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Environmental heterogeneity and biotic interactions mediate climate impacts on tropical forest regeneration

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Abstract

Predicting the fate of tropical forests under a changing climate requires understanding species responses to climatic variability and extremes. Seedlings may be particularly vulnerable to climatic stress given low stored resources and undeveloped roots; they also portend the potential effects of climate change on future forest composition. Here we use data for ca. 50,000 tropical seedlings representing 25 woody species to assess (i) the effects of interannual variation in rainfall and solar radiation between 2007 and 2016 on seedling survival over 9 years in a subtropical forest; and (ii) how spatial heterogeneity in three environmental factors—soil moisture, understory light, and conspecific neighborhood density—modulate these responses. Community-wide seedling survival was not sensitive to interannual rainfall variability but interspecific variation in these responses was large, overwhelming the average community response. In contrast, community-wide responses to solar radiation were predominantly positive. Spatial heterogeneity in soil moisture and conspecific density were the predominant and most consistent drivers of seedling survival, with the majority of species exhibiting greater survival at low conspecific densities and positive or nonlinear responses to soil moisture. This environmental heterogeneity modulated impacts of rainfall and solar radiation. Negative conspecific effects were amplified during rainy years and at dry sites, whereas the positive effects of radiation on survival were more pronounced for seedlings existing at high understory light levels. These results demonstrate that environmental heterogeneity is not only the main driver of seedling survival in this forest but also plays a central role in buffering or exacerbating impacts of climate fluctuations on forest regeneration. Since seedlings represent a key bottleneck in the demographic cycle of trees, efforts to predict the long-term effects of a changing climate on tropical forests must take into account this environmental heterogeneity and how its effects on regeneration dynamics play out in long-term stand dynamics.

KEYWORDS
climate refugia, density dependence, drought, seedling dynamics, solar radiation

1 | INTRODUCTION

Interannual climate variability is a major driver of community dynamics and a potentially important axis of niche partitioning in forest ecosystems (Clark et al., 2016). However, little is known about the role of interannual climate fluctuations in driving the dynamics of these communities, especially for diverse tropical rainforests (Zuidema et al., 2013). Since climate-change models project rapidly increasing surface temperatures in tropical regions (Diffenbaugh & Scherer, 2011) and precipitation declines for large parts of the

tropics (Christensen et al., 2007; Mora et al., 2013; Sherwood & Fu, 2014), this knowledge gap impedes our ability to anticipate the effects of climate change on tropical rainforests.

Observations from long-term forest-monitoring networks in tropical forests have shown that high temperatures and extreme drought events can result in lower tree growth and fecundity (Clark, Clark, & Oberbauer, 2010; Feeley, Joseph Wright, Nur Supardi, Kassim, & Davies, 2007; Lasky, Uriarte, & Muscarella, 2016) and elevated mortality (Chazdon, Redondo Brenes, & Vilchez Alvarado, 2005; Phillips et al., 2010; Uriarte, Lasky, Boukili, Chazdon, & Merow, 2016). Studies also demonstrate significant variation in species responses to climatic variability; early successional species appear to be more susceptible to drought than late-successional trees (Chazdon et al., 2005; Uriarte et al., 2016) and dry habitat specialists have high survival during drought (Comita & Engelbrecht, 2009; Engelbrecht, Kursar, & Tyree, 2005). The associations between climate and tropical tree performance, however, remain understudied (Zuidema et al., 2013). This is in part because we lack an understanding of the environmental and biotic factors that mediate species responses to climate in forest communities.

Spatial heterogeneity in water availability at local and regional scales can buffer or exacerbate impacts of climate fluctuations on tropical forests. There is ample evidence that precipitation is a major driver of species distributions at regional scales (Baltzer, Davies, Bunyavejchewin, & Noor, 2008; Engelbrecht et al., 2007). At local scales, topographic heterogeneity and drainage networks generate spatial heterogeneity in soil moisture (Daws, Mullins, Burslem, Paton, & Dalling, 2002) that can also shape the fine-scale distribution of species (Engelbrecht et al., 2007; Harms, Condit, Hubbell, & Foster, 2001). Since tree growth and productivity are often strongly limited by water availability in tropical forests (Silva, Kellner, Clark, & Clark, 2013), individual trees of drought-sensitive species that fare poorly under drought conditions may be able to persist in moist microsites (Comita & Engelbrecht, 2009; Daws, Crabtree, Dalling, Mullins, & Burslem, 2008; Daws et al., 2002). On the other hand, water logging can also generate anoxic soil conditions (Silver, Lugo, & Keller, 1999) and reduce tree growth and survival (Born et al., 2015).

Plant growth and productivity in tropical forests are also strongly constrained by solar radiation, particularly in regions where growth is not limited by rainfall (Banin et al., 2014; Churkina & Running, 1998; Dong et al., 2012; Fyllas et al., 2017; Graham, Mulkey, Kitajima, Phillips, & Wright, 2003; Guan et al., 2015; Huete et al., 2006; Nemani et al., 2003; Wright & Calderon, 2006). Across the tropics, fluctuations in cloud and aerosol abundance and characteristics drive variability in irradiance among years (Hatzianastassiou et al., 2012; Nemani et al., 2003; Rich, Clark, Clark, & Oberbauer, 1993; Wielicki et al., 2002). In some regions of the tropics including the Caribbean, interannual variation in radiation is also associated with the dynamics of Saharan dust emission and transport (Chami, Mallet, & Gentili, 2012). The impacts of such fluctuations on vegetation will likely depend on heterogeneity in the understory light environment that result from gap formation and stand development processes

(Nicotra, Chazdon, & Iriarte, 1999). Although high solar radiation can inhibit photosynthesis and growth, and potentially decrease survival for understory plants (e.g., seedlings) growing under full light conditions (i.e., gaps) (Comita et al., 2009; Krause et al., 2012), it is more likely to lead to higher growth and survival under the low-light environments that characterize tropical forest understories (Nicotra et al., 1999). For example, Dong et al. (2012) demonstrated that temporal variability in radiation influenced tree growth for individuals in the understory with greater growth during years of high solar radiation. How interannual variation in solar radiation interacts with the understory light environment to shape forest regeneration dynamics has received limited attention.

