Implications of a long-term mast seeding cycle for climatic entrainment, seedling establishment and persistent monodominance in a Neotropical, ectomycorrhizal canopy tree

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Abstract
In Guyana, we examined temporal variability and ecological consequences of seed-based reproduction in the ectomycorrhizal, monodominant leguminous canopy tree Dicymbe corymbosa using an extensive 2003–2017 dataset encompassing two masting events. Annual seed output, predation and nutrient investment were recorded in primary D. corymbosa forests. Seedling establishment, survival and growth were monitored. Mast seeding occurred in 2003 and 2016 and low seeding events occurred every 3–4 years, separated by non-reproductive years. In accordance with predicted climatic entrainment of regional masting, El Niño-intensified dry seasons preceded each masting event but not low seeding events. The regularly variable seeding pattern by D. corymbosa suggests that innate supra-annual periodicity may initiate D. corymbosa flowering. Internal resource thresholds may also contribute to periodicity, but El Niño-associated intensified dry seasons appear necessary to entrain mass flowering and successful mast seeding across the region. In accordance with a predator satiation hypothesis, seed predation was proportionally higher during low seed years. Competitive gains from the 2016 masting event were evidenced by strong replenishment of declining seedling pools.

KEYWORDS
Detarioideae, Dicymbe, El Niño, Fabaceae, Guiana Shield

1 | INTRODUCTION

Mast seeding (or “masting”) is the supra-annual synchronous heavy fruiting of a plant (Kelly & Sork, 2002). Mast seeding is exhibited primarily by iteroparous perennial woody plants and is best known from temperate ecosystems (e.g., many Fagaceae, Pinaceae; Crone & Rapp, 2014; Herrera, Jordano, Guitlan, & Traveset, 1998; Kelly & Sork, 2002; Koenig & Knops, 2000; Sork, 1993). While a recent masting review failed to elaborate on tropical mast seeding (Pearse, Koenig, & Kelly, 2016), significant examples are known in Asian Dipterocarpaceae (Ashton, 1987; Janzen, 1974) and Neo- and Afro-tropical Fabaceae (Henkel, Mayor, & Woolley, 2005; Newbery, Chuyong, & Zimmerman, 2006). Dicymbe corymbosa Spruce ex Benth. (Fabaceae subfam. Detarioideae) is a canopy tree from the central Guiana Shield that provides a classic example of mast seeding in a monodominant tree in lowland tropical moist forest (Henkel, 2003; Henkel et al., 2005). The species meets the requirements for “persistent monodominance” as it dominates >60% of the over-, mid-, and understory individuals in a stand, and lacks edaphic specialization (Connell & Lowman, 1989). Dicymbe-dominated forests cover much of the lower elevation terrain in the central Pakaraima Mountains of Guyana (Degagne, Henkel, Steinberg, & Fox, 2009; Fanshawe,
1952. **Dicymbe corymbosa** exhibits several life history traits which, taken together, are unique among tropical tree species worldwide. These include: (a) the ectomycorrhizal (ECM) habit (Henkel, Terborgh, & Vilgalys, 2002), (b) broad edaphic amplitude (Henkel, 2003), (c) cumulative shoot and root reiterative growth leading to large, multi-stemmed, clonal individuals of indeterminate age (Woolley, Henkel, & Sillett, 2008) and (d) episodic, large-scale sexual recruitment through mast seeding (Henkel et al., 2005). This collusion of evolved traits allows partial escape from density-dependent effects on recruitment, control over above- and belowground resources, and competitive exclusion of sympatric non-ECM tree species, ensuring **D. corymbosa** spatiotemporal dominance (e.g., Henkel et al., 2005; McGuire et al., 2008; Smith et al., 2017; Woolley et al., 2008).

Henkel et al. (2005) detailed the 2003 mast seeding event in the central Pakaraima Mountains of Guyana. This mast featured regional synchrony, high stand-level reproductive resource investment, and ballistic/barochorous seed dispersal. Density-dependent mortality effects were low, and a large shade-tolerant seedling cohort was established. Regional entrainment of this masting event was posited to be due to an intensified dry season coincident with the 2002–2003 El Niño Southern Oscillation (hereafter “El Niño”) event. However, there remains uncertainty with regards to climatic initiation and entrainment of **D. corymbosa** seeding events and the ecological importance of mast and non-mast years in long-term seedling recruitment.

Because of uncertainty in the causes of masting, including the roles of resource, biotic and climatic factors in driving regional entrainment (Crone & Rapp, 2014; Koenig, Knops, Carmen, & Pearse, 2015; Pearse et al., 2016), we planned to track the reproductive behavior of **D. corymbosa** through a complete masting cycle. This would allow accurate determination of the coefficient of variation of seeding in the species (sensu Kelly, 1994) for comparison to other masting species, assessment of relationships of flowering with regional weather cues, and shed light on the competitive consequences of variable seeding. Following the 2003 mast, data were obtained annually over an unexpectedly long inter-mast period spanning 2004–2015, within which three low seed years occurred. With the super El Niño and teleconnected intensified dry season conditions for northern South America arising in late 2015 and extending into 2016, we predicted that a **D. corymbosa** mass flowering would occur in February–March of 2016, followed by a mast seeding event, and designed field work accordingly. In addition to fully documenting the 2016 mast, we specifically asked: (a) Is there a proximal relationship between weather variables, seeding patterns and resource relations over an extended period encompassing non-reproductive, low seed and mast seeding years?, (b) With comparable datasets between mast years and low seed years, is there evidence for a predator-satiation evolutionary mechanism?, and, (c) What are the impacts of a long inter-mast period on **D. corymbosa** seeding populations and persistent monodominance?

## 2 MATERIALS AND METHODS

### 2.1 Study site

The study was conducted in monodominant **D. corymbosa** forest along the Upper Potaro River in Guyana’s Pakaraima Mountains. Study plots were located within a 15-km radius of a permanent base camp near the Potaro River (5°18’04.8” N; 59°54’40.4” W), with elevations of 700–750 m above sea level. The site was situated in an undulating valley 20 km east of Mt Ayanganna, and was densely forested with primarily **Dicymbe**-dominated and to a lesser extent mixed forests of the *Eschweilera–Licania* association (Degagne et al., 2009; Fanshawe, 1952). In the **D. corymbosa**-monodominant stands no other ECM tree species occur (McGuire et al., 2008). Regional synchrony of **D. corymbosa** seed production was assessed along a 37-km transect from the Upper Potaro to the Upper Ireng River (Henkel et al., 2005). Details of climate, geology, soils, forest structure and the 2003 masting event can be found in Henkel et al. (2002, 2005) and Henkel (2003).

### 2.2 Study plots

In 2003, five 50× 50 m² (0.25-ha) study plots (P1–P5) were randomly positioned within 2 km of the Potaro base camp in larger areas of monodominant **D. corymbosa** forest (Henkel et al., 2005). Two additional Upper Potaro 0.25-ha plots (P6–P7) were added in 2005, with P6 located 1.5 km southeast of the base camp, and P7 located 5 km southwest of the base camp. In 2009, three spatially distant 0.25-ha plots (P8–P10) were added along the 37-km Potaro-Ireng transect. P8 was located 15 km east of the base camp, P9 was located 10 km east of the base camp and P10 was located 9 km east of the base camp, all on low, flat ridges. In July 2016, an additional spatially distant plot (P11) was established 37 km south of the base camp on a slope with brown sand soil near the Upper Ireng River. Similar to P1–P5, P6–P11 were heavily dominated by **D. corymbosa** with soils that were uniformly acidic and low in extractable P (<12 ppm; Henkel et al., 2005). Twenty 3 × 3 m² (9 m²) seed traps were randomly positioned on the ground in each study plot to annually assess **D. corymbosa** seedfall.
Seeds and fruit valves were counted in each seed trap at the mid-July peak dispersal period and during the end of the dispersal period in late August. In most years, all traps had no or very few seeds or valves, and these were considered non-reproductive years. In 2006, 2009 and 2013, it was evident that a small scale but synchronous seeding event was occurring and seed traps were visited more frequently between mid-July to early September. Seeds and valves were counted and post- and pre-dispersal predation was recorded using methods described below. Reproductive biomass and mineral nutrient investment for the 2006, 2009 and 2013 low seed years were calculated using the mean seed and valve dry weights taken from 100 bulk grab samples of composite collections made across plots P1–P5 following the methods described below. In each of the original masting plots P1–P5, new seedlings established during these low seed years in the 2 × 4.5 m² (9 m²) survivorship subplots (up to 10 per plot; Henkel et al., 2005) were tagged and survivors counted annually up through July 2017, along with surviving seedlings and saplings from the pre-2003 and 2003 cohorts. For logistical reasons, survivorship was not sampled at 96 and 132 months.

