University of Reading

Conspecific density and the reproductive ecology of trees — implications for species coexistence

by

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Abstract

The successful production and development of seeds can be fraught with challenges, as plants must simultaneously attract pollinators and escape enemies which feed on the developing seeds. Interactions with insect pollinators and predators can be dependent on the local abundance of resources (flowers or seeds) available to them, sometimes causing variation in seed production and survival across gradients of host plant densities. Where insects are host-specific, density-dependent patterns of seed predation can promote the coexistence of tree species by suppressing the recruitment of species which are locally abundant. Although this mechanism has received substantial attention, density-dependent seed mortality caused by insects in the canopy has been largely overlooked. In this thesis, I explore the impacts of plant-insect interactions on seed production and pre-dispersal seed development to better understand the potential roles of these interactions in plant community dynamics. I first investigate the phenomenon of premature fruit drop in a community of tropical forest trees and conclude that seed losses at the pre-dispersal stage are significant and could be triggered by pre-dispersal seed predators. In the same forest, I then explore how premature fruit drop varies with the local density of conspecific trees, demonstrating that seed mortality associated with premature fruit drop is highest where conspecific trees are locally abundant. Next, I investigate the parallel processes of fruit set and fruit drop through field surveys focusing on a tropical (*Jacaranda copaia*) and a temperate (*Crataegus monogyna*) tree species. At the population-level I find conspecific density-dependent patterns of premature fruit drop but no evidence to suggest that fruit set varies with conspecific density in either of the studied tree populations. Taken together, the results presented in this thesis provide evidence that density-dependence in plant-insect interactions at the pre-dispersal stage can be widespread, and highlight the potential role of these interactions in promoting the coexistence of plant species in natural forest systems.

Declaration

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

Eleanor E. Jackson

Author contributions for each data chapter are detailed below.

Chapter 2

Eleanor E. