Revised: 13 July 2018

Resilience of seed production to a severe El Niño-induced drought across functional groups and dispersal types

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PRIMARY RESEARCH ARTICLE

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Funding information

National Science Foundation, Grant/Award Number: DEB-1053237 ; Biological and Environmental Research, Grant/Award Number: DE-SC0014363 ; Schweizerischer Nationalfonds zur Förderung der Wissenschaftlichen Forschung, Grant/Award Number: P3P3PA_167760; US Department of Energy; Office of Science

Abstract

More frequent and severe El Niño Southern Oscillations (ENSO) are causing episodic periods of decreased rainfall. Although the effects of these ENSO-induced droughts on tree growth and mortality have been well studied, the impacts on other demographic rates such as reproduction are less well known. We use a four-year seed rain dataset encompassing the most severe ENSO-induced drought in more than 30 years to assess the resilience (i.e., resistance and recovery) of the seed composition and abundance of three forest types in a tropical dry forest. We found that forest types showed distinct differences in the timing, duration, and intensity of drought during the ENSO event, which likely mediated seed composition shifts and resilience. Drought-deciduous species were particularly sensitive to the drought with overall poor resilience of seed production, whereby seed abundance of this functional group failed to recover to predrought levels even two years after the drought. Liana and wind-dispersed species were able to maintain seed production both during and after drought, suggesting that ENSO events promote early successional species or species with a colonization strategy. Combined, these results suggest that ENSO-induced drought mediates the establishment of functional groups and dispersal types suited for early successional conditions with more open canopies and reduced competition among plants. The effects of the ENSO-induced drought on seed composition and abundance were still evident two years after the event suggesting the recovery of seed production requires multiple years that may lead to shifts in forest composition and structure in the long term, with potential consequences for higher trophic levels like frugivores.

KEYWORDS

climate change, drought-deciduous, ENSO, evergreen, forest succession, lianas, plant-climate interactions, reproductive phenology, tropical forests

1 | INTRODUCTION

El Niño Southern Oscillations (ENSO) are episodic events that are associated with warmer and drier conditions in tropical forests around the globe, and many climate change scenarios project the frequency and severity of these events to increase (Cai et al., 2014; Dai, 2013; Huang & Xie, 2015). Although predictions of the timing and intensity ENSO events have improved, the impacts on forest

demographic rates remain poorly understood, especially as ENSO events simultaneously alter growth, mortality, and reproductive processes that are mediated by multiple mechanisms including physiological responses, biological interactions, and abiotic variables (Allen et al., 2017; Bebber, Brown, & Speight, 2004; Itoh et al., 2012; Maza-Villalobos, Poorter, & Martínez-Ramos, 2013; O'Brien, Leuzinger, Philipson, Tay, & Hector, 2014; O'Brien, Reynolds, Ong, &

Hector, 2017). Therefore, assessing the effects of ENSO events on forest demography while incorporating multiple variables across species, functional groups, and forest communities is important for improving our understanding and in turn predictions of the effects of ENSO-induced drought.

Seed production is an important process in tropical forests because it determines forest regeneration and diversity as well as providing food sources for vertebrates and invertebrates (Granados, Brodie, Bernard, & O'Brien, 2017; Vazquez-Yanes & Orozco-Segovia, 1993). Reproduction rates depend on multiple variables including the synchronization of flowers and pollinators (Augspurger, 1981), resource availability during the development of flowers and fruits (Ågren, 1989; Ågren, Ehrlén, & Solbreck, 2008; Borchert, 1983) and environmental conditions during production and dispersal of seeds and fruits (Primack, 1987). Furthermore, tree seeds develop over fairly long periods from weeks to months and disturbances at any point in the development can impact seed production (Borchert, 1983; Primack, 1987). Therefore, reproduction in forests is sensitive to shifts in climatic variables-such as changes in temperature and precipitation associated with ENSO events-that affect the diversity, quality, and abundance of seeds produced in a forest (Lasky, Uriarte, & Muscarella, 2016). This sensitivity in conjunction with the difficulty of tracking seed production over temporal scales relative to tree growth and survival has led to an understudied demographic rate in tropical forests (Mendoza, Peres, & Morellato, 2017), especially in terms of episodic climatic fluctuation such as ENSO events (but see Detto, Wright, Calderón, & Muller-Landau, 2018).

Multiple variables contribute to community-level seed production in tropical forests (Lasky et al., 2016). The composition of the forest community can promote stability in seed production as species and functional groups may vary in reproductive strategies (Borchert, 1983; Primack, 1987). For example, evergreen and drought-deciduous tree species in tropical dry forests have different resource allocation strategies, which may be effected by different climatic variables (Álvarez-Yépiz et al., 2017; Reich & Borchert, 1984). In addition, seed production between drought-deciduous and evergreen species may have unique temporal responses to dry conditions because drought-deciduous species may require additional time to regrow leaves before seed development (Borchert, 1983; Detto et al., 2018; Reich & Borchert, 1984). In contrast to tree species, lianas may have a distinctly different vulnerability to drought than trees and appear to be increasing in abundance in tropical forests (DeWalt et al., 2010; Schnitzer, 2005; Schnitzer & Bongers, 2011). These three functional groups represent different drought strategies whereby lianas adjust osmotic potentials to maintain turgor (Maréchaux, Bartlett, Iribar, Sack, & Chave, 2017), evergreen trees maintain function through cavitation resistance (Adams et al., 2017; Markesteijn, Poorter, Paz, Sack, & Bongers, 2011) and drought-deciduous trees avoid desiccation by shedding leaves (Mcdowell et al., 2008). These strategies might have effects on the maintenance of seed production during drought and the temporal recovery of seed production following drought (Wright & Calderon, 2006), and assessing variation in seed production across functional groups may provide insights into the variables that mediate responses to climatic variability.

In addition to the mechanistic importance of functional traits and groups for understanding plant responses, the effect of climatic fluctuations on dispersal types offers insights into the cascading impacts on other trophic levels (Curran & Leighton, 2000; Curran & Webb, 2000; Frankie, Baker, & Opler, 1974) as well as the spatial distributions of regeneration in forests recovering from climatic disturbance (Caughlin, Ferguson, Lichstein, Bunyavejchewin, & Levey, 2014). Previous studies in seasonally dry forests have suggested that fleshy fruited species and wind-dispersed seeds have different fruiting phenologies (Frankie et al., 1974), indicating that they might respond differently to climatic variability and drought. If tree species dependent on vertebrate dispersal are sensitive to ENSO events, then the effects will cascade to frugivores that depend on those seeds (van Schaik, Terborgh, & Wright, 1993). Alternatively, if wind-dispersed seeds are negatively impacted by ENSO events, then species distributions within forests may become underdispersed or clumped, which can in turn influence other processes such as competition (Caughlin, Ferguson, Lichstein, Zuidema, et al., 2014).

For tropical dry forests, which have a seasonal dry period, drought may negatively affect forest demographic rates through either reducing the annual rainfall or through a drier and longer dry season (Allen et al., 2017; Murphy & Lugo, 1986). However, these two components reduce water availability below typical levels either for the dry season or the wet season (Guan et al., 2015). Therefore, assessing annual water deficit encompasses both periods, and the response of forest demographic rates both during (resistance) and after (recovery) drought relative to predrought levels determines the resilience of the ecosystem process-for example seed production (Ingrisch & Bahn, 2018: Mitchell et al., 2016). This temporal component is important as functional groups or dispersal types could maintain seed production during drought (high resistance) but have slow recovery to predrought production, or alternatively, seed production could decrease rapidly during drought (low resistance) but recover quickly after drought (overall resilient). Therefore, understanding the impact of ENSO-induced drought on seed production requires assessing responses through time relative to predisturbance conditions.

Here, we examine the composition and abundance of seeds from a seed rain dataset across different forest types spanning four years in a tropical dry forest in Costa Rica, which included one of the most severe ENSO events on record (Figure 1a). The dataset included a predrought period before the ENSO event, a drought of approximately 12 months and two years postdrought, which allowed us to assess resistance and recovery of seed production to drought. First, we assessed the species composition of the seed rain in three forest types across the four years of sampling to highlight differences in community-level responses. We posit that the forest types, which consist of different species and proportions of functional groups, will differentially respond to the timing, duration, and intensity of the ENSO event. Second, we assessed the impacts of ENSO-induced drought on seed abundance from two perspectives that are not