2.3 | Inter-mast monitoring 2004 to 2015

Undamaged seeds and fruit valves were removed and counted from each seed trap in P1–P7 at 5-day intervals from 20 June to 28 July, then in early September after the end of seed dispersal. Given the ballistic/barochorous mechanism of seed dispersal in D. corymbosa (described in Henkel et al., 2005), seed and valve removal every 5 days from an individual trap ensured that all seeds and valves present in the trap at the next visit were mature and had fallen in the previous 5 days, and allowed summing of the total inputs over the entire sampling period (see Zagt, 1997 for the similar congener Dicymbe alstonii). Damaged seeds and fruit valves were separated and sorted into predation categories and counted at each sampling event, based on direct observation of predators and/or damage symptoms. Pre- and post-dispersal predation categories were: (a) ant feeding on seeds (primarily harvester ants; post-dispersal), (b) larval bore holes in fruit valves and seeds (putatively Bruchidae, Coleoptera; pre-dispersal; Janzen, 1969), (c) bird-diagnostic tears and rips of fruit valves (macaw and parrot; pre-dispersal), (d) fungal hyphal growth and putrescence of seeds in the absence of animal damage (pre- and post-dispersal) and (e) terrestrial vertebrate tooth marks on seeds (post-dispersal). For the spatially distant plots P8–P10, these counts were performed in early and late July and early September. The most distant plot, P11, was counted once for all seeds and fruit valves in early September. Subsequently, seed traps in all plots were revisited 1 year post-mast on 5 July and 30 August.

2.5.2 | Seedfall and predation

Seedfall and predation

2.5 | 2016 mast flowering, seedfall, predation, reproductive resource investment and seedling establishment

2.5.1 | Flowering

In late February 2016, the proportion of sun-exposed crown branches bearing flowers was recorded for all D. corymbosa canopy trees in P1–P10. Frequency and intensity of pollinator visitation during full anthesis was also qualitatively noted. Abscission of flower parts other than ovaries was complete by mid-March.
Reproductive mineral investment for the 2016 mast was estimated for each plot by multiplying the mean nutrient concentration of each reproductive component by the mean dry mass quantity \((m^{-2})\) of that component extrapolated to a kg ha\(^{-1}\) basis.

2.5.4 Seeding establishment and survival

New 2016 mast seedlings were tagged and counted in September 2016 in each of the P1–P5 seedling survivorship subplots established in 2003 (Henkel et al., 2005). Total area sampled in these long-term survivorship subplots was 469 m\(^2\) \((n = 10\) 9-m\(^2\) subplots for P1–P4; \(n = 31\) 3-m\(^2\) subplots for P5). Some subplots were lost due to tree falls. Surviving 2016 mast seedlings were recensused at 6- and 12-month intervals in 2017.

2.6 Seedling growth 2007–2017

Annually within P1–P5 from 2007–2010, and subsequently in 2017, up to six seedlings from each of the pre-2003 seeding and 2003 seeding cohorts were randomly selected within each survivorship subplot and their height measured from ground level to the uppermost apical bud. Seedling height values used in subsequent analyses were the average height per subplot. In July 2017, hemispherical photography was used to quantify percentage canopy openness directly above each survivorship subplot. A north-oriented digital color photograph was taken at the center of each subplot using a Canon EOS Rebel T3 camera (Canon Inc., Tokyo, Japan) fitted with a Rokinon 8 mm F3.5 fisheye lens (Samyang Optics Co., Masan, South Korea) held level at 2 m above the ground (“fisheye” setting). The photographs were analyzed with GapAnalyzer 2.0 software using standard protocols given in Frazer, Canham, and Lertzman (1999).

2.7 Climatic data

For the period 1996–2017, satellite-derived outgoing long wave radiation (OLR) monthly anomalies (deviation of outgoing re-radiated energy from the long-term monthly mean) and precipitation anomalies on a 2.5° lat/long grid resolution centered on the Potaro site (5°N, 60°W) were downloaded from the International Research Institute for Climate Prediction (http://iridl.ldeo.columbia.edu/maproom/Global/). This time span encompassed an observed 1998 and the quantified 2003 and 2016 \(D.\ corymbosa\) mast seeding events. Additional anecdotal information concerning dry season conditions following El Niño events was obtained from local inhabitants of the region, including indigenous farmers and miners. Monthly OLR anomalies are positively correlated with reduced cloud cover and increased solar irradiance of the forest canopy, and negatively correlated with precipitation, in northeastern South America in the months following strong El Niño events in the central Pacific (Kogan, 2000; Lyon & Barnston, 2005).