Because the spatial distribution and density of individual species partially reflects underlying environmental heterogeneity and climate affects not only trees directly, but also their competitors, symbionts, and natural enemies, the impacts of climate variability on tropical forests are further complicated by the degree to which this heterogeneity influences biotic interactions (Blois, Zarnetske, Fitzpatrick, & Finnegan, 2013; Jactel et al., 2012). Although mesic sites may act as a refuge during drought, individuals in moist sites could also experience intense competition for water with neighbors or stronger effects from specialist enemies, negating the buffering effect of moisture during drought. Several studies suggest that enemy-mediated conspecific effects are amplified under wet and warm conditions (Bachelot, Kobe, & Vriesendorp, 2015; Comita et al., 2014; Givnish 1999; Swinfield, Lewis, Bagchi, & Freckleton, `; Thompson, Alvarez-Loayza, Terborgh, & Katul, 2010). On the other hand, many pathogens can tolerate a wider range of water stress than the plants they infect, and the combination of pathogen infection and moisture stress on host plants can increase disease severity (Desprez-Loustau, Marcais, Nageleisen, Piou, & Vannini, 2006; Jactel et al., 2012). Similarly, both the competitive environment and interactions with enemies may vary with light availability. Stem densities of early successional species are particularly high in gaps and insect herbivores may respond to the high quality and quantity of leaves at these sites (Coley & Barone, 1996; Dalling & Hubbell, 2002; Richards & Coley, 2007). Consequently, herbivore pressure may be highest in high light areas, especially when water is not limiting (i.e., rainy seasons or years, Richards & Windsor, 2007).

Seedlings may be particularly vulnerable to abiotic stress (e.g., dry, low-light conditions) given the low stored resources of seedlings and the relatively undeveloped roots (Comita & Engelbrecht, 2014). This life stage also appears most vulnerable to pressures from pathogens and herbivores which may be altered under a changing climate (Jactel et al., 2012). Yet, the relationship between climate variability and recruitment is poorly understood (Clark et al., 2016). Advanced regeneration in seedlings provides clues to future stand composition; as a result, the effects of climate extremes on seedling survival are a harbinger of the potential effects of climate variability on future forest composition. Here we examine the effects of interannual variation in precipitation and solar radiation between 2007 and 2016 on annual seedling survival for 25 woody species and how these effects are modulated by fine-scale abiotic heterogeneity in light and soil

moisture and by biotic interactions with conspecifics. We address the following questions:

1. What is the impact of interannual variation in precipitation and solar radiation on seedling survival? We expected seedling survival to decline in years of low rainfall and solar radiation. On the other hand, anoxic conditions associated with water logging during wet years may reduce seedling survival leading to nonlinear responses to rainfall.

2. How does spatial heterogeneity in soil moisture and light availability modulate species responses to interannual variation in solar radiation and precipitation? We hypothesized that high soil moisture and light availability will act synergistically to enhance seedling survival across all years but these effects will be most marked in years with low precipitation (for soil moisture) and high radiation (for light). The rationale is that high rainfall will buffer moisture deficits in dry microsites and that the positive effects of high solar radiation will most benefit seedlings growing in relatively open sites where light can reach the understory. Conversely, anoxic conditions associated with water logging during wet years may reduce seedling survival, particularly in moist microsites. High light conditions may also lead to desiccation and lower seedling survival in high radiation years and instead, favor seedlings growing in areas with lower understory light levels.

3. How do effects of conspecifics vary with site and climate conditions? We expected high conspecific density to reduce seedling survival, particularly during years of high precipitation and solar radiation and in sites with high soil moisture or light availability where enemies would be more likely to occur at high densities. On the other hand, unfavorable conditions may exacerbate negative conspecific effects if seedlings become more vulnerable to enemies or competition intensifies when water and light resources are limiting.

2 | MATERIALS AND METHODS

2.1 | Study site

The Luquillo Forest Dynamics Plot (LFDP) is a 16-ha permanent plot located in subtropical wet forest of NE Puerto Rico (18°20′°N, 65°49′°W). Mean annual rainfall in the LFDP is ~3,500 mm/year and elevation ranges from 333 to 428 m a.s.l. Soils are formed from volcaniclastic rock. The dominant soil types are Zarzal, a deep and well-drained oxisol, and Cristal, a deep but poorly drained ultisol. Spatio-temporal variation in soil moisture is influenced by topography and soil type (Johnston, 1992; Silver et al., 1999). Since 1990, all free-standing woody stems >1 cm dbh (diameter at 1.3 m height) in the LFDP have been mapped, identified to species, and measured approximately every 5 years (Thompson et al., 2002).

Interannual variation in precipitation in Puerto Rico is primarily driven by the NAO (Jury, Malmgren, & Winter, 2007). Climate models derived from field and satellite data predict a decrease in rainfall of 5%–50% over the next 100 years for the Caribbean (Khalyani,

Harmsen, Terando, Quinones, & Collazo, 2016; Neelin, Munnich, Su, Meyerson, & Holloway, 2006). Periodic droughts are expected to influence the distribution of drought-susceptible seedlings in the most drought-prone areas of the forest (e.g., well-drained ridges) eventually, through repeated drought events, influencing the distribution of adult trees. Seasonal variation in solar irradiance at the site reflects changes in maximum zenithal sun angle (Zimmerman, Wright, Calderón, Pagan, & Paton, 2007), whereas interannual variation is associated with the dynamics of Saharan dust emission and transport (Chami et al., 2012).

2.2 | Data

2.2.1 | Seedling data

In 2007, 360 1-m^2 seedling plots were established on each side of a trail that runs north-south through the LFDP (Figure S1). Seedlings in these plots have been mapped, identified to species, and measured for root collar diameter annually since 2007. New seedlings are added to the census each year as they appear. Censuses are conducted between March and May, the driest time of the year. For this study, we used data from annual seedling censuses collected from 2007 through 2016. There was no minimum seedling size cut off. Species were included in the analyses if there were more than 200 survival observations over this period. On the basis of these criteria, we analyzed data for 27,899 individual seedlings representing 25 species and 51,425 survival observations. These data account for ca. 95% of observed seedlings over the study period (Table 1).

