

RESEARCH ARTICLE

Pre-dispersal seed predation could help explain premature fruit drop in a tropical forest

Eleanor E. Jackson¹  | S. Joseph Wright²  | Osvaldo Calderón² | James M. Bullock³  | Tom Oliver¹  | Sofia Gripenberg¹ 

¹School of Biological Sciences, University of Reading, Reading, UK

²Smithsonian Tropical Research Institute, Balboa, Republic of Panama

³UK Centre for Ecology and Hydrology, Wallingford, UK

Correspondence

Eleanor E. Jackson

Email: e.e.jackson@pgr.reading.ac.uk

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Abstract

1. Pre-dispersal seed mortality caused by premature fruit drop is a potentially important source of plant mortality, but one which has rarely been studied in the context of tropical forest plants. Of particular interest is premature fruit drop triggered by enemies, which—if density dependent—could contribute to species coexistence in tropical forest plant communities.
2. We used a long-term (31 year) dataset on seed and fruit fall obtained through weekly collections from a network of seed traps in a lowland tropical forest (Barro Colorado Island, Panama) to estimate the proportion of seeds prematurely abscised for 201 woody plant species. To determine whether enemy attack might contribute to premature fruit drop, we tested whether plant species abscise more of their fruit prematurely if they (a) have attributes hypothesised to be associated with high levels of enemy attack and (b) are known to be attacked by one enemy group (insect seed predators). We also tested (c) whether mean rates of premature fruit drop for plant species are phylogenetically conserved.
3. Overall rates of premature fruit drop were high in the plant community. Across all species, 39% of seeds were abscised before completing their development. Rates of premature seed abscission varied considerably among species and could not be explained by phylogeny. Premature seed abscission rates were higher in species which are known to host pre-dispersal insect seed predators and species with attributes that were hypothesised to make them more susceptible to attack by pre-dispersal enemies, namely species which (a) have larger seeds, (b) have a greater average height, (c) have temporally predictable fruiting patterns and (d) are more abundant at the study site.
4. *Synthesis.* Premature fruit drop is likely to be a major source of seed mortality for many plant species on Barro Colorado Island. It is plausible that pre-dispersal seed enemies, such as insect seed predators, contribute to community-level patterns of premature fruit drop and have the potential to mediate species coexistence through stabilising negative density dependence. Our study suggests that the role of pre-dispersal enemies in structuring tropical plant communities

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should be considered alongside the more commonly studied post-dispersal seed and seedling enemies.

KEYWORDS

determinants of plant community diversity and structure, forest dynamics plot, frugivory, fruit abortion, granivory, herbivory, immature fruit drop, Janzen–Connell hypothesis, plant–herbivore interactions

1 | INTRODUCTION

Seed production and seed survival are critical elements in the life cycle of a plant, giving rise to the next generation and mediating population- and community-level dynamics (Clark et al., 2007; Green et al., 2014; Maron & Crone, 2006; Turnbull et al., 2000). Mortality events that happen in early life can be a bottleneck for the recruitment of individuals to a population, with sometimes disproportionate effects on community composition (Fenner & Thompson, 2005; James et al., 2011; Rother et al., 2013; Roughgarden et al., 1988; Turnbull et al., 2000). A number of processes contribute to the success or failure of a developing seed, including nutrient availability (Bertamini & Nedunchezian, 2005; Martinez-Alcantara et al., 2012), microclimatic conditions (Einhorn & Arrington, 2018), weather (Najeeb et al., 2017; Reichardt et al., 2020) and interactions between the plant and other organisms. For plant species relying on biotic pollination, visits from pollinators are crucial for reproductive success, often manifesting as a direct positive correlation between pollinator visitation rate and seed set (Karron et al., 2006; Steffan-Dewenter et al., 2001). Following successful pollination, the developing seed might be a target for a range of enemies, including pre-dispersal insect seed predators (Fenner & Thompson, 2005), with deleterious effects on fitness.