We examined the relationship between summed monthly OLR and precipitation anomalies that were apparent during the period of August to March immediately preceding each known 1998–2016 seeding event (i.e., three mast and three low seeding events). In the central Pakaraima Mountains, this period encompasses the beginning of two typically short dry seasons (August–October and February–March) and through the period of flower anthesis (late February), pollination, and the beginning of fruit development (early March). The increased canopy irradiance and associated photoassimilative boosts could stimulate reproductive investment during these months (Graham, Mulkey, Kitajima, Phillips, & Wright, 2003). Anomalies were also summed from the backcasted 2 years prior August to March period to account for the possibility of current year flower initiation responding to the previous year’s environmental cues, a proximal relationship implicated in other masting species (Kelly et al., 2013; Newbery, Chuyong, & Zimmerman, 2006).

2.8 Statistical analyses

All data were graphically analyzed using JMP 13.1.0 statistical software (SAS Institute Inc., Cary, North Carolina) and statistically tested in either JMP or the R 3.3.1 Statistical Environment (R Core Team, 2016). Mixed effect regression models were fit with the lme4 package (Bates, Mächler, Bolker, & Walker, 2015). Plot, or subplot within plot, was treated as a random effect to accommodate any unique clustered variances associated with environmental conditions. All linear model fits were assessed for violations of normality and heteroscedasticity. Hypothesis testing of explanatory variables used Likelihood Ratio tests with Type III ANOVA Satterthwaite approximation of degrees of freedom in the lmerTest package (Kuznetsova, Brockhoff, & Christiansson, 2017).

Specifically, seedfall during mast and low seed years were compared using mixed effect models comparing the seedfall during two quantified mast seeding events to the three low seed years. The random effect of plot permitted comparison across years differing in plot number. Seedling height in 2017 was regressed against canopy openness using linear mixed effect models of the log value of seedling height with the random effect of plot (P1–P5). Decadal seedling growth rates of the pre-2003 and the 2003 seeding cohorts were compared for the period of 2007–2017 using...
the random effects of subplot nested within plot. For both seedling correlation analyses, marginal (fixed) and conditional variance (defined as both fixed and random factors) $R^2_{GLMM}$ values were reported as goodness-of-fit statistics using the MuMIn package (Bartoń, 2017), as defined in Nakagawa and Schielzeth (2012). Pre-dispersal and post-dispersal predation plot values for combined mast seed years ($n = 14$) and combined low seed years ($n = 27$) were compared using a nonparametric Wilcoxon rank sum test. Cumulative August–March monthly OLR and precipitation anomalies for each of years 1998–2016 were summled and a logistic test with $\chi^2$ approximation used to predict mast seeding or low seeding years.

3 | RESULTS

3.1 | Reproductive behavior during the inter-mast years

During the years 2004, 2005, 2007, 2008, 2010, 2011 and 2012 no seed output was detected for *D. corymbosa*. These years were considered non-reproductive. Low seed years occurred in 2006, 2009 and 2013 in which seedfall was recorded at low but consistent levels in all traps and plots sampled, with mean ($\pm$SE) seeds m$^{-2}$ of 2.3 $\pm$ 0.4 (2006), 3.6 $\pm$ 0.4 (2009) and 3.2 $\pm$ 0.7 (2013) (Figure 1).

The proportion of post-dispersal seed predation during low seed years was significantly higher than that of mast years ($p < .001$, Figure 2), as was pre-dispersal fruit predation ($p < .001$, data unavailable for the 2003 mast; Figure 3).

![Figure 1](image1.jpg)

**FIGURE 1** Estimated seed fall in *Dicymbe corymbosa* plots from 2003 to 2016. Black box plots represent the two observed mast years and gray box plots represent low seed years. Seed fall in 2003 was measured in P1–5, 2006 in P1–P7, and 2009–2016 in P1–P10. Median values are shown in white, and quartiles with solid fill. Seed fall in the two mast years was significantly higher than that of low seed years based on a random effect model comparing the fixed effect of masting and the random effect of plot ($p < .001, F = 68.8$)

![Figure 2](image2.jpg)

**FIGURE 2** Post-dispersal seed predation for *Dicymbe corymbosa* for low seed years and mast seeding years. Predation was significantly higher during low seed years ($n = 27; p < .001$, nonparametric Wilcoxon rank sum test). Median values are shown in white, quartiles with solid fill, and an outlier in red

![Figure 3](image3.jpg)

**FIGURE 3** Pre-dispersal fruit predation for *Dicymbe corymbosa* for low seed years and mast seeding years. Predation was significantly higher during low seed years ($n = 27$) relative to mast seeding years ($n = 14; p < .0001$, nonparametric Wilcoxon rank sum test). Median values in are shown in white and quartiles with solid fill