2.2.2 | Climate data

Meteorological data were collected using a nearby (distance ~300 m) weather station connected to a Campbell 10X data logger (Campbell Scientific, Logan, UT, USA). To assess the effects of interannual climate variation on seedling survival, we calculated the total amount of rainfall in the year preceding the census of each seedling plot. We also calculated average daily daytime solar radiation (short and long wave) between each census interval using data from a LiCOR LI200X pyranometer (LI-COR Biosciences, Lincoln, NE, USA). Aerosol measurements are derived from the Ozone Monitoring Instrument (OMI) on NASA's EOS Aura satellite. The measurements are in the form of the aerosol index (AI), which is calculated based on the difference between the amount of ultraviolet (UV) light that the dust-filled atmosphere scatters compared to the amount of UV the atmosphere would backscatter without dust.

2.2.3 | Environmental data for seedling plots

We quantified a number of local factors that can affect seedling survival: understory light availability, soil moisture, and density of conspecifics. Initial analyses indicated that soil type did not substantially influence seedling survival so we excluded this variable from

TABLE 1 Species included in the analyses

Species	Family	Life form (Guild)	Number of seedling-years (2007–2016)	% of total no. of seedlings (2007–2016)	Mean annual survival rates (%)
Caseria arborea	Flacourtiaceae	Tree (S)	280	0.51	88.21
Dacryodes excelsa	Burseraceae	Tree (L)	3,949	7.25	15.67
Drypetes glauca	Euphorbiaceae	Tree (L)	254	0.47	67.32
Eugenia domingensis	Myrtaceae	Tree (L)	459	0.84	64.92
Guarea guidonia	Meliaceae	Tree (S)	4,784	8.78	51.94
Heteropteris laurifolia	Polypodiaceae	Liana	1,827	3.35	70.28
Hippocratea volubilis	Hippocrateaceae	Liana	4,739	8.8	55.80
Hirtella rugosa	Rosaceae	Tree (L)	259	0.48	84.56
Inga laurina	Leguminosae	Tree (S)	1,274	2.34	80.46
Inga vera	Leguminosae	Tree (S)	220	0.41	77.73
Manilkara bidentata	Sapotaceae	Tree (L)	490	0.90	78.78
Matayba domingensis	Sapindaceae	Tree (L)	257	0.47	51.75
Myrcia leptoclada	Myrtaceae	Tree (S)	315	0.58	95.24
Ocotea leucoxylon	Lauraceae	Tree (S)	1,074	1.97	82.03
Ocotea sintenisii	Lauraceae	Tree (S)	845	1.55	75.86
Paullinia pinnata	Sapindaceae	Liana	1,803	3.34	31.06
Piper glabrescens	Piperaceae	Shrub (S)	329	0.61	83.59
Prestoea acuminata	Arecaceae	Palm (L)	16,001	29.38	53.01
Rourea surinamensis	Connaraceae	Liana	6,399	11.75	65.04
Roystonea borinquena	Arecaceae	Palm (S)	913	1.68	24.10
Securidaca virgata	Polygalaceae	Liana	3,033	5.62	52.52
Sloanea berteriana	Elaeocarpaceae	Tree (L)	258	0.47	66.67
Tabebuia heterophylla	Bignonaceae	Tree (S)	242	0.44	85.12
Tetragastris balsamifera	Burseraceae	Tree (L)	1,003	1.84	73.88
Trichilia pallida	Meliaceae	Tree (L)	418	0.77	83.97

We selected all 25 species that had more than 200 seedling-year observations between 2007 and 2016. Total number of seedling-years is the number of observations included in the analyses, not the number of individuals. Successional guild: S, secondary forest species; L, late successional; shade-tolerant species.

analyses. To quantify variation in light availability among seedling plots, we used a camera with a fisheye lens (Nikkor, Nikon Inc., Tokyo, Japan) positioned at 1 m height at the center of each seedling plot under uniform light conditions. Pictures were taken each year in conjunction with the seedling census and were analyzed following the Ridler and Calvard (1978) algorithm. We quantified light availability using the Gap Light Index (GLI), a measure of canopy openness (Canham 1988). To assess spatial variation in water availability, we used a Hydrosense II soil moisture probe (Campbell Scientific) in each plot over a 4-year period (2012–2016). Since soil moisture can change rapidly after individual rainfall events and we wanted to capture the effects of precipitation extremes (i.e., drought) on soil moisture, measurements were taken at the same location in each plot using an adaptive sampling scheme. We sampled whenever precipitation over the previous 7, 14, 21, and 28 days was less than the lower 5% quantile for those intervals in observed historical precipitation at the site. Historical precipitation was based on meteorological data collected between 1975 and 2010

(Table S1). For the analyses presented here, we used median plot-level soil moisture calculated using all measurements taken over this 4-year period that were lower than the 5% historical quantile. In effect, this metric captures spatial heterogeneity in soil moisture across seedling plots, with an emphasis on characterizing dry conditions.

We also considered plant neighborhood factors that could influence seedling survival, including conspecific seedling density in the plot and the sum of conspecific basal area basal tree area in a 15-m radius around each seedling plot. Previous analyses in the LFDP (Uriarte, Canham, Thompson, Zimmerman, & Brokaw, 2005) showed that a 15-m radius captured neighborhood interactions between individual trees. Preliminary analyses showed no effect of conspecific basal area on seedling survival and no negative effect of heterospecific seedling density on survival so we excluded these variables from subsequent analyses. Pairwise correlations between conspecific seedling densities and environmental covariates were uniformly low ($r < .15$), assuaging concerns about collinearity.

2.3 | Statistical analyses

We modeled individual seedling survival using annual censuses conducted from 2007 to 2016. For each seedling we modeled survival as a function of root collar diameter at the start of the interval (*size*), understory light levels (*light*), our soil moisture metric *(SM)*, conspecific seedling density (*cons*), and two climate variables: total precipitation (*precip*) and average daily solar radiation in the interval between the seedling censuses. The soil moisture metric was the same across years for any given plot while the other covariates changed from year-to-year. The model also includes a quadratic term for soil moisture to account for the possibility that anoxic condition induced by water logging, which are common at the site (Silver et al., 1999), would reduce seedling survival.