FIGURE 1 Moving cumulative rainfall for previous 12 months. (a) Rainfall was summed across the previous 12 months from January 1981 until December 2017. Gray bars represent the four periods with more than two consecutive months of less than 1,000 mm moving 12-month cumulative rainfall. (b) The moving 12-month cumulative rainfall for the period of seed fall sampling from January 2014 until December 2017 for the Palo Verde site (gray) and Santa Rosa sites (black). We assumed the drought began at cumulative rainfall below 1,000 mm (solid vertical lines) and ended after more than 2 months of cumulative rainfall above 1,000 mm (dashed vertical lines). The two sites showed different timing, duration and intensity of drought

completely orthogonal (i.e., the roles of the categorical variables are not mutually exclusive) to test two hypotheses. (a) Functional groups will be differentially affected by ENSO-induced drought with reduced seed abundance in drought-deciduous species relative to evergreen and liana species, and (b) seed dispersal types will show contrasting patterns in response to ENSO-induced drought, which has implications for seedling regeneration and vertebrates.

2 | MATERIALS AND METHODS

2.1 Study sites

This study was carried out Parque Nacional Palo Verde located in the Área de Conservación Arenal-Tempisque (10.358 N, 85.358 W) and in Sector Santa Rosa, formerly known as Parque Nacional Santa Rosa located in the Área de Conservación Guanacaste (10.848 N, 85.628 W) in northwestern Costa Rica. At Parque Nacional Palo Verde, we sampled a single forest type consisting of a mixture of drought-deciduous and evergreen species (referred to as Palo Verde throughout). We sampled in two distinct forest types in Sector Santa Rosa: (a) a typical diverse tropical forest consisting of a mixture of drought-deciduous and evergreen species (referred to as Santa Rosa throughout) and (b) an evergreen forest dominated by the live oak *Quercus oleoides* with low abundance of co-occurring drought-deciduous and evergreen species (referred to as Santa Rosa Ok throughout). All plots in the three different forest types consisted of secondary forest in various stages of recovery from grazing, and plots spanned a gradient of forest age within each forest type. Details of forest composition and soil types can be found in Powers, Becknell, Irving, and Perez-Aviles (2009). The average annual rainfall (SD) at the Palo Verde site from 2008 to 2017 was ~1,600 mm (465), and at the Santa Rosa sites from 1981 to 2017, average rainfall (SD) was ~1,700 mm (700). The dry season typically lasts about 5 months between January and May, and the mean annual temperature is approximately 25°C. The ENSO event from late 2014 to 2016 was the longest and most intense drought in the area since 1983 to 1984 (Figure 1a).

2.2 Seed sampling

Six plots of 20×50 m were placed within each of the three forest types (18 plots in total) stratified by stand age. These plots are a subsample of a larger 84 plot network and are broadly representative of the variation across the landscape (Becknell & Powers, 2014; Powers et al., 2009). Along a center transect running the length of the plot, four seed traps were placed every 10 m (10, 20, 30 and 40 m). The dimension of the traps was 50×50 cm and they were mounted 75 cm above the ground on square rebar frames. Traps were lined with plastic screening with ~1 mm mesh size. Seed sampling was carried out monthly beginning in October of 2013 until December of 2017. All seeds and fruits in the traps were counted, identified to species, and assigned to a functional group (drought-deciduous, evergreen or liana) based on Powers and Tiffin (2010) and dispersal type (vertebrate, gravity/autochory and wind) based on

Hilje, Calvo-Alvarado, Jiménez-Rodríguez, and Sánchez-Azofeifa (2015). See Supporting Inforamtion Table S1 for the list of species, their functional groups, dispersal types, and seed mass (from Vargas, Werden, & Powers, 2015). The Poaceae spp. (grasses) were excluded from the all analysis due to their difficulty to identify and the focus on forest species.