3.2 | 2016 flowering

A regionally synchronous *D. corymbosa* mass flowering event occurred in late February 2016, with canopy trees in full anthesis in all *D. corymbosa* monodominant stands. Heavy flowering ranged from 75 to 100% of sun exposed
crown branches for all canopy trees in each of P1–P10. The large flowers at full anthesis were 2–3 cm diameter, with cream-colored petals, in masses on exposed crown branches. Observed pollinators were bees, with numerous daytime visits to anthetic flowers. Within 2–3 days of opening, an individual flower's petals abscised and fell to the forest floor. The observed mass flowering in February across all plots was corroborated by the dry masses of abscised flower parts ranging from 30.4 to 99.4 g m\(^{-2}\) across P1–P10 in July (Table S1).

### 3.3 | 2016 seed output, synchrony, predation and reproductive investment

The seedfall mean (±SE) values for *D. corymbosa* during the 2016 mast for P1–P10 ranged 2.8 ± 0.3 to 17.5 ± 2.3 seeds m\(^{-2}\), with a global mean across plots of 8.9 ± 1.5 seeds m\(^{-2}\) (Table S1). This global mean approached the 12.5 ± 1.6 seeds m\(^{-2}\) seen in the 2003 mast and was significantly higher than those of the low seed years (Figure 1). Extrapolations to the stand level yielded a mean estimate of 89,999 seeds ha\(^{-1}\), ranging from 27,778 to 174,778 seeds ha\(^{-1}\) across the 10 plots (Table S1). Plots with lower seed output (e.g., P5, P6) had sustained some recent treefall loss of reproductive crown branches. Regional synchrony in masting was inferred by the uniform seed production measured in the Upper Potaro plots P1–P7, the Potaro-Ireng transect plots P8–P10 9–15 km distant, and 37 km distant plot P11 on the Upper Ireng River (with 6.2 ± 0.4 seeds m\(^{-2}\); Table S1). Subsequently, no seed output was detected in 2017. The calculated population level coefficient of variation (CV\(_p\); SD across all years divided by the mean seed output across all years) for *D. corymbosa* from 2003 to 2017 was 1.87.

Proportional seed predation was low during the 2016 mast. Pre-dispersal predation by beetle larvae (14.4%) was greater than that by birds (1.3%). Post-dispersal predation by several species of ant averaged 10.9 ± 0.8% of seeds on the ground, with fungal damage found in only 3% of seeds. Post-dispersal predation by vertebrates was essentially absent; only five seeds out of 17,208 that were directly examined had small rodent tooth marks, and no evidence was found of ground-turning by peccaries or seed scatter-hoarding by agoutis. Some interplot variation in predation levels was recorded (Table S1), but even in plots with higher post-dispersal predation (e.g., P3) the amount of seeds that escaped predation to germinate and establish seedlings amounted to tens of thousands ha\(^{-1}\).

Seeds were flattened-orbicular in shape and ranged from 2 to 4 cm diameter across the longest axis. Mean 2016 seed dry mass was 5.2 g per seed, very close to the mean of 5.1 g recorded in the 2003 mast (Henkel et al., 2005). Valves of the dry dehiscent legumes were flattened-elongate and ranged from 10 to 40 cm in length with up to 13 seed pockets; mean dry mass was 19.1 g per valve. Mean dry mass of flower parts was 66.9 g m\(^{-2}\). Extrapolated to the stand level, combined dry mass of seeds, fruit valves and flower parts of the 2016 mast averaged 3,117 ± 327 kg ha\(^{-1}\) across P1–P10 (range 1,444–4,884 kg ha\(^{-1}\); Table S1). Concomitant mineral nutrient investment in reproductive parts was: N: 41.2 ± 5.0 kg ha\(^{-1}\); P: 1.6 ± 0.2 kg ha\(^{-1}\); K: 12.5 ± 1.7 kg ha\(^{-1}\); Ca: 5.6 ± 0.7 kg ha\(^{-1}\); and Mg: 3.2 ± 0.4 kg ha\(^{-1}\). The average reproductive resource investment values for dry mass and minerals of the 2003 and 2016 mast events were generally two-fold greater than those of the low seed years (Table 1).

### 3.4 | Leaf litter relative to reproductive resource investment

Over a 4-year period spanning 2004–2008 *D. corymbosa* average annual leaf litterfall dry mass was estimated at 1,664 kg ha\(^{-1}\) year\(^{-1}\), whereas the average of the 2003 and 2016 mast years' reproductive litterfall dry masses was 45% higher at 3,048 kg ha\(^{-1}\) year\(^{-1}\) (Table 1). Average mast year reproductive investment of mineral nutrients ranged from 20 to 40% higher than that of annual leaf litterfall for N, K and Ca, and was 69% higher for P, although Mg mast investment was 63% lower (Table 1).