Survival of seedling *i* in year *t* in plot *p* for species *s* was modeled using generalized linear mixed models (GLMM) as:

$$\text{survival } e_{itps} \sim \text{Bern}(y_{itps})$$
$$\begin{aligned} y_{itps} = \beta_0 &+ \beta_{size} \times size_{itp} + \beta_{rain} \times rain_t + \beta_{rad} \times radiation_t + \beta_{cons} \\ &\times \log(cons_{tps}) + \beta_{light} \times light_{tp} + \beta_{soil\ moist} \times SM_{tp} + \beta_{soil\ moist2} \\ &\times SM_{tp}^2 + \theta_s + \gamma_i \end{aligned} \quad (1)$$

where θ_s are normally distributed species random effects and γ are random effects associated with repeated observations of individuals. We used an iterative approach to model building by first adding random species effects for the intercept and for each covariate (random slopes). We evaluated fit for each model and added interactions required to test our hypotheses (see Section 2.3.1 below). Because rainfall can have both positive and negative effects on survival, we also evaluated a model that incorporated a linear and a quadratic term for rainfall. However, this model consistently underperformed models with just a linear term so we excluded it from further consideration. To facilitate interpretation and accelerate convergence, all environmental covariates were standardized by subtracting their means and dividing by their standard deviations computed across the whole dataset (all species) prior to analyses (Gelman & Hill, 2007). Because the large range of abundances lead to high interspecific variation in conspecific seedling densities (Table 1), this covariate was standardized within species. Root collar diameter was also standardized within species. Collinearity was formally assessed using Variance Inflation Factor (VIF) for the model with only main effects (Equation 1).

The formulation in Equation (1) could be difficult to interpret if the range of values of environmental covariates differ across species (e.g., if seedlings of a given species only germinate and recruit at sites with high light availability or soil moisture) (Bafumi & Gelman, 2006). To verify that this was not the case, we calculated the 10%, 50%, and 90% quantiles of environmental covariates (understory light and soil moisture) and found no consistent differences among species (Table S2). We also conducted separate analyses for each species using models that included the same covariates plus individual as a random effect. All analyses were conducted using R Statistical software (R Development Core Team, 2016). We fitted models using the "lme4" package in R (Bates, Maechler, & Bolker, 2013).

Goodness of fit was evaluated using marginal and conditional R^2 for multilevel models (Johnson, 2014; Nakagawa, Schielzeth, & O'hara, 2013). Model selection for fixed effects was based on AIC and chi-square statistics. We evaluated the significance of random effects (intercepts and slopes) by fitting reduced models (without a given random effect) and calculating likelihood ratio tests via ANOVA (Pinheiro & Bates, 2000).

2.3.1 | Hypothesis testing

To assess the impact of interannual variation in climate (solar radiation and precipitation) on seedling survival and how these varied across species (Question 1), we coupled best linear unbiased parameters (BLUP) of slopes for these covariates from the community-level mixed model with parameters from individual species analyses. We evaluated whether environmental heterogeneity in soil moisture and understory light levels modulate the effects of interannual variation in rainfall and solar radiation (Question 2) by considering significant pairwise interactions between these variables at both the community and individual species scales. Finally, we examined interactive effects of conspecific density, environment and climate on seedling survival by including interactions among these variables in the models (Question 3).

3 | RESULTS

3.1 | Overview

Annual rainfall was extremely variable during the study period, ranging from 5,570 mm in 2010 to 2,035 mm in 2015, with an average of 3,800 mm (Figure 1). Average daily solar radiation was also highly variable from year to year, ranging between 523.9 to 644.6 W/m² with an average of 569.36 W/m². Variation in solar radiation was driven primarily by aerosol inputs ($R^2 = .47$). Although precipitation and solar radiation are typically strongly correlated at finer temporal scales, the correlation between the two climate variables at annual scales was low ($r = .02$).

The seeding community in the LFDP was extremely dynamic between 2007 and 2016 with marked fluctuations among years in the number of seedlings that recruited, lived, and died (Figure 2). These community-scale patterns were largely driven by 6 of the 25 species included in the study—two tree species (*D. excelsa* and *G. guidonia*), a palm (*P. acuminata*) and three lianas (*H. volubilis*, *R. surinamensis*, and *S. virgata*)—which together accounted for ca. 72% of seedlings observed between 2007 and 2016 (Table 1). Annual rates of seedling survival varied substantially among species, ranging from 15% for *D. excelsa* to 95% for *M. leptoclada* (Table 1; Figure S2). For the most part, abundant species had lower survival rates (Pearson' r between log species abundance and instantaneous annual survival rate, $r = -0.54$) with some exceptions (e.g., the palm, *R. borinquena*).

The best-fit mixed models for probability of seedling survival included main and species-specific effects (random slopes) for all the environmental covariates: precipitation, radiation, soil moisture (linear
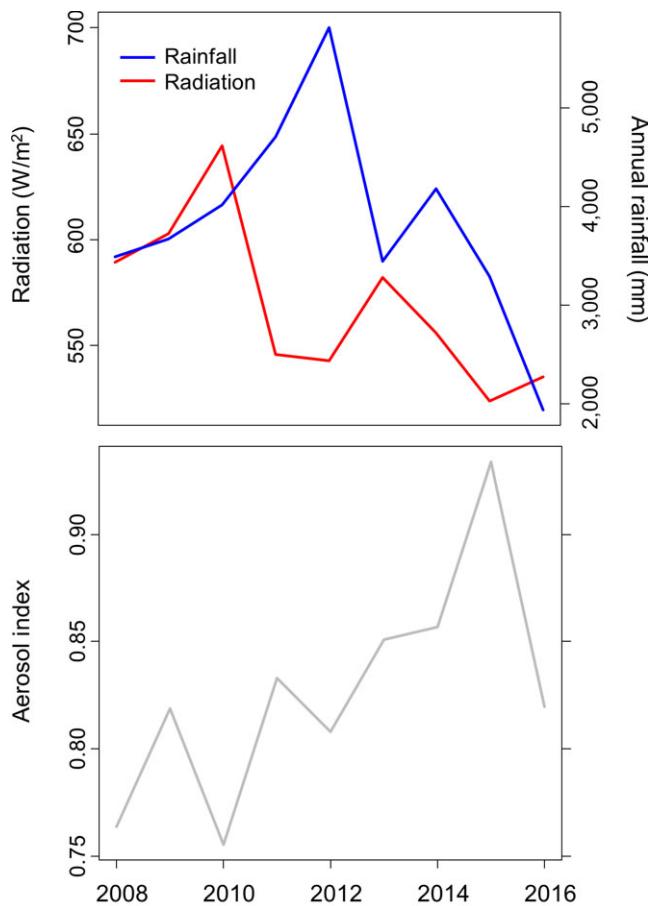
FIGURE 1 Interannual variation in total annual precipitation, solar radiation, and the Aerosol Index across census years at the study site. AI is a unitless measurement of the effect of aerosols on backscattered UV radiation. AI ranged from 0.75 in 2009 to 0.93 in 2014 over the study period. For context, AI values in the dustiest regions of the world are ~5. Puerto Rico averages its highest values in June and July with ~1

and quadratic terms), and light availability (Table S3). Among covariates, seedling size had the strongest relationship with survival (Table S3), where larger seedlings had significantly higher survival. Synergistic effects of light and solar radiation and of rainfall and soil moisture on seedling survival were supported by the data. The strength of negative density dependence varied with rainfall, heterogeneity in soil moisture, and understory light. (Table S2). Goodness-of-fit metrics for the community-scale survival mixed model were marginal $R^2 = .07$ and conditional $R^2 = .33$, whereas individual species conditional and marginal R^2 values ranged broadly (Table S4).

