on seedlings of drought-sensitive species than seedlings of drought-resistant species (Figure 2). Specifically, species with higher moisture affinity values experienced large increases in mortality rates during the El Niño census interval compared with a typical year—up to a 39% (12.8%–77.4% CI) relative increase in seedling mortality rates during the El Niño for species with the highest moisture affiliation (Figure 2a,c). In contrast, species with low moisture affinity values showed no increase in seedling mortality in the El Niño year (Figure 2c). Experimentally assessed drought sensitivity was also a strong predictor of mortality response to El Niño (Figure 2b,d). Species with the highest drought sensitivity ($DS = 100$) experienced a 251% relative increase in mortality (124%–468% CI) during the El Niño year compared with a typical year (Figure 2d), whereas the least drought-sensitive species ($DS = 0$) had slightly lower mortality in the El Niño census interval compared with non-El Niño years (Figure 2b).

3.3 | Wetter forests had stronger mortality responses during El Niño

To determine whether the impact of the El Niño differed for drier versus wetter forest sites along the rainfall gradient, we related responses in seedling mortality rates during the 2015–16 El Niño in each of the eight forests to the respective long-term average dry season severity (1961–1990), the absolute dry season severity during the 2015–16 El Niño, and the relative anomaly in dry season severity during the El Niño compared with the long-term average. For all three metrics, we found that wetter forests, that is, those with the mildest dry seasons, experienced the strongest relative increase in seedling mortality in response to the El Niño (Figure 2; Table S3). For example, two of the wettest forests, Santa Rita and San Lorenzo, experienced a 25% (6%–44% CI) and 57% (26%–92% CI) increase in mortality during the El Niño, respectively, whereas the forest with the strongest dry season in the El Niño year, Panamá Pacífico, exhibited no increase in mortality in the El Niño year relative to other years (–34 to 8% CI; Figure 2b). The three dry season severity metrics were moderately to strongly correlated with each other (Figure S2) and had similar ability to predict forest mortality response (Table S3).