### 3.5 | Seedling survivorship

Twelve months after establishment of the 2003 mast seedlings, total *D. corymbosa* seedling density (i.e., pre-2003 and 2003 cohorts) was >8 seedlings m\(^{-2}\), with an across-plot range of 41,000–92,000 seedlings ha\(^{-1}\) (Henkel et al., 2005). New seedlings were subsequently established at low densities during the low seed years of 2006, 2009 and 2013 (Figure 4). Collective 2004–2015 annual mortality rate of seedlings across cohorts was 5%; total surviving density had declined to 3.2 seedlings m\(^{-2}\) by June 2015, 1 year prior to the 2016 mast seeding (Figure 4). Seventy eight percent of these surviving seedlings were ≥ 13 years of age, of either the 2003 mast cohort (1.5 seedlings m\(^{-2}\)) or the pre-2003 group (1 seedling m\(^{-2}\)). Only 22% (0.7 seedling m\(^{-2}\)) of the surviving seedlings were from the low seed years of 2006, 2009 and 2013.

The 2016 mast seeding produced 3.2 new seedlings m\(^{-2}\) across P1–P5. Of these 2016 seedlings, 2.9 seedlings m\(^{-2}\) had survived after 6 months. After 12 months 2.6 seedlings m\(^{-2}\) had survived, restocking the across-cohort total standing pool to an average of nearly 5.8 seedlings m\(^{-2}\), with an estimated range of 34,200–68,000 seedlings ha\(^{-1}\) (Figure 4). By this time, 75% of all living seedlings
were derived from the 2003 and 2016 masting events, 15% were from the low seed years, and 10% were from the pre-2003 age group. Similarly, 43.1% of the 144 saplings (i.e., 1–10 cm diameter individuals) monitored since 2003 were still alive in 2017.

### 3.6 | Seedling growth 2007–2017

Seedling height was positively correlated with canopy openness in 2017 for both pre-2003 seedlings and 2003 cohort seedlings ($R^2_c = 0.34$ and $0.31$, respectively, when plot specific variance was accounted for; $p = .014$) (Figure S1). For the 11 year period (2007–2017) average annual seedling growth rates were nearly identical for pre-2003 and 2003 seedlings at 1.04 and 1.05 cm growth year$^{-1}$ ($p < .001$), respectively, when accounting for plot and subplot specific variance (Figure S2).

### 3.7 | El Niño-related climate effects and D. corymbosa seeding

The three known $D. corymbosa$ masting events of 1998, 2003 and 2016 were preceded by El Niño-driven sustained positive monthly OLR anomalies in Guyana's Pakaraima Mountains (Figures 5 and S3). Negative precipitation anomalies followed the same pattern (Figure 5). Local inhabitants of the Upper Potaro study region reported dramatic increases in daily sunshine in the 1997–1998 and 2002–2003 dry seasons (Henkel et al., 2005), as well as in the 2015–2016 dry season reported here, in each case with greatly reduced surface water flows and numerous accidental forest fires associated with slash and burn farming. The summed August–March monthly OLR anomalies preceding the 1998, 2003 and 2006 mast seedings at 1.04 and 1.05 cm growth year$^{-1}$ ($p < .001$), respectively, when accounting for plot and subplot specific variance (Figure S2).
2013 did not follow strong, prolonged El Niño events or sustained positive monthly OLR anomalies in the preceding August–March period (Figures 5 and S3). For non-seeding years, the summed preceding August–March OLR anomaly values were generally low. An exception was that the sustained August–March positive OLR and negative precipitation anomalies in 2009–2010 did not result in a detectable seeding event in 2010 (Figures 5 and 6a,b). Backcasting of the August–March period to 2 years prior to reproduction had no predictive power for either masting or low seeding events (Figure 6c,d).

4 | DISCUSSION

4.1 | Climate variables, seeding patterns, and resource relations over a long inter-mast interval

Over 2003–2017, all stands of D. corymbosa exhibited high inter-annual variability in seeding, with two synchronous masts and three low seed years occurring in the 15 year period. The resulting CV of 1.87 is similar to that described for masting, wind-pollinated, predator-dispersed seed plants (i.e., 1.77, Kelly & Sork, 2002), but much higher than that described from other biotically pollinated and abiotically dispersed species based on a meta-analysis of 570 seeding variability studies of >6 years duration (i.e., 0.74; Kelly & Sork, 2002). It may be that CV values alone poorly differentiate bimodal, supra-annual seeding species from annually seeding species that have high year-to-year variability in seed production (Norden et al., 2007).