3.2 | Effects of interannual variation in solar radiation and precipitation on seedling survival

Community-wide survival did not respond to interannual variation in rainfall (Figure 3; Table S3). The absence of a community-level response, however, obscured large variation in species-specific responses, which ranged from negative to positive (Figures 3 and 4;
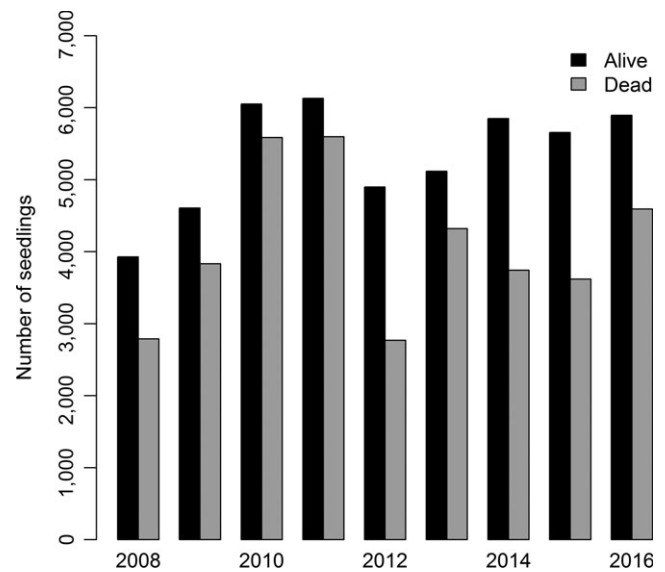

FIGURE 2 Community-wide variation in recruitment and seedling demography between 2007 and 2016. Note that numbers were calculated for each census interval (i.e., 2008 represents survival between the 2007 and 2008 censuses)

Table S5). Overall, rainfall was a significant driver of seedling survival for 8 of 25 species in the individual species analyses (Figure 4; Table S5). Of those species that showed significant responses to rainfall, the two palms, *P. acuminata* and *R. borinquena*, and the late-successional tree species, *D. excelsa*, presented increases in survival during high rainfall years, whereas four of the five lianas species plus one tree species, *M. bidentata*, experienced marked declines in survival during years of high rainfall (Table S5).

Solar radiation had a positive effect on seedling survival at the community level, as we had hypothesized (Figure 3). Although there were also marked differences in species responses to temporal fluctuations in radiation, the range of responses was far narrower than observed for rainfall. Among the seven species showing significant responses to solar radiation in individual species analyses, only survival of *D. excelsa* seedlings declined during high irradiance years, whereas for the remaining six species survival increased in years of high radiation (Figure 4; Table S5). These six included four of the five liana species and two tree species, *G. guidonia* and *P. acuminata*.

3.3 | Impacts of spatial heterogeneity in soil moisture and light availability on seedling survival

When pooling all species in the community, seedling survival exhibited a nonlinear response to soil moisture, as we had hypothesized (Figure 3). From the 25 species included in the analyses, 10 showed significant positive linear responses to high soil moisture conditions and no species responded negatively to linear increases in soil moisture (Figure. 4; Table S5). Four species exhibited nonlinear responses to soil moisture: survival of seedlings for two lianas (*S. virgata* and *R. surinamensis*) and one tree species (*T. pallida*) increased and then decreased with soil moisture (Table S5). Seedling survival for the palm *P. montana* increased exponentially at high soil moisture levels.
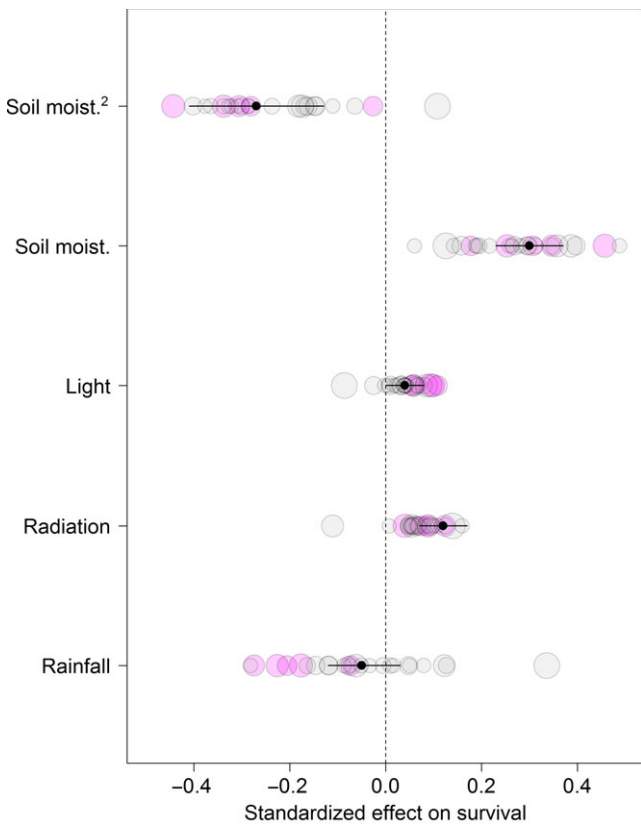
FIGURE 3 Standardized effect size of covariate relationships with survival. Black dots indicate mean parameter values and black lines the 95% confidence of the community-level responses. Circles show Best Linear Unbiased Parameter of random slopes for the community-wide mixed model, demonstrating the wide interspecific variability in survival associations with each covariate (Equation 1). Lianas are shown in pink, trees and palms in gray. Size of circles is proportional to seedling abundance. Values for individual species analyses are provided in Table S5. Note that covariates were standardized using the z-transformation (Section 2)

Community-wide survival was higher at high understory lights conditions (Figure 3; Table S3). The response to high understory light levels had weaker support in individual analyses than those observed for soil moisture, with only seven species, including the five lianas, showing increased survival under high light conditions, and two species, the palms *P. acuminata* and *R. borinquena* experiencing lower survival at high light levels (Figure 4; Table S5).