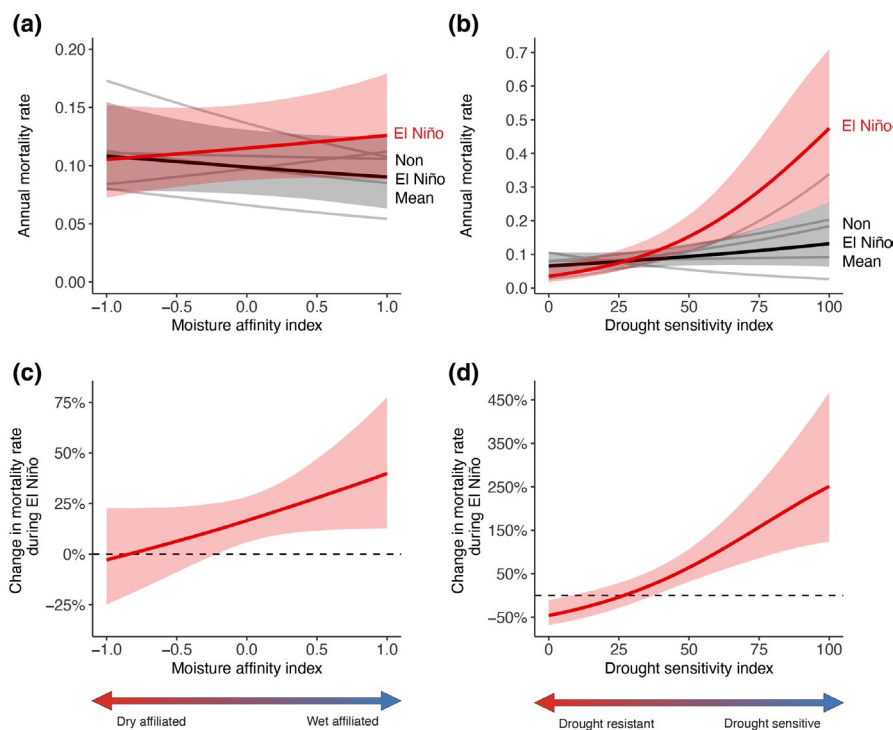


FIGURE 2 Mortality response to the 2015–16 El Niño dry season is dependent on species' moisture affinity and drought sensitivity. Annual mortality rates for seedlings during the 2015–16 El Niño census interval (red solid line), in each of five censuses taken during non-El Niño years (grey lines), and the average mortality rates across these non-El Niño censuses (black line) based on their (a) moisture affinity and (b) drought sensitivity. Shaded regions indicate the 95% credible interval. Predicted change in mortality during the 2015–16 El Niño census interval compared with average mortality rate in non-El Niño years dependent on (c) species' moisture affinity and (d) species' drought sensitivity. Dashed line indicates no change in mortality during the census interval covering El Niño. Shaded regions indicate the 95% credible interval

4 | DISCUSSION

As extreme climate events like the 2015–16 El Niño are predicted to become more common over the next century, an understanding of their impacts on tropical forests is crucial for predicting the consequences of global change for tropical forest composition, diversity, and function. Because extreme El Niño events occur infrequently and are hard to predict far in advance, relatively few studies have been able to provide detailed accounts of their impact on tropical forest dynamics. Due to long-term monitoring projects in place at multiple sites along a rainfall gradient, we were able to document the effects of this severe El Niño on tropical forest seedlings and assess how impacts varied both within and among communities. Specifically, we demonstrated that overall seedling mortality was elevated during the census interval covering the 2015–16 El Niño year, with the largest increases in mortality observed for drought-sensitive species and wetter forest sites along the gradient. Our results highlight the vulnerability of drought-sensitive species and communities to severe El Niño events in moist tropical forests. Because early life stages are a critical bottleneck in the life cycle of trees, these impacts on seedling mortality may alter future forest composition, with potential implications for species diversity and ecosystem function.