4.1.1 | Regional entrainment to El Niño teleconnections

Population-wide synchronization of masting requires entrainment of flowering, typically in response to a broad environmental cue (Pearse et al., 2016). There is evidence across the Guiana Shield that the intensified dry season conditions of reduced cloud cover and increased solar irradiance provide such a cue (Hammond & ter Steege, 1998; ter Steege & Persaud, 1991; Thomas, 2001). The last three D. corymbosa masting events were preceded by strong Pacific El Niño conditions and in western Guyana highly positive OLR anomalies persisted for several months leading up to the February–March flowering period relative to all other years (Figures 5 and 6a,b). These conditions have also been repeatedly corroborated on the ground by local inhabitants of the Upper Potaro
study region for multiple El Niño events from 1997–2016. It is possible that these consecutive months of prolonged high irradiance provide both the entrainment cue for mass flowering and the non-structural carbohydrates (NSC) necessary to "fuel" the enormous carbon investment in masting. While NSC data are currently lacking for *D. corymbosa*, the results of other studies corroborate such a mechanism. Accumulation of NSC immediately prior to a masting event has been observed in tropical and temperate canopy trees (Newbery, Chuyong, & Zimmerman, 2006; Piovesan & Adams, 2001; Sork, 1993; Wright, Carrasco, Calderón, & Paton, 1999; Wright & Van Schaik, 1994) followed by NSC depletion after masting (Miyazaki, Hiura, Kato, & Funada, 2002; Sala, Hopping, McIntire, Delzon, & Crone, 2012). Additionally, NSC storage between masting events appears minimal (Hoch, Siegwolf, Keel, Korner, & Han, 2013; Ichie et al., 2013) and during masting fruit bearing branches appear carbon autonomous (Hasegawa, Koba, Tayasu, Takeda, & Haga, 2003; Hoch, 2005). Such results further implicate a possible connection between elevated irradiance and carbon gain prior to masting.

4.1.2 | Low seed years

Summed OLR or precipitation anomalies did not differentiate non-reproductive years from low seed years in the months prior to, or 1 year preceding, flowering (Figure 6). Therefore, apart from some other unknown regularly occurring environmental cue, it is possible that the phenologically synchronous low seed years are internally entrained. Unlike the "alternate year bearing" seen in *D. altsonii* (Zagt, 1997), *D. corymbosa* reproduction appears intrinsically separated by 3–4 years (e.g., 2003, 2006, 2009, 2013, 2016, and corroborated by an observed flower bud initiation in January 2019; T. W. Henkel, personal observation). In this scenario, a sufficiently long but predictable flowering periodicity may allow accumulation of mineral nutrients capable of supporting mast fruiting during El Niño events (discussed further below).

Admittedly, our data set is of short duration relative to the indeterminate lifespan of *D. corymbosa* trees (Woolley et al., 2008). Nonetheless, the aforementioned periodicity mechanism could also explain the lack of reproduction in 2010 despite the intensified dry season conditions in preceding months (Figures 5 and 6a,b). For instance, a 2010 mast may have failed because the preceding low seed year resulted in extensive resource depletions, with the subsequent enhanced dry season irradiance insufficient to initiate flowering in such an "off" year (Borchert, 1983; Tucker, 2003). This idea is akin to the "match-mismatch" hypothesis developed by Cushing (1969, 1990) to describe how climatic variation affects fish recruitment. As a result of the interaction of innate periodicity and climatic cycles the increasing frequency of extreme El Niño events over the next 50 years (Cai et al., 2014) could alter both the magnitude and frequency of resource pulses in *D. corymbosa* forests as posited for Malaysian dipterocarps (Chen et al., 2018).

4.1.3 | Mineral nutrient proximate drivers

Proximate controls over supra-annual seeding include constraints imposed by resource limitations to flower or
fruit/seed production (Pearse et al., 2016). Reproductive events can temporarily exhaust internal nutrient supplies and select for alternating patterns in reproduction as seen in many species of wild and cultivated trees (e.g., Davis, 1957; Lloyd, 1980; Newbery, Chuyong, & Zimmerman, 2006; Rosecrance, Weinbaum, & Brown, 1998). *Dicymbe corymbosa* may have resource constraints that favor extended supra-annual periodicity in flowering which, as posited here with an interval of 3–4 years, could allow for multi-year replenishment of resources depleted by seeding events of any scale.