3.4 | Interactive effects between climate and environmental factors

Spatial heterogeneity in understory light levels mediated the effects of interannual fluctuations in solar radiation on community-wide seedling survival. When aggregating all 25 species, increases in survival observed during years of high radiation were most pronounced for seedlings growing at high light, a pattern consistent with solar radiation limitation at sites with high canopy openness but not in shaded areas where radiation cannot reach the understory (Figure 5a; Table S5).

Individual species analyses confirmed this finding for *G. guidonia*, *H. volubilis*, *O. sintenisii*, *P. pinnata*, *P. acuminata*, and *S. virgata*, where the positive effects of high solar radiation on survival only accrued to seedlings growing in sites with high levels of understory light (Table S5). In contrast, survival of *S. berteriana* seedlings decreased with radiation when growing in high understory light conditions.

Seedling survival in dry sites increased slightly in high rainfall years while the opposite was true for seedlings growing in wet sites (Figure 5b; Table S3). Two species, *I. laurina* and *R. surinamenesis* paralleled the community pattern (Table S5). Community-wide survival did not support a significant interaction between rainfall and the nonlinear soil moisture term (Table S3). Individual species analyses only uncovered nonlinear effects of soil moisture and rainfall on seedling survival for one species, the liana *R. surinamensis* (Table S5).

3.5 | Interaction effects between environmental factors and conspecifics on seedlings survival

High conspecific density reduced seedling survival at the community scale, consistent with expectation of Janzen–Connell effects (Figure 3; Table S3). Nevertheless, individual species analyses uncovered large differences among the 25 species in responses ranging from negative in *G. guidonia*, *H. volubilis*, *P. pjnnata*, *P. acuminata*, *S. virgata*, and *S. berteriana* to positive for *H. laurifolia* and *D. excelsa* (Figure 4; Table S5).

When pooling all species, the negative effects of conspecifics on survival were most marked during high rainfall years (Figure 6a). In the individual species analyses, models of seedling survival for 7 of the 25 species included significant interactions between rainfall and conspecific density. The negative effects of conspecific density were intensified by high rainfall conditions for *O. laurina*, *P. pinnata*, *R. surinamensis*, *S. berteriana*, and *T pallida* but ameliorated for *H. volubilis* and *G. guidonia* (Table S5).

Our analyses also revealed interactions between soil moisture and the effects of conspecifics. Specifically, seedlings in plots with low soil moisture exhibited exacerbated negative responses to high conspecific density, in accordance with stronger density dependent effects in dry sites (Figure 6b). In individual species analyses, four species, *P. pinnata*, *P. acuminata*, *S. berteriana*, and *T. pallida* experienced tronger negative effects at dry sites, following the community-wide trend. (Table S5).

Spatial heterogeneity in understory light levels also influenced the strength of conspecific densities on seedling survival (Figure 6c; Table S5). Specifically, the negative effects of conspecifics on survival were slightly more marked under high light conditions. This was also the case for two species, *H. laurifolia* and *P. acuminata*, in analyses of individual species data (Table S5).

Variation in solar radiation did not influence the effects of conspecifics on seedling survival at the community level (Table S3). Nevertheless, four species in the individual species analyses responded to the interactive effects of these two factors, showing that the effects of high irradiance were weaker at high conspecific densities (Table S5).
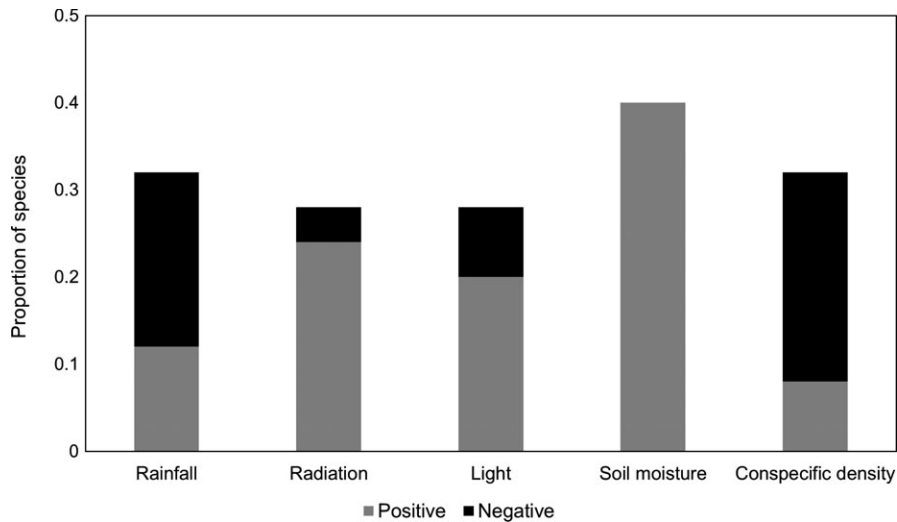
FIGURE 4 Proportion of 25 tropical wet forest species analyzed showing significant responses to spatial environmental heterogeneity and interannual climate variability. Gray denotes positive effects of the covariate on survival and black negative effects
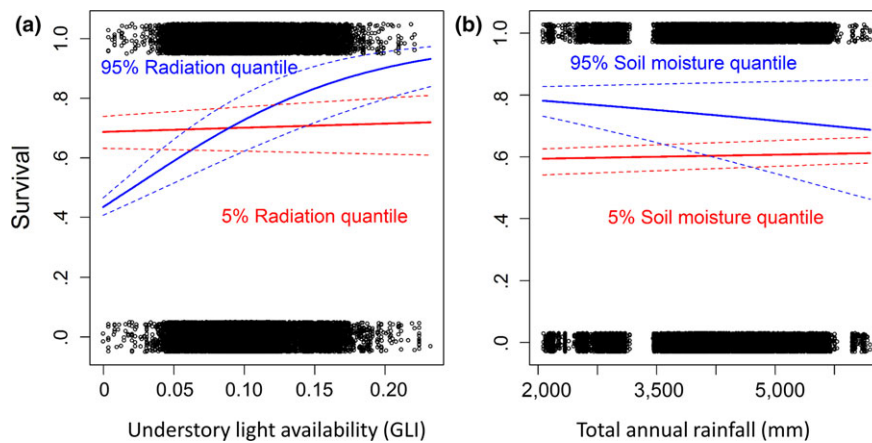
FIGURE 5 Seedling survival responses to the interactive effects of (a) solar radiation and understory light, (b) rainfall and soil moisture