A commonly observed phenomenon in plants is that some fruits are prematurely abscised, that is, they drop from the mother plant prior to completing their development. Plant species which regularly abscise a large proportion of their fruits form a taxonomically and ecologically diverse group (Stephenson, 1981) and it is currently unknown whether shared ancestry contributes to variation in rates of premature fruit drop across species. The ecological and agricultural research literature reports several causes of premature fruit drop. For example, changes in resource availability, through mechanisms such as herbivory (Stephenson, 1980), leaf shading (Einhorn & Arrington, 2018) and drought (Nussbaumer et al., 2020; Pérez-Pérez et al., 2008; Reichardt et al., 2020), can trigger premature fruit drop due to competition for resources among fruits (Bawa & Webb, 1984; Goubitz et al., 2002; Stephenson, 1981). Developmental or genetic abnormalities (Bradbury, 1929; Forino et al., 1987; Kraus, 1915), pollen quality (Goubitz et al., 2002) and damage to fruits through abiotic means, for example frost (Rodrigo, 2000; Rodrigo et al., 2006; Tagliasacchi et al., 2006), can trigger an individual to drop fruits which are unlikely to reach maturity and thereby minimise the cost to the parent plant (Stephenson, 1981). Damage by natural enemies can also lead to premature drop, often through seed/fruit predation or pathogen attack (Akinsanmi et al., 2016; Boucher & Sork, 1979; Planes

et al., 2014). Regardless of the exact mechanism causing premature fruit drop, the resulting seed mortality could—if it reduces the number of viable seeds produced by the plant—have important effects on plant population and community dynamics (Turnbull et al., 2000).

The phenomenon of premature fruit drop, including its causes and wider consequences, remains largely unexplored in the context of tropical forest plants (but see Bawa & Webb, 1984; Jones & Comita, 2010). Of particular interest is the potential for enemy-triggered premature fruit drop which, if widespread and showing patterns of positive density dependence (e.g. locally abundant species experiencing higher levels of premature fruit drop), could be a mechanism that contributes to the coexistence of plant species in these highly diverse systems (Chesson, 2000). Although the role of plant enemies in maintaining high local diversity of plant species has received substantial attention in the context of tropical forest plant communities since Janzen's (1970) and Connell's (1971) seminal papers, the bulk of research conducted to date has focused on enemies attacking seeds or young seedlings after their dispersal from the mother plant (e.g. Comita et al., 2014; Holl & Lulow, 1997; Levi et al., 2019). While pre-dispersal seed mortality has been highlighted as a potentially important source of mortality and facilitator of high local plant diversity in tropical forests (Gillett, 1962; Gripenberg, 2018; Janzen, 1970), enemy attack in the period prior to seed dispersal—as the fruit is developing—is only rarely considered in this context (e.g. Jones & Comita, 2010).

Taking advantage of a 31-year dataset on seed and fruit rain in the well-studied woody plant community of Barro Colorado Island, Panama, we relate patterns of premature fruit drop for 201 plant species (trees, shrubs, lianas) to (a) plant phylogeny, (b) plant traits and population attributes hypothesised to be associated with high levels of enemy attack and (c) previously documented patterns of attack by one enemy group (insect seed predators) known to trigger premature fruit drop in other settings (Follett, 2002; Tzanakakis et al., 1997). Through this approach, we assess whether enemies such as pre-dispersal seed predators are likely contributors to premature fruit drop and explore the potential consequences for plant biodiversity maintenance in tropical forests.

If pre-dispersal seed enemies are important contributors to premature fruit drop, we predict the following relationships between plant species traits (or population attributes) and levels of premature fruit drop:

1. **Positive relationship between seed mass and the proportion of seeds prematurely abscised.** Larger seeds are more valuable as

a food source to potential seed predators (Fenner et al., 2002). Additionally, large seeds might be exposed to predation from a wider range of seed predators (Greig, 1993; Mucunguzi, 1995) and for a longer period of time (Moles & Westoby, 2003); but see (Moles et al., 2003).

2. **Positive relationship between average tree height and the proportion of seeds prematurely abscised.** Taller tree species are more apparent to enemies because of a positive relationship between tree height and fruit crop size (Castagneyrol et al., 2013; Gripenberg et al., 2019a; Janzen, 1968).
3. **Negative relationship between investment in mechanical seed defences and the proportion of seeds prematurely abscised.** Species that invest large amounts of resources in seed protection are less vulnerable to seed predation (e.g. Kuprewicz & García-Robledo, 2010).
4. **Negative relationship between temporal crop size variation and the proportion of seeds prematurely abscised.** Species with more stable fruiting patterns over time are more prone to seed enemy attack, since they provide a more stable resource for seed enemies (Janzen, 1976).
5. **Positive relationship between temporal overlap in fruit production by other species and the proportion of seeds prematurely abscised.** Species fruiting at times of the year when many other species fruit experience lower seed predation due to satiation of generalist seed enemies (Kelly, 1994; Toy, 1991; Toy et al., 1992).
6. **Positive relationship between the local abundance of conspecifics and the proportion of seeds prematurely abscised.** Species with a high local population size are likely to be more prone to pre-dispersal enemy attack since the abundance of resources available to host-specific enemies will be higher (Hanski, 2001; Pacala & Crawley, 1992).

Finally, we predict that levels of premature fruit drop will be higher in plant species known to be attacked by pre-dispersal insect seed predators at our study site than for plant species for which such interactions have been looked for, but not detected (Gripenberg et al., 2019a).

2 | MATERIALS AND METHODS

Barro Colorado Island (BCI; 9°9'N, 79°51'W) is a 16 km² island situated in Gatun Lake in the Panama Canal, which supports semi-deciduous tropical forest with a 35-m tall canopy. The Smithsonian Tropical Research Institute is custodian of the Barro Colorado Nature Monument and Barro Colorado Island on behalf of the Republic of Panama. The BCI 50-ha forest dynamics plot was the first to be established within the CTFs-ForestGEO plot network in 1982 (Anderson-Teixeira et al., 2015). Since 1987, weekly censuses of seed rain have been conducted within the 50-ha plot as part of a research project coordinated by S. J. Wright (e.g. Wright et al., 1999, 2003, 2005; Wright & Calderon, 1995). The first set of seed traps ($n = 200$) was established in 1987 and has been continuously monitored since then. These seed traps are located at 13.5 m intervals on alternating sides of and 4–10 m from 2.7 km of pre-existing trails

within the 50-ha plot. Another 50 traps were added in naturally occurring tree fall gaps within the 50-ha plot between 2002 and 2004 and have been monitored since. A final set of 200 traps were established 2 m from each of the 200 original traps in 2011 and were censused for 23 months. Each trap consists of a 0.8 m tall PVC frame and 1 mm mesh covering 0.5 m² of forest floor. In weekly censuses, all fruits and seeds encountered in each trap are identified to species, counted and categorised as mature or immature. In the context of the long-term seed rain study, very young fruits collected in the traps immediately or shortly after flowering are termed 'aborted'. These were not included in this study. Fruits labelled as 'immature' were dropped several weeks to months later. The distinction between immature and mature fruits was based on the examination of endocarps: If the endocarp of seeds within a fruit is filled with material that is solid (rather than hollow or filled with liquid or soft substances), then the fruit was considered mature. Our species-specific estimates of rates of premature seed abscission are based on the relative frequencies of mature and immature fruits. Since we did not conduct systematic germination trials across the full range of species, we cannot rule out the possibility that some of the seeds scored as immature would be able to germinate. We are still confident that in the vast majority of cases, the seeds inside fruits scored as immature are indeed inviable (given the timing at which the bulk of premature fruit drop happens in many species) and that premature fruit drop typically translates to seed mortality in the studied plant community.

In this study, we used information on fruits and seeds from woody plant species (trees, shrubs and lianas) recorded in the traps during the period 1988–2018 (31 full calendar years). All analyses and data preparation were conducted in R v 4.0.5 (R Core Team, 2021). Counts of fruit in the traps were multiplied by species-specific average seed-to-fruit ratios (S. J. Wright, unpubl. data) and added to the number of seeds. For each species, the weekly counts ($n = 1,615$ censuses) of mature and immature seeds were then summed across all seed traps. This was done separately for each full calendar year in the dataset. Since 90% of species fruit only once during a calendar year, and since few species fruit in the December–January period, this approach will typically generate data on overall fruit drop rates for individual fruiting events. Not all species were encountered in every single year, but in total there were 5295 unique species × year combinations in the original dataset. Species × year combinations with fewer than 10 fruits or individual seeds were omitted to ensure a representative sample size, yielding a total of 3,286 observations in the final dataset.

To assess whether enemy attack is likely to have contributed to observed rates of premature fruit drop, we tested whether plant species with attributes hypothesised to signal susceptibility to enemy attack (see Section 1) prematurely abscised a larger proportion of their seeds. Additionally, for one pre-dispersal enemy group—insect seed predators—we were able to test whether species which are known to be attacked, prematurely abscised a larger proportion of their seeds. Plant attributes and associations between insect seed predators and plant species were obtained from previously

archived data collected from plant individuals at BCI (Gripengberg et al., 2019a, 2019b; Wright et al., 2010). Information on how plant traits and population attributes were estimated, and their original sources are provided in Table 1.