Fruit valves and flower parts constituted >70% of the total *D. corymbosa* mast reproductive litter and this material entered the detritus pool. Mineral nutrients contained therein could potentially be lost to leaching. Recovery of these mineral nutrients by extensive ectomycorrhizas may therefore be imperative, especially for P which is barely detectable in mineral soils at <12 ppm, and Ca which is mined directly from leaf litter (Mayor & Henkel, 2006). The average reproductive dry mass inputs from the two masting events was ca. 3.0 t ha$^{-1}$, nearly twice the average annual leaf litter inputs of ca. 1.7 t ha$^{-1}$. Masting P and Ca investments were 69 and 39% greater, respectively, than that lost to annual leaf litterfall (Henkel et al., 2005; Table 1). Such large investments suggest that P accumulation during prolonged inter-mast periods may be a prerequisite for masting on oligotrophic tropical soils, as proposed for African detarioids (Chuyong, Newbery, & Songwe, 2000; Newbery, 2005; Newbery, Alexander, & Rother, 1997; Newbery, Chuyong, & Zimmerman, 2006) and the Bornean dipterocarp *Dryobalanus aromatica* (Ichie & Nakagawa, 2013). In contrast, temperate masting trees in ECM Fagaceae appear more limited by N (Han, Kabeya, Iio, Inagaki, & Kakubari, 2014; Smaill, Clinton, Allen, & Davis, 2011), reflecting global gradients in relative nutrient availability (Mayor et al., 2015).

### 4.2 Predator satiation and masting

Selection for mast seeding requires an ultimate evolutionary driver to favor increased synchrony in supra-annual reproduction (Pearse et al., 2016). Hypothesized drivers for masting evolution include predator satiation (i.e., seed predators consume a smaller proportion of large seed crops) and pollination efficiency (i.e., higher cross-pollination in heavy-flowering years) (Bogdziewicz, Espelta, Muñoz, Aparicio, & Bonal, 2018; Crone & Rapp, 2014; Janzen, 1974). In the case of *D. corymbosa*, preliminary evidence supports a role for predator satiation due to the significantly higher proportional predation during low seed years relative to mast years. Given the absence of a vertebrate-based seed dispersal mechanism in *D. corymbosa*, the low phytochemical defense compounds of *D. corymbosa* seeds (Henkel et al., 2005), along with current seed predation performed largely by insects, it is conceivable that invertebrate predator selection pressure may have been a driver for a predator satiation mechanism, as recently posited for Bornean dipterocarps (Iku et al., 2017). However, prior vertebrate-based selective forces for masting evolution cannot be ruled out (Janzen, 1971, 1974; Waller, 1993). Additionally, chemical defense of seeds may have been lost after the evolution of masting. All told, there are limitations to the tractability of questions which address how extant community ecology of long-lived trees may have been shaped by macro-evolutionary processes (Johnson & Stinchcombe, 2007).

### 4.3 Seedlings and monodominance

Stand-wide expanses of *D. corymbosa* seedlings benefit from periodic mast seeding to maintain their high densities necessary for persistent monodominance. Over the 2003–2015 period prior to the 2016 mast, 83% of pre-2003 and 75% of 2003 mast seedlings had died, and seedling contributions from the three intervening low seed years were minimal. Density-dependent seedling mortality is the rule for tropical tree species regardless of whether they exhibit masting or monodominance (Queenborough, Burslem, Garwood, & Valencia, 2007). The long-term dataset reported here for *D. corymbosa* suggests that without a subsequent masting event the standing seedling and sapling pool would continue to decline, albeit slowly. Conversely, the near-term survival of *D. corymbosa* seedlings in deep shade, necessary to maintain the standing seedling stock, may be dependent on rapid ectomycorrhization – a trait not shared with competing species in *D. corymbosa* forest (Henkel, 2003; McGuire et al., 2008). The rare transition of an individual *D. corymbosa* seedling to sapling, pole and ultimately canopy tree must be very slow and dependent on small, transient light gaps resulting from stem attrition of highly reiterated, stand-dominating adult trees (Newbery, Chuyong, Zimmerman, & Praz, 2006; Woolley et al., 2008). The positive correlation between canopy openness and seedling heights in 2017 (Figure S1) provided a glimpse of such gap-driven seedling growth. All told, mast seeding may play a fundamental role in maintaining *D. corymbosa* dominance, by providing the periodic pulse of shade-tolerant seedlings necessary for slow, but inexorable, accession to the canopy.

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REFERENCES


**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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