4 | DISCUSSION

This study revealed a strong positive association between annual seedling survival and solar radiation while rainfall had a neutral—albeit highly variable—effect on survival. Individual species analyses showed that high soil moisture has a far more consistent effect on seedling survival than year-to-year variation in total rainfall. Fine-scale environmental heterogeneity (e.g., soil moisture and canopy openness) and to a lesser degree, biotic interactions, modulated the impacts of fluctuations in rainfall and solar radiation from year to year. We suggest that the study of climate impacts on tropical forests would benefit from a shift from the perspective that climate influences trees directly to one that embraces the role of environmental heterogeneity and biotic interactions in mediating plant community responses.

4.1 | Effects of interannual variation in solar radiation and precipitation on seedling survival

Most studies of climate impacts on tropical forests have focused on drought and temperature. However, plant growth and productivity may be more strongly limited by solar radiation than by water

availability in several tropical regions (Dong et al., 2012; Graham et al., 2003; Nemani et al., 2003). This limitation may be particularly marked for plants growing in the understory where the light environment is highly unpredictable (Chazdon & Pearcy, 1991; Dong et al., 2012; Nicotra et al., 1999). Consistent with these findings, our study demonstrated a strong and consistently positive relationship between seedling survival and solar radiation with only one species of the 25 included in the study exhibiting lower survival during years of high radiation. To our knowledge, our results provide the first clear demonstration of a relationship between seedling survival and temporal fluctuations in incoming solar radiation. The large spread in solar radiation values among years at our site mainly reflects attenuation of photosynthetically available radiation due to Saharan dust inputs (Chami et al., 2012). Although the drivers of variation in Saharan dust emission and transport are not well understood (Prospero & Mayol-Bracero, 2013), recent studies suggest inputs are likely to decline (Evan, Flamant, Gaetani, & Guichard, 2016) with potential consequences for tropical forest regeneration. At the same time, a recent study of global trends in solar radiation found dimming of solar radiation over the last decade in several regions of the tropics as a result of increases in aerosol emissions and cloud cover (Hatzianastassiou et al., 2012). Regardless of drivers, any directional
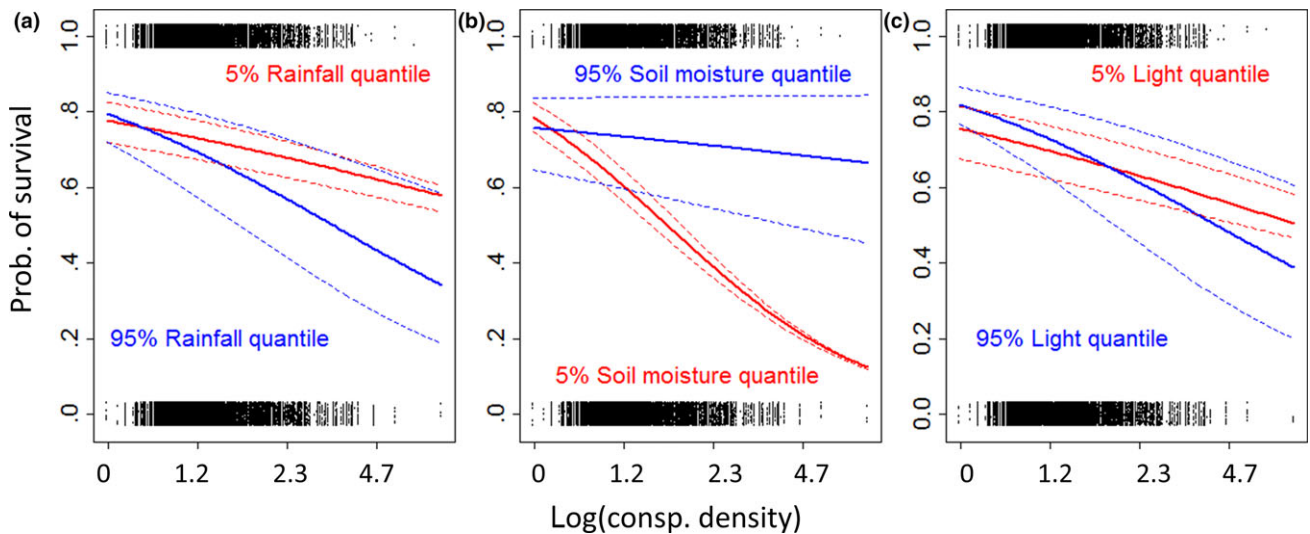
FIGURE 6 Seedling survival responses to the interactive effects of the number of conspecific seedlings and (a) rainfall, (b) soil moisture, and (c) understory light

change in solar radiation will likely influence forest regeneration and the dynamics of tropical forests.

When aggregating all 25 species, annual rainfall did not influence seedling survival. This result is surprising given that 2015 was an extremely dry year at the study site and seedlings are thought to be extremely sensitive to changes in water availability. Although a handful of field studies spanning year-to-year variation in precipitation found lower seedling survival in dry seasons and years (Comita & Engelbrecht, 2014; Delissio & Primack, 2003; Marod, Kutintara, Tanaka, & Nakashizuka, 2002), supplemental irrigation led to increases in seedling mortality in other experimental studies (Swinfield et al., 2012; Thompson et al., 2010). The absence of a community-wide response may simply reflect averaging across divergent species responses.