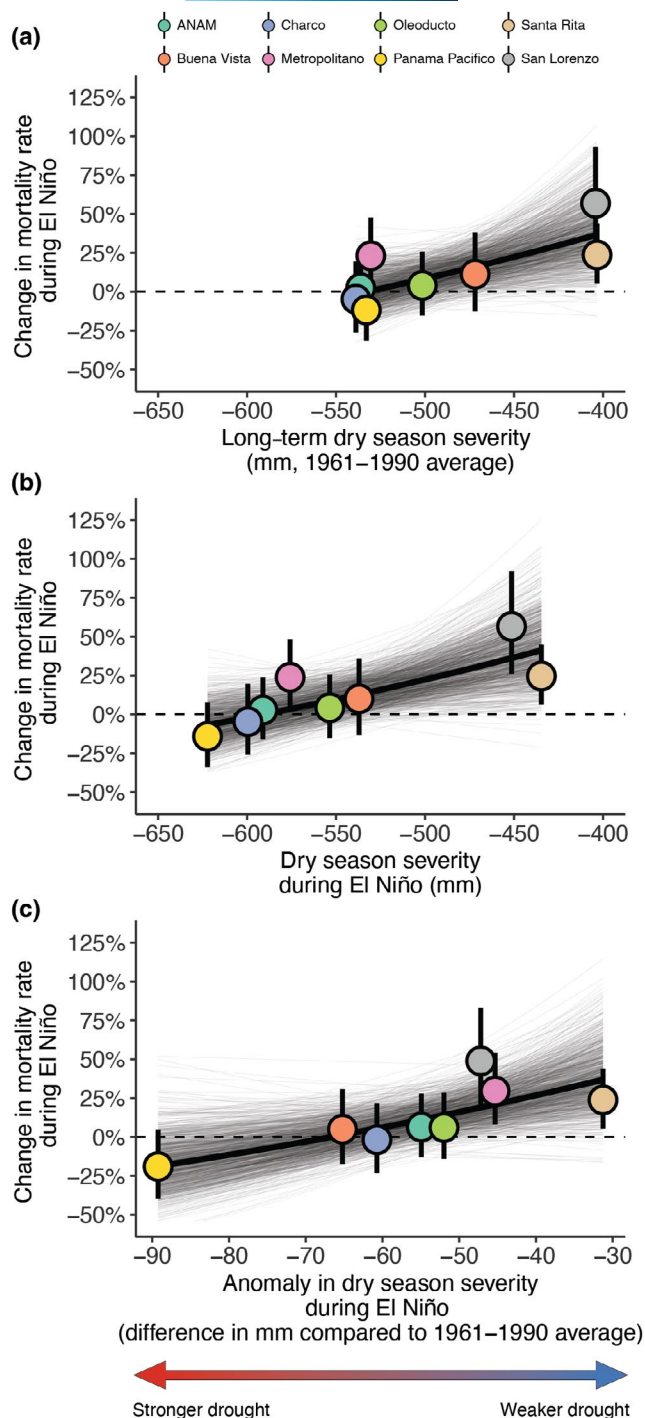
For predicting the impact of extreme climate events on hyperdiverse natural systems such as tropical forests, understanding how individual species respond to severe droughts will be necessary. Our study illustrates that adult tree distribution patterns across a moisture gradient provide predictive insight into species' mortality responses to severe drought at an early and critical life history stage, with species affiliated with wetter sites being more sensitive to drought than species affiliated with drier sites. Previous studies have linked directly measured plant drought sensitivity with tropical tree species' distributions across moisture gradients (Engelbrecht et al., 2007; Esquivel-Muelbert et al., 2017), providing support for using regional data on species occurrence and moisture affinity as an index of drought resistance. Experimentally assessed drought sensitivity (Engelbrecht et al., 2007) was an especially strong predictor of mortality response during El Niño for the 34 species in our study for which experimental data were available. While performing drought experiments or directly measuring functional traits related to drought response will likely improve predictions of the impact of extreme climates on individual species (Barros et al., 2019), these types of traits remain difficult to collect for many species in diverse communities. However, it is possible to estimate species' moisture affinity from spatial distributions for hundreds to thousands of species using already available data from online databases, herbarium collections, and large-scale plot networks (e.g., BIEN, Tropicos, RAINFOR, AFRITRON; Enquist et al., 2016; Lewis et al., 2009; Malhi et al., 2002) in combination with hierarchical Bayesian modeling (Condit et al., 2013), which may improve our ability to predict species drought responses in tropical regions.

The ability of species-level drought sensitivity metrics to predict responses to the 2015–16 El Niño indicates that the El Niño event

influenced seedling survival largely via severe decreases of water availability. However, other factors besides water availability are known to drive tropical tree seedling dynamics (Johnson et al., 2017), and many of those factors also vary during El Niño events. For example, cloud cover is reduced and solar irradiance is increased during El Niño events, which has been shown to result in higher flower and seed production in tropical trees (Wright & Calderón, 2006). Tropical tree seedlings tend to be severely light limited in the forest understory, especially in wetter forests, which have fewer deciduous species in the canopy and more cloud cover (Brenes-Arguedas et al., 2011; Umaña et al., 2021). As such, the potential negative effects of drought on seedling survival during El Niño events may be offset by potential positive effects of increased light availability. In addition, biotic interactions that influence seedling survival, such as plant-pathogen interactions, are also influenced by precipitation in tropical forests (Milici et al., 2020). Therefore, to fully understand and predict the future trajectories of tropical forests, we need an integrated understanding of how extreme climate events alter multiple abiotic and biotic factors to determine species-specific responses across various life stages.

A key strength of this study is that we were able to compare how multiple forest communities across a rainfall gradient responded to the 2015–16 El Niño. Understanding how regional differences in local environmental conditions, such as moisture availability, influence response to climate is critical for generating predictions of how forest communities will respond to climate change (Anderegg et al., 2019). Interestingly, the driest forests in our study did not show a significant change in seedling mortality during the El Niño year. Our results, thus, support the hypothesis that drier forests in our study region are less sensitive to the negative impacts of El Niño-associated drought, at least at the seedling stage. This could be due to drier forests having communities of species pre-adapted to extreme drought because of long-term selection for drought resistance during the annual dry season or past severe drought events. Supporting this, seedling communities in drier forests in our study region were composed of species with lower mean drought sensitivity and lower moisture affinity indices compared with wetter sites (Figure S5). It is important to note, however, that tropical dry forests are not immune to severe drought events. For example, the severe drought related to the 2015–16 El Niño event caused elevated tree mortality in later life stages for many tree species in tropical dry forest in Costa Rica (Powers et al., 2020).

Although observing higher mortality increases in wetter forests and in seedlings of more drought-sensitive species may not seem surprising, our results contrast with previous studies on larger trees both within the same study region and elsewhere in the humid tropics. A study of the effect of the 1997–98 El Niño on saplings and trees at three sites along the same rainfall gradient in Panama found elevated mortality only at the driest site (Condit et al., 2004). Similarly, a study in the Amazon found tree mortality increases were strongest at sites experiencing the most intense drought (Phillips et al., 2010). Whether this is due to differences in the effects of drought across tree life stages or differences in the severity and



duration of the drought events themselves is unclear. Contrary to expectations, the strongest mortality increases in our study occurred in the forest that experienced the weakest drought anomaly (i.e., El Niño year compared with long-term conditions). This may be because forests experiencing a strong drought anomaly during the 2015–16 El Niño also tended to have more severe dry seasons on average over longer time periods (1961–1990; Figure S1), making it difficult to tease apart the relative influence of anomalous versus long-term conditions within our study. Despite being among the most severe droughts in Panama's recent history (Spinoni et al., 2019), and drier forests in our study area experiencing the strongest

FIGURE 3 Mortality response to the 2015–16 El Niño by forest plot. Change in community-wide seedling mortality at eight forests across the Isthmus of Panama in relation to (a) long-term dry season severity (1961–1990 average), (b) dry season severity during the 2015–16 El Niño, and (c) the anomaly in dry season severity during the 2015–16 El Niño compared with long-term averages. Dry season severity is a metric of dry season intensity, defined as the most extreme cumulative rainfall deficit during the dry season, where more negative values indicate stronger drought. Bars extending from points indicate the 95% credible interval in mortality change at each forest. The solid black line indicates the fit of a linear regression between mortality change and the corresponding dry season metric. Thin gray lines are 1000 samples from the posterior distribution to visualize uncertainty in regression fit

drought anomalies (Figure 3c), the 2015–16 El Niño may not have been severe enough to push seedling populations in drier forests beyond the climatic limits they can tolerate (Anderegg et al., 2019). However, there remains the possibility of this occurring during more extreme droughts in the future.

We demonstrated that an extreme El Niño event can lead to a substantial short-term increase in seedling mortality and that increases in seedling mortality rates can be predicted based on moisture affinities of adult trees and experimentally assessed seedling drought sensitivity. It remains to be determined if these impacts persist over time and how they may impact future patterns of species diversity and composition. Future climate change and increased frequency of severe El Niño events may affect forest composition by filtering seedlings of drought-sensitive species from communities, especially in wetter forests, leading to an increase in relative abundance of drought-resistant species (Corlett, 2016). Long-term demographic monitoring of tropical forests will be a key component of efforts to understand how these important ecosystems will respond to climate change over the next century (Brodribb et al., 2020).

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CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTION

Liza S. Comita, Bettina M. J. Engelbrecht, and F. Andrew Jones conceived the study. Owen T. Lewis, S. Joseph Wright, and Lars Markesteijn contributed to study design and establishment. Lars Markesteijn, Liza S. Comita, Eric Manzané-Pinzón, and Luke Browne participated in data collection. Luke Browne performed data analysis with input from Liza S. Comita. Luke Browne wrote the first draft of the manuscript, and all authors contributed to interpretation and writing. All authors approve of the submitted version of the manuscript.

DATA AVAILABILITY STATEMENT

Full model code, data, and instructions to reproduce all statistical analyses in this study are available on figshare: <https://doi.org/10.6084/m9.figshare.14204258>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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