2.3 | Defining drought

Instead of using a temporal definition of the ENSO event that began at the end of 2014 and ended at the end of 2016, we defined the drought empirically as a moving 12-month cumulative total below 1,000 mm (Figure 1), which is approximately less than one standard deviation below the mean rainfall. We chose a 12-month period because smaller increments emphasized the natural precipitation fluctuations between the wet and dry seasons, and as drought can effect either of these periods through decreased rainfall during the wet season or lengthening the dry season, using 12-month cumulative rainfall encompasses both periods (Guan et al., 2015; Murphy & Lugo, 1986). Furthermore, seed production is predominantly during the dry season (Figure 2), and flowering and fruit development often depends on resources of the previous year, which further emphasizes the importance of using 12-month cumulative rainfall. Therefore, the drought period was determined separately for each conservation area based on the rainfall data collected at Santa Rosa and Palo Verde. This method provided a guantifiable definition of drought and allowed the two sites to vary in the timing and duration of drought based on the moving 12-month cumulative total.

2.4 | Statistical analysis

To assess the compositional shifts due to rainfall and time, we used a constrained analysis of proximities on the Jaccard distance matrix of monthly presence-absence data (pooled to the plot level) and the constraining terms year (a factor with four levels; 2014, 2015, 2016, and 2017) and moving 12-month cumulative rainfall (a continuous variable). Because forest types had distinct compositions (Powers et al., 2009), this analysis was performed separately for each forest type. We tested the significance of the constraining terms with a permutation test. If the inertia in the permuted models (null model with no constraining terms) was lower than in the constrained model, then the association was considered statistically significant. If the overall model was significant, then we tested the significant effect of each constraining variable with moving 12-month cumulative rainfall tested before year. These analyses were performed with R statistical software (version 3.3.2; https://r-project.org). The constrained analysis of proximities was performed with the capscale function (Legendre & Anderson, 1999), and the permutation test was carried out with the anova.cca function in the VEGAN package.

To assess the importance of functional groups and dispersal types on seed abundance during drought, we first partitioned months into predrought, drought, and postdrought periods based on the moving 12-month cumulative rainfall, which allowed us to assess resistance 5273



FIGURE 2 Seed production over the 4 years of sampling. The three panels are for (a) Palo Verde, (b) Santa Rosa, and (c) Santa Rosa Oak. The different lines and points represent the six different plots in each forest type and are included to just show the within forest type variability. Most seed fall occurred during the dry season each year (i.e., January to July)

(drought period) and recovery (postdrought period). We analyzed seed abundance as a function of rainfall period (a factor with three levels: predrought, drought, and postdrought), forest type (a factor with three levels: Palo Verde, Santa Rosa, and Santa Rosa Oak), functional group (a factor with three levels: drought-deciduous, evergreen, and liana) and all two-way interactions using a generalized-linear mixed-effects model. The same analysis was performed with dispersal type (a factor with three levels: vertebrate, wind, and gravity/autochory) WILEY— Global Change Biology

instead of functional group. We used a negative-binomial distribution with a log link function and random terms for plot nested within forest type (a factor with 18 levels), plot nested in forest type nested in period (a factor with 54 levels), plot nested in forest type nested in year (a factor with 72 levels), forest type nested in year (a factor with 12 levels), and functional group/dispersal type nested in year (a factor with 12 levels). See Supporting Information Table S2 for the ANOVA table of Wald statistics and variance components for functional group and Supporting Information Table S3 for dispersal type. All generalized-linear mixed-effects models were performed with the asreml-R package (ASReml 3, VSN International, UK) in the R statistical software (version 3.3.2; https://r-project.org).

3 | RESULTS

3.1 | Drought timing and intensity

Although the two conservation areas are less than 80 km apart, they showed distinctly different drought patterns (Figure 1b). The drought at Palo Verde started in October 2014 and went to November 2015, had a 12-month duration, and had a minimum moving 12-month cumulative rainfall of 750 mm. By contrast, the drought at the Santa Rosa and Santa Rosa Oak forest types began in April 2015 to June 2016, lasted 14 months, and reached a minimum moving 12-month cumulative rainfall of 625 mm. Therefore, the drought at Palo Verde had an earlier timing, shorter duration, and lower intensity than the Santa Rosa types.

3.2 | Seed rain

Over the four-year period, we identified ~18,000 seeds from 67 species among the three forest types (Figure 2). The seed rain composition of the three forest types (see Supporting Information Table S1 for the species list) was differentially affected by moving 12-month cumulative rainfall and year (Figure 3). Palo Verde was not significantly affected by the constraining terms (p = 0.1 for the overall model) while the constraining terms significantly affected Santa Rosa (p = 0.002 for the overall model) and Santa Rosa Oak (p = 0.002 for the overall model). However, the effect on the Santa Rosa composition was driven by year (p = 0.001) while the Santa Rosa Oak composition was different across the moving 12-month cumulative rainfall gradient (p = 0.001).