The lack of an association between rainfall and community-wide survival does in fact mask substantial differences in species responses at the study site. Comparative experimental studies elsewhere have demonstrated large variation among species in performance under drought (Engelbrecht et al., 2005, 2007). Such differences reflect variation in water use strategies, including among others, rooting depth, deciduousness, water storage capacity, hydraulic architecture, and ability to regulate stomatal conductance (Comita & Engelbrecht, 2014). In our study, four of the six species showing negative responses to rainfall in individual analyses were lianas. Schnitzer (2005) suggested that the deep roots and efficient vascular systems of lianas enable them to suffer less water stress during seasonal droughts, giving them a competitive advantage over other woody plants. This strategy, however, may make them less competitive than tree seedlings in wetter conditions (Schnitzer, 2005). The fact that conspecific effects were more pronounced during years of high rainfall lend support to this idea. Interspecific variability in responses to rainfall may also reflect carryover effects of seed size on the seed-to-seedling transition (Muscarella et al., 2013). Seedlings of large-seeded species that rely on cotyledon resources

well beyond germination may be particularly prone to desiccation during drought (Pritchard et al., 2004).

4.2 | Effects of soil moisture and light availability and interactions with climate on seedling survival

Seedling survival was higher in moist microsites at the community level and for all species for which results were significant. Topographic heterogeneity drives soil moisture at this study site with ridges being more drought-prone than valleys (Johnston, 1992; Silver et al., 1999). The strong showing of soil moisture as a consistent predictor of seedling survival supports findings elsewhere demonstrating the importance of soil moisture and topography in driving forest regeneration (Comita & Engelbrecht, 2009).

Soil moisture also modulated the effects of rainfall for some species. Survival responses of species that responded positively to high rainfall were slightly higher in dry sites, suggesting that moist sites buffer the effects of drought on regeneration (Dobrowski, 2011). For species that exhibited a negative response to rainfall, the positive effect of soil moisture on survival was only evident in years of low rainfall. Drought may increase seedling survival for these species in high soil moisture environments due to alleviation of anoxic soil conditions created by water logging, a common occurrence in areas with low topographic relief at the study site (Silver et al., 1999). These results highlight the need to consider the impacts of habitat favorability on plant demography across years and seasons since results are likely to vary depending on natural climate variability (Comita & Engelbrecht, 2009).

A large number of studies including this one support the notion that light availability is a primary driver of plant demography in the understory of tropical forests (Kobe, 1999; Montgomery & Chazdon, 2002). Previous studies at the site showed that seedling growth and survival increase during the high light conditions that follow hurricane disturbance (Comita et al., 2009); this longer dataset supports

these results. Only two species, the palms *P. acuminata* and *R. borin-quena*, had lower survival at high understory light conditions. Lower survival for these species at such high light conditions could be due to desiccation or sun scald of seedlings growing under more open canopies. To some degree, these patterns represent life-history variation in responses to light where seedlings of shade-tolerant species tend to have higher survival in the shade, whereas seedlings of light-demanding species experience high mortality under low light, but have a strong growth response to canopy openings (Wright et al., 2010).

Understory light also exacerbated the positive effects of high solar radiation on seedling survival at the community scale. Greater canopy light interception reduces the average amount and variability in transmitted solar radiation (Canham et al. 1990). The large number of positive interactions between light and radiation results from the fact that individuals not severely light-limited can respond most to year-to-year variation in solar irradiance. To our knowledge, this is the first study to examine the synergistic effects of temporal variation in solar radiation and understory light availability on forest regeneration dynamics. Since solar radiation differs substantially between years (Dong et al., 2012; Wielicki et al., 2002), our findings might also explain why several field studies of seedling demography have failed to uncover significant light effects (Lin et al., 2014).

4.3 | Interactions between environmental factors and conspecific density on seedlings survival

Although direct effects of climate extremes on forests are well documented, there is growing consensus that indirect effects from biotic interactions can have large impacts (Allen et al., 2010; Clark et al., 2016). In this study, we found that the negative effects of conspecific density on seedling survival were amplified during years of high rainfall. Several recent studies suggest that enemy-mediated conspecific effects are exacerbated under wet and warm conditions (Bachelot et al., 2015; Comita et al., 2014a,b; Swinfield et al., 2012). This pattern could result from increased abundance of herbivores and pathogens in wet years (Coley & Barone, 1996; Jactel et al., 2012).

At the same time, the negative effects of conspecifics on seedling survival were more pronounced in dry microsites consistent with the expectation that negative density-dependent forces are stronger at unfavorable sites. Species partition water resources by utilizing a variety of water use strategies (e.g., root depth, Meinzer, Johnson, Lachenbruch, Mcculloh, & Woodruff, 1999) and competition for water among conspecifics may be particularly intense in drier sites. A recent rainfall manipulation experiment found that that seedling competition for water was more intense among conspecifics leading to lower seedling survival growth (O'Brien, Reynolds, Ong, & Hector, 2017). Low soil water availability can also place seedlings under physiological stress, making them more susceptible to pathogens. Often, pathogens can tolerate lower water stress than the plants they infect and the combination of pathogen infection and moisture stress on hosts can increase disease severity (Desprez-Loustau et al., 2006). An

alternative explanation is that pathogen and insect populations are more resource limited at dry microsites, and can only have a negative impact on seedlings beyond a threshold density of conspecifics.

Our analyses also found that negative density dependent effects were more pronounced in high light gap environments, in accordance with a previous study at the site (Comita et al., 2009). Seedlings of light-demanding species that tend to dominate gaps have shorter-lived leaves which may be more palatable to enemies (Coley & Barone, 1996; Mccarthy-Neumann & Kobe, 2008). Alternatively, asymmetric competition for light with larger conspecifics may be stronger in gaps (Uriarte, Canham, Thompson, & Zimmerman, 2004).

In conclusion, species responses to interannual climate variability are highly variable and dependent on their environment and neighborhood. Efforts to predict the long-term effects of a changing climate on tropical forests must take into account the effects of this environmental heterogeneity and how its effects on regeneration dynamics play out in long-term stand dynamics. Although there is less consensus among models regarding tropical drought than tropical temperature increases (Good, Jones, Lowe, Betts, & Gedney, 2013), most models do predict stronger droughts over Central America and the Caribbean (Neelin et al., 2006; Maloney et al. 2014), West Africa, and peninsular S.E. Asia (Zelazowski, Malhi, Huntingford, Sitch, & Fisher, 2010) and the Amazon basin (Joetzjer, Douville, Delire, & Ciais, 2013), which holds the largest intact tropical forest on earth. Climate change models also project a substantial increase in extreme precipitation associated with tropical storm events in the North Atlantic (Knutson et al., 2010). Given that economic development will likely lead to increases in atmospheric aerosols in many tropical regions (Hatzianastassiou et al., 2012; Wild, 2009), greater attention to the role of interannual variability in solar radiation on forest regeneration is also warranted.

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