To assess the relationship between rates of premature fruit drop and each variable of interest, we constructed generalised linear mixed models (GLMMs) with binomial distributions using the `LME4` package (Bates et al., 2020). The number of prematurely abscised seeds and the number of viable seeds were combined into a single two-column binomial response variable. The explanatory variable was plant attribute (listed in Table 1) or the presence of insect seed predators, with plant species and year as random effects. Since for most explanatory variables, data were only available for a subset of plant species, each was tested independently (i.e. as continuous covariates in separate models). Two of the explanatory variables (local abundance of conspecifics and seed mass) were log-transformed and all explanatory variables were standardised (mean = 0, $SD = 1$) to aid model fitting and interpretation. The package `DHARMA` (Hartig, 2020) was used to generate scaled residuals by simulation from the fit models. The scaled residuals were plotted with `DHARMA` to verify the models were specified correctly. The Durbin–Watson statistic was used to test for temporal autocorrelation in the scaled model residuals for each plant species. The models were additionally fit with an AR(1) covariance structure using `GLMMTMB` (Brooks et al., 2021) to assess

the effect of potential temporal autocorrelation on the results. We assessed pairwise correlations between explanatory variables with Spearman's rank correlation coefficient, to test for multicollinearity. Results were visualised using `GGPLOT2` (Wickham, 2016) as model coefficient estimates and 95% confidence intervals.

To explore whether shared ancestry contributes to similarities in premature fruit drop among species within the community, we estimated the phylogenetic signal (the tendency for related species to be more similar than species drawn at random from the phylogenetic tree) in the proportion of seeds prematurely abscised. We used a previously archived phylogeny (Gripengberg et al., 2019b), which included 184 of the 201 plant species in our dataset, and species-specific mean proportions of seeds prematurely abscised for the phylogenetic analyses. Both Pagel's lambda (Pagel, 1997, 1999) and Blomberg's K (Blomberg et al., 2003) were estimated using 'phylosig' in the `R` package `PHYTOOLS` (Revell, 2012). The 'contMap' function was used to visualise phylogenetic signal in mean premature seed abscission as a continuous trait mapped onto the phylogenetic tree.

3 | RESULTS

Premature fruit drop in the BCI forest dynamics plot is common. Of the 1,222,863 fruits collected in the seed traps across all years and plant species, 632,835 (52%) were immature. Taking into account

TABLE 1 Plant traits and population attributes which are hypothesised to influence susceptibility to attack by seed enemies and descriptions of how they were estimated, as obtained from previously archived data (Gripengberg et al., 2019a, 2019b)

Plant attribute	Description of data used
Seed mass	Data on species-specific seed masses were available in the form of mean dry seed mass (g) where a 'seed' is defined to include the endosperm and embryo only. For most species, the mean seed mass was based on an average of 5 seeds collected from 5 individuals and dried to constant mass at 60°C (for some species, sample sizes were slightly lower).
Tree height	For each species, the average height (m) of the 5 tallest tree individuals in the 50-ha forest dynamics plot was used as an estimate of tree size. Data on this variable are available for free-standing species only.
Investment in mechanical seed defences	A dataset on species-specific protective tissue content was used as a measure of the degree of investment in mechanical seed defences, which reflected the proportion of diaspore mass made up by protective tissue (e.g. endocarps and seed coats) rather than seed mass. These data were obtained by dissecting diaspores into three parts: seed (embryo plus endosperm only), appendages to enable dispersal by wind and material to protect the seed. All materials were oven-dried at 60°C for at least 72 h and then weighed for dry mass. The protective tissue content was taken as the dry weight of the seed protection material divided by the diaspore dry weight.
Temporal crop size variation	As a measure of the extent of interannual variation in the size of the seed crop, a variable analogous to the variable CV_{year} in (Wright et al., 2005) was used, but implemented on a larger dataset involving more species and in which seed fall for each trap was averaged across a longer time period (1987–2010) than in the primary publication.
Temporal overlap in fruit production by other species	A subset of the fruit and seed rain dataset used in this study was used to calculate this metric. The subset was published in association with the study by (Wright et al., 2016) and included weekly counts of reproductive parts of plant species found in the first 200 traps between January 1987 and December 2014. For each species in this subset, temporal overlap in fruit production was calculated as the total number of other species observed to fruit in the same week as a given species.
Local abundance of conspecifics	The local abundance of reproductive-sized adult trees was estimated using data from the 2010 census of the ForestGEO plot (Condit, 1998; Condit et al., 2019). To estimate the number of reproductive adults in the 50-ha plot, species-specific maximum diameter at breast height (DBH_{max}) was extracted and individuals with a DBH larger than $0.5 \times DBH_{\text{max}}$ (the known size threshold for tree reproduction; Visser et al., 2016) were counted.

the (species-specific) mean numbers of seeds per fruit, this corresponds to 3,159,062 (39%) out of a total of 8,062,517 seeds being dropped from the tree as either immature single diaspores or as part of immature fruits. No prematurely abscised seeds were collected for 29 species, of these, 20 species (69%) had fewer than 100 seeds collected across the 31-year period. Of the remaining 172 species, 57 abscised more than 50% of total seeds when averaged across the 31-year study period (Figure 1).

Correlations between the explanatory variables were relatively weak (Figure S1). Of 867 species \times model combinations, 47 (5%) showed significant positive temporal autocorrelation (Durbin-Watson statistic <1 and $p < 0.05$) and 29 (3%) showed significant negative temporal autocorrelation (Durbin-Watson statistic >3 and $p < 0.05$) in the model residuals. Fitting the models with an AR(1) covariance structure to account for potential temporal autocorrelation had no effect on our results. Other than investment in mechanical seed defences, all the investigated plant attributes demonstrated a relationship with the proportion of seeds prematurely abscised at $p < 0.05$ (Figure 2; Table S1). All observed relationships with premature seed abscission rate, other than temporal overlap in fruit production, were in line with our predictions. We saw a clear positive effect on proportion of seeds prematurely abscised by four of the plant attributes: local abundance, seed mass, temporal overlap in fruit production (i.e. whether a plant species fruits at a time of the year when many other species are fruiting) and tree height. We detected a negative relationship between the proportion of seeds prematurely abscised and two of the studied plant attributes: temporal crop size variation and investment in mechanical seed defences. In our dataset, 28% of plant species had no known associations with insect seed predators on BCI. Plant species known to be attacked by at least one species of insect seed predator abscised a larger proportion of their seeds prematurely.

Estimates of phylogenetic signal in the mean proportion of seeds abscised were low ($K = 0.002$, $p = 0.10$; $\lambda = 0.33$, $p < 0.005$; Figure 3).

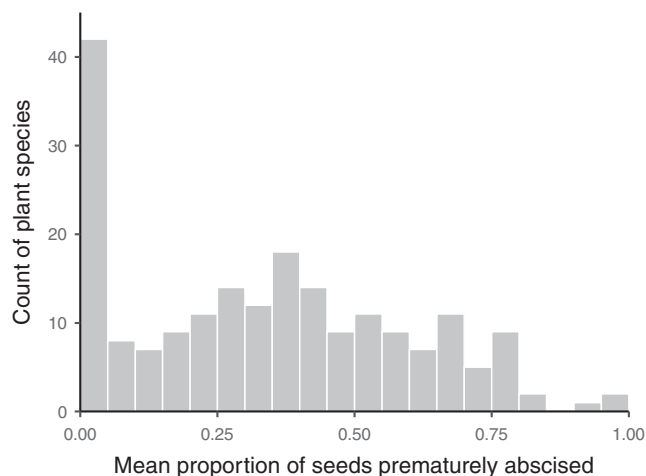


FIGURE 1 Average rates of premature seed abscission for 201 woody plant species on Barro Colorado Island. The proportion of seeds prematurely abscised per year for each plant species is averaged across 31 years to give the means presented here

4 | DISCUSSION

Although patterns of mortality at early stages in the life cycle of tropical forest plants can be important determinants of the structure of populations and communities at later life stages (Green et al., 2014), survival at the very earliest stages—when developing seeds are still attached to their mother plant—has rarely been studied in tropical forests (Gripengberg, 2018; but see Bawa & Webb, 1984; Jones & Comita, 2010). Our analysis of premature fruit drop in 201 woody plant species in the 50-ha forest dynamics plot on Barro Colorado Island, Panama, reveals that premature fruit drop is a widespread phenomenon at this site and likely to be an important source of seed mortality in the plant community, responsible for the deaths of up to 39% of all seeds initiated. Rates of seed abscission showed a weak phylogenetic signal, suggesting that shared ancestry can only explain a small amount of the variation observed across plant species. We found that five of the six plant attributes which we had predicted would be associated with enemy attack demonstrated a clear relationship with premature seed abscission. A key aim of our study was to assess whether plant species attacked by one group of pre-dispersal seed enemies—insect seed predators—show higher levels of premature fruit drop than species not attacked by this enemy guild. We found that plant species known to be attacked by insect pre-dispersal seed predators had higher rates of seed abscission. This suggests that these insects may play a role in triggering premature fruit drop.

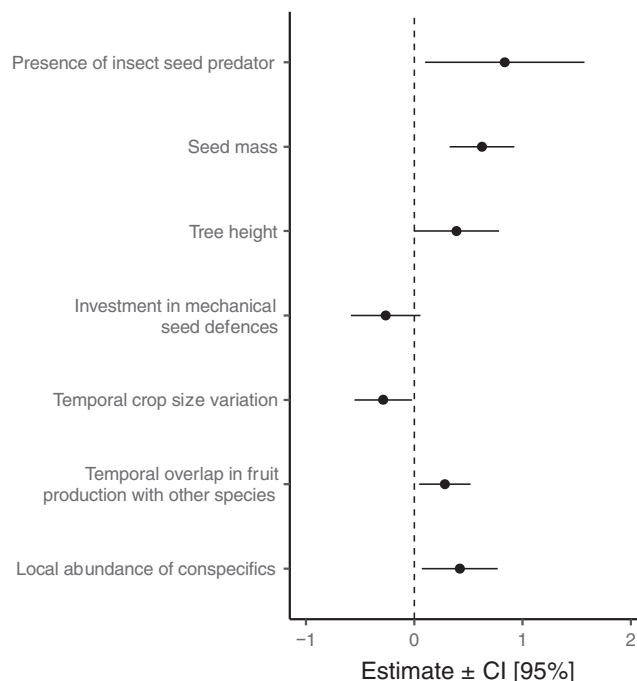


FIGURE 2 Relationships between premature seed abscission rates and plant attributes hypothesised to reflect likelihood of attack by seed enemies. Positive estimates represent increased premature seed abscission rates with increased attribute values, and the opposite for negative effects. Points are coefficient estimates from generalised linear mixed effects models. Error bars denote 95% confidence intervals

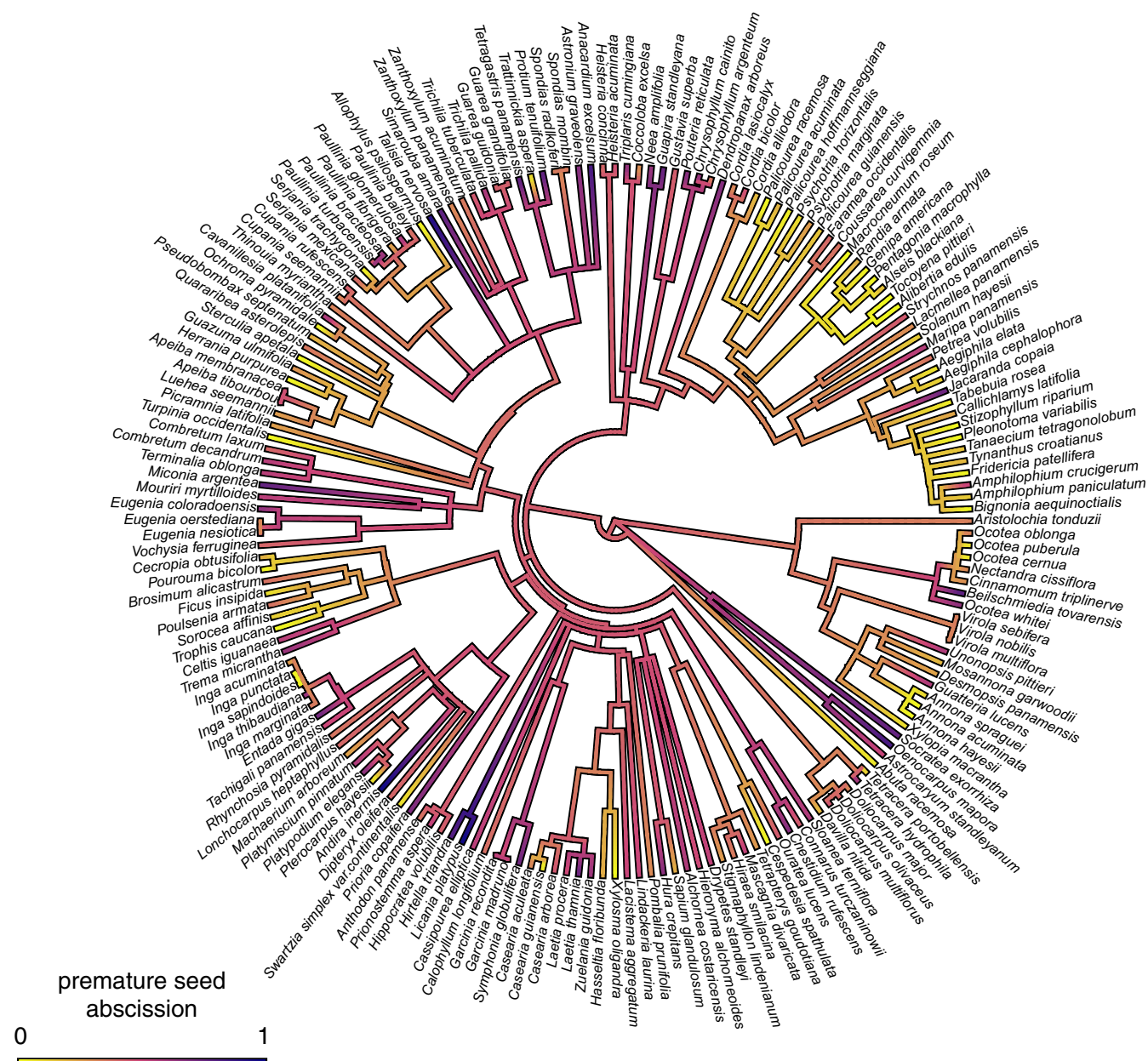


FIGURE 3 Reconstructed evolution of premature seed abscission rates for 184 woody plant species on Barro Colorado Island, Panama, using continuous character mapping. Based on the mean proportion of seeds prematurely abscised ($n = 31$ years), where yellow = lower proportion of seeds prematurely abscised, and purple = higher proportion of seeds prematurely abscised

The association between rates of premature seed abscission and traits hypothesised to make species more prone to seed predator attack is in agreement with previous studies of leaf herbivory in tropical forests, which have found that interspecific variation in enemy attack can be explained by variation in defensive traits (Cárdenas et al., 2014; Coley, 1983, 1988; Schuldt et al., 2012). Plant species with attributes associated with abundant resources for enemies, such as a large seed mass and high local abundance, prematurely abscised a larger proportion of their developing seeds. In addition to providing a larger food resource, species with larger seeds may also be exposed to pre-dispersal seed enemies for a longer period of time, as larger seeds take longer to develop (Moles & Westoby, 2003). Locally abundant plant species are also more likely to be colonised

by, and to support larger populations of host-specific enemies (Hanski, 2001; Pacala & Crawley, 1992). In this study, taller plant species had higher rates of premature fruit drop. Canopy trees are likely to have larger seed crops and be more apparent to seed predators than understorey trees and shrubs (Castagneyrol et al., 2013; Janzen, 1968). Both a greater average height and high local abundance of conspecifics could increase the 'apparency' of species to seed predators (Feeny, 1976). Leaf herbivory is also known to cause premature fruit drop (Petzold et al., 2009) and some traits (e.g. local abundance) which increase apparency to seed predators, probably also increase apparency to herbivores, possibly contributing to some of the observed relationships between plant traits and fruit drop (Floater & Zalucki, 2000; Hughes, 2012).

Species which had a temporal overlap in fruiting times with many other species tended to have higher rates of premature seed abscission. This contrasts with our prediction that an abundance of fruit at the wider community-level would result in the satiation of generalist seed predators, thereby reducing levels of attack and premature seed abscission. A greater abundance and diversity of fruits, however, could support larger populations of generalist seed and fruit predators. This would not be the case if the enemies triggering premature fruit drop were host specific, as we know is the case for at least one pre-dispersal enemy guild: In a previous study (Gripengberg et al., 2019a), we found that the insect seed predators of Barro Colorado Island are highly host specific. Seed predators were reared from seed samples representing 478 woody plant species. The majority (80%) of reared seed predators were associated with only one plant species, and the remaining 20% were relatively restricted in their host ranges. The positive relationship between temporal overlap in fruit production by other species and rates of premature fruit abscission can possibly be explained by the fact that species which fruit at the same time as many other species in our dataset also fruit for a longer time period (see Figure S2). Species that produce fruits for a long period of time (e.g. several months of the year) may be more likely to be found by seed predators (Moles & Westoby, 2003).

In line with our predictions, we found that plant species with greater variation in crop size between years had lower rates of premature fruit drop, which could be due to a temporally unstable food resource reducing enemy populations. Our prediction of a negative relationship between investment in mechanical seed defences and premature seed abscission did not yield statistical support, although we did detect an effect in the predicted direction. Plants invest approximately the same amount of biomass in seed defensive structures as they do in producing embryo and endosperm tissues (Moles et al., 2003). Reducing crop size in some years and investing in mechanical seed defences both come at the cost of producing fewer offspring. If pre-dispersal seed enemies are causing selection for these traits, given we found that across the studied plant community up to 39% of seeds are lost via premature fruit drop, they could be important selective agents in tropical forest plants.

Our observation that plant species which were locally abundant in the 50-ha forest dynamics plot lost more seeds before maturation, should be of key interest to ecologists interested in species coexistence mechanisms in diverse tropical forests. A long-standing question in tropical forest ecology is what allows so many plant species to coexist in highly diverse tropical forest systems (Wright, 2002). A prerequisite for stable coexistence is negative density dependence (Chesson, 2000): locally abundant species must have lower population growth rates than species that are rare in the local community. Our analyses suggest that there might be fitness costs (i.e. higher pre-dispersal seed mortality) associated with being a locally common plant species. The fact that species known to be attacked by specialist insect seed predators also exhibited higher levels of premature fruit drop further suggests that natural enemies might be causing negative density dependence, as envisaged by the Janzen–Connell hypothesis (Connell, 1971; Janzen, 1970). Although current

evidence is circumstantial, our study suggests that pre-dispersal enemies contribute to negative conspecific density dependence and possibly to species coexistence (see also Gripengberg, 2018).

While our study suggests that enemy-triggered premature fruit drop could be a major source of seed mortality in tropical forests with important implications for species coexistence, some caution needs to be taken when interpreting the results presented here. First, our study uses a correlative approach, and although the observed relationships between plant species attributes and patterns of premature fruit drop could be caused by enemies, there may be other triggers of premature fruit drop, unrelated to enemies, that cause the same relationships. As an example, tree height—which is hypothesised to increase ‘apparency’ to seed enemies—also correlates with light availability. (Nevertheless, the fact that we found a positive relationship between tree height and premature fruit abscission suggests that light limitation is unlikely to be a major driver of interspecific patterns of premature fruit drop.) Second, while our study suggests that a substantial proportion of seeds die as a result of premature fruit drop that is possibly triggered by natural enemies, we do not know whether those seeds would have survived to maturity in the absence of enemies. It has been suggested that many plant species produce more flowers and fruits than they can realistically support through to maturation (Stephenson, 1981), to account for the possibility that some of them will fail to be cross-fertilised. In the context of tropical forest trees, Ghazoul and Satake proposed the ‘sacrificial sibling hypothesis’ which suggests that rather than aborting inbred seeds at an early stage, trees might retain surplus low-quality fruits to act as sinks for seed predators, diluting the negative effects of seed predation on overall tree fitness (Ghazoul & Satake, 2009). Although logistically challenging, manipulative experiments which measure reproductive output of trees in the presence or absence of seed predators would be helpful for the interpretation of our results in the context of plant fitness. Third, it might be argued that the methodological approach taken in our study could have overestimated rates of premature fruit drop, as the displacement of mature fruits from the canopy by seed dispersers could potentially result in an inflated proportion of immature fruits relative to mature fruits in the traps. However, since we see no reason why mature seeds would not be just as likely to be brought into the traps by dispersal agents as they are to be removed from the canopy above them, and as we have summed counts of seeds and fruits collected from traps spread across the 50 ha plot, we believe that the premature fruit drop rates quantified in this study are representative of the reality.

In summary, our study suggests that premature fruit drop could be a major source of seed mortality on Barro Colorado Island, and that pre-dispersal seed enemies may be causing some of the observed premature fruit drop. Although often overlooked in favour of the better-known post-dispersal enemies, enemies which attack seeds before dispersal could play an important role in shaping tropical forest community structure. Our results have hinted that pre-dispersal enemies could be driving selection for plant traits and contributing to species coexistence through stabilising negative

density dependence. In light of these results, we encourage ecologists to consider events which happen in the very earliest life stages of plants when investigating tropical plant communities.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

S.G., E.E.J. and S.J.W. conceived the idea for the study, which was developed following discussions with J.M.B. and T.O.; S.J.W. established the seed trap network on BCI and coordinated data collection and curation (including collection of seed trait data); O.C. collected the data on seed and fruit rain; E.E.J. developed the statistical methodology, supported by S.G., J.M.B. and T.O.; E.E.J. conducted formal analyses, visualisations and wrote the initial draft. All authors contributed to subsequent revisions.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13867>.

DATA AVAILABILITY STATEMENT

Data on species-specific yearly seed abscission rates are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.4mw6m909j> (Calderón et al., 2022). Data on plant population attributes and seed predator attack have previously been archived in public data repositories <https://doi.org/10.5061/dryad.230j5ch> (Gripengberg et al., 2019b) and are related to the article (Gripengberg et al., 2019a). All code relating to the manuscript is in a repository on GitHub at <https://github.com/ee-jackson/premature-fruit-drop> and archived on Zenodo at <https://doi.org/10.5281/zenodo.5767681> (Jackson et al., 2021).

ORCID

Eleanor E. Jackson  <https://orcid.org/0000-0002-9884-2972>

S. Joseph Wright  <https://orcid.org/0000-0003-4260-5676>

James M. Bullock  <https://orcid.org/0000-0003-0529-4020>

Tom Oliver  <https://orcid.org/0000-0002-4169-7313>

Sofia Gripengberg  <https://orcid.org/0000-0002-8788-2258>

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