Functional groups mediated seed abundance across rainfall periods and forest types (Figure 4). Drought-deciduous and evergreen species had significantly fewer seeds at the Palo Verde type both during drought (difference between predrought and drought = -4.3 log-seeds, 95% CI: -6.1 to -2.6) and during postdrought (difference between predrought and postdrought = $-4.9 \log$ -seeds, 95% CI: -7.7 to -2.1) periods. The effect of drought on these two functional groups at Santa Rosa and Santa Rosa Oak types was not significantly different from predrought seed abundance. However, there was a lag effect on droughtdeciduous species whereby seed abundance was significantly reduced relative to predrought seed abundance after the return of rainfall in both the Santa Rosa (difference between predrought and postdrought = -2.4 log-seeds, 95% CI: -4.4 to -0.4) and Santa Rosa Oak (difference between predrought and postdrought = -2.3 log-seeds, 95% CI: -4.2 to -0.4) types. Seed abundance of liana species was mostly unaffected by drought, with seed abundance remaining consistently similar among predrought, drought and postdrought periods for all forest types except for significantly fewer seeds during drought relative to predrought at the Palo Verde forest type (difference between predrought and drought = $-2.1 \log$ -seeds, 95% CI: -4.0 to -0.1).

Seed abundance during and after drought was not significantly different on average among dispersal types but instead varied by



FIGURE 3 Constrained PCoA of seed communities in each forest type. PCoA of Palo Verde (a), Santa Rosa (b) and Santa Rosa Oak (c) forest types after constraining for the 4 years of sampling and the moving 12-month cumulative rainfall (black line; Rain). The gray text represents species with an identifier for the functional group and dispersal type (DW, drought-deciduous and wind; LW, liana and wind; DV, drought-deciduous and vertebrate; EV, evergreen and vertebrate; LV, liana and vertebrate; DG, drought-deciduous and gravity; LG, liana and gravity)

forest type (Figure 5). Palo Verde had significantly fewer seeds during drought and postdrought periods for all dispersal types (Figure 5b) while in Santa Rosa and Santa Rosa Oak forest types, wind-dispersed seed abundance was maintained during drought and postdrought periods (Figure 5d.f). However, in Santa Rosa and Santa Rosa Oak forest types, seed abundance was lower for both vertebrate and gravity dispersed seeds during drought (Figure 5d,f). Furthermore, there were lag effects for vertebrate-dispersed seeds whereby seed abundance was significantly lower during recovery for Santa Rosa (difference between predrought and postdrought = -2.6 log-seeds, 95% CI: -4.9 to -0.3) and Santa Rosa Oak (difference between predrought and postdrought = $-2.9 \log$ -seeds, 95% CI: -5.2 to -0.7). The same pattern was found for gravity dispersed seeds at Santa Rosa (difference between predrought and postdrought = $-2.9 \log_{-1}$ seeds, 95% CI: -5.1 to -0.6) and Santa Rosa Oak (difference between predrought and postdrought = -3.2 log-seeds, 95% CI: -5.4 to -1.0).

4 | DISCUSSION

Our assessment of seed composition and abundance in three forest types in tropical dry forests before, during, and after an ENSO-induced drought found differential responses among functional groups and dispersal types through time. Interestingly, seed abundance, but not composition, at Palo Verde was more significantly impacted than the Santa Rosa forest types despite a shorter and less intense drought, which indicate the unique forest composition mediated these responses. Our findings of significant regional variation in seed production in response to drought suggest that studies conducted at isolated field stations may not reflect overall responses across the landscape; thus, such studies should be extrapolated to broader spatial scales with caution. Within functional groups, drought-deciduous species had reduced seed production during drought and continued to decline in abundance even after the return of typical rainfall. By contrast, lianas, and to a lesser extent evergreen species, maintained seed abundances during and after drought suggesting a high degree of resistance and overall resilience to ENSO-induced drought for these two groups. Vertebrate and gravity dispersed seeds were the most inhibited by drought showing an overall low resilience of larger seeded species even after nearly 2 years postdrought. Overall, these results suggest that ENSO-induced drought promoted small seeded species (i.e., lianas and wind-dispersed species) that would be typical of early successional species with a colonization strategy.

4.1 | Composition shifts

Forest types showed distinct patterns in seed community composition in response to interannual cycles and rainfall quantity. The effect of drought on forest function is often partitioned into four variables: (a) timing, (b) intensity, (c) frequency, and (d) duration (Mitchell et al., 2016), and the different species compositions likely responded differently to these variables. Palo Verde seed Global Change Biology –WILEY

composition was not significantly different among years or across rainfall quantity, which was likely due to the earlier onset (October 2014 to November 2015), shorter duration (12 months), or less intense drought (750 mm minimum moving 12-month cumulative rainfall). The drought at the Santa Rosa and Santa Rosa Oak forest types started later (at the end of the dry season; April 2015 to June 2016) was longer (14 months) and more intense (625 mm minimum moving 12-month cumulative rainfall). Therefore, forest type differences between Palo Verde and the Santa Rose types could be due to either timing, duration, intensity, or some combination of the three. These variables are likely working in conjunction with the different unique compositions among forest types.

However, the differences between Santa Rosa and Santa Rosa Oak can be separated into timing and intensity effects. The community at Santa Rosa was significantly different among years suggesting timing was important while Santa Rosa Oak showed a pattern whereby months with more similar moving 12-month cumulative rainfall had more similar seed composition (i.e., an effect of drought intensity). These results suggest that different forest compositions can vary in their sensitivity to temporal and intensity variables of drought (Mitchell et al., 2016), which is likely due to the underlying species sensitivities within these different forest communities (O'Brien, Ong, & Reynolds, 2017). Again, this regional variation in forest responses to drought underscores that we need phenological datasets that are both long term (Detto et al., 2018; Pau et al., 2013) and distributed over geographic/spatial gradients (Mendoza et al., 2017).

4.2 | Functional groups

In addition to regional variation, we also found variation in how functional groups responded to drought. Seed production of drought-deciduous species was most sensitive to the ENSO-induced drought followed by evergreen and lianas. Furthermore, drought-deciduous species showed prolonged negative effects even with the return of typical rainfall conditions, which suggests lag effects on this functional group which may be due to prioritizing leaf flushing over reproduction after drought (Borchert, 1983).

Lianas species were on the opposite end of the spectrum with similar seed numbers across all sampling periods at all forest types. Liana numbers are increasing in many tropical forests around the globe due to increasing drought and seasonality (DeWalt et al., 2010; Schnitzer & Bongers, 2011). Our results suggest the maintenance of seed production by liana individuals during drought may contribute to the increasing liana abundance found in tropical dry forests. Maintained seed production during drought relative to trees may lead to more rapid germination and establishment of lianas after drought thereby promoting liana establishment over trees, especially in newly formed gaps created by drought-induced mortality (Schnitzer & Carson, 2010). Coupling seed numbers with seedling establishment following drought is needed to support this hypothesis, but our results indicate that the liana seed bank is maintained during ENSO events. As lianas repress reproductive output by trees (García



FIGURE 4 Seed abundance as a function of functional group. Seed abundance (95% CI) as a function of rainfall period for Palo Verde (a, b), Santa Rosa (c, d), and Santa Rosa Oak (e, f) forest types. The left panels (a, c, e) are absolute estimates (log-scale) for predrought, drought, and postdrought periods of drought-deciduous (\bigcirc), evergreen (\blacksquare), and liana (\blacksquare) functional groups. The right panels (b, d, f) are the difference between predrought and drought (resistance) and predrought and postdrought (recovery) abundance. If confidence intervals cross the gray line at zero, then differences are statistically indistinguishable from predrought levels. Abundance is on the log-scale for readability

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FIGURE 5 Seed abundance as a function of dispersal types. Seed abundance (95% CI) as a function of rainfall period for Palo Verde (a, b), Santa Rosa (c, d), and Santa Rosa Oak (e, f) forest types. The left panels (a, c, e) are absolute estimates (log-scale) for predrought, drought, and postdrought periods of vertebrate (O), gravity (•), and wind (•) dispersal types. The right panels (b, d, f) are the difference between predrought and drought (resistance) and predrought and postdrought (recovery) abundance. If confidence intervals cross the gray line at zero, then differences are statistically indistinguishable from predrought levels. Abundance is on the log-scale for readability

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León, Martínez Izquierdo, Mello, Powers, & Schnitzer, 2018), increasing liana abundance coupled with drought-induced decreases in seed production of trees could further exacerbate potential food shortages for frugivores, as lianas tend to have wind-dispersed seeds.

Seed abundance in evergreen species showed a strong interactive effect with forest type whereby only evergreen species in Palo Verde had reduced seed production during the ENSO event. The difference in response between the forest types is likely due to unique species that are present at the Santa Rosa forest types but not found at Palo Verde (i.e., only three evergreen species were shared among the forest types). Therefore, even though functional groups explained large differences in responses, it appears that species-level differences may explain forest type-level differences within functional groups (O'Brien, Ong, et al., 2017).

4.3 | Dispersal types

Vertebrate-dispersed seeds were the most negatively affected by the ENSO event with reduced seed production at all forest types after the onset of drought and continuing even with the return of typical rainfall. This result suggests that ENSO-induced drought will have cascading negative effects on frugivores due to reduced food production (Harrison, 2001; Lasky et al., 2016). Furthermore, the gravity dispersed seeds-the second largest seed size after vertebrate dispersed—showed significant reductions by the recovery period, which indicates an overall reduced quantity of large seeded species that could severely impact resources for frugivores. By contrast, wind-dispersed species-with significantly smaller seedsmaintained production across all periods, again, consistent with the fact that lianas tend to have wind-dispersed seeds and liana seed production was less affected by drought. This continued seed production of small seeded species would suggest a feedback whereby drought-induced mortality of the overstory creates gaps that promote the establishment of small seeded species with a colonization strategy (Dalling & Hubbell, 2002; Muller-Landau, 2010). Therefore, ENSO events may not only induce overstory mortality but support the establishment of early successional species. However, the longterm impact on forest regeneration will be determined not only by seed production, but overstory mortality, and comprehensive results on long-term forest demographic rates will need to include effects at all stages of development.

Our results provide detailed support of long-term data on ENSOinduced drought effects on seed fall (Detto et al., 2018). Both functional groups and dispersal types showed lag effects on seed production as evidenced by low seed abundance of larger seeded species even 2 years after typical precipitation levels had returned. However, detailed analysis at longer time-scales is necessary to understand the effects on species demographic rates, especially for species that do not produce seeds on annual cycles (Chapman, Wrangham, Chapman, Kennard, & Zanne, 1999) or that display masting behavior (e.g., *Quercus oleoides*) which may have longer recovery times than annual seed producers. Our assessment of a four-year seed rain dataset that includes a severe ENSO-induced drought suggests strong negative effects on drought-deciduous species and larger seeded species that depend on vertebrates for dispersal. These asymmetric impacts on larger seeded species coupled with increased canopy openness due to drought-induced mortality of canopy trees will favor the establishment of smaller wind-dispersed seeds such as lianas and tree species with a colonization strategy, thereby promoting secondary successional process. Furthermore, seed abundance of drought-deciduous and vertebrate-dispersed seeds had yet to recover to predrought quantities even two years after the drought suggesting these ENSO events set these forests to earlier successional stages that have long-term impacts on the forest composition and structure.

ACKNOWLEDGEMENTS

MOB was supported by the Swiss National Science Foundation through an Advanced Postdoc Mobility Fellowship (P3P3PA_167760). The plots were set up and monitored with funding from the National Science Foundation CAREER Grant DEB-1053237 and US Department of Energy, Office of Science, Office of Biological and Environmental Research, Terrestrial Ecosystem Science (TES) Program under award number DE-SC0014363 to JSP. We thank Camila Pizano and two anonymous reviewers for comments that improved the manuscript.

AUTHOR CONTRIBUTIONS

MOB analyzed the data and wrote the manuscript. DPA carried out the sampling, sorted and identified seeds, and maintained the experimental infrastructure. JSP setup and designed the sampling strategy and contributed to writing and revision.

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How to cite this article: O'Brien MJ, Peréz-Aviles D, Powers JS. Resilience of seed production to a severe El Niño-induced drought across functional groups and dispersal types. *Glob Change Biol.* 2018;24:5270–5280. <u>https://doi.org/10.1111/</u>gcb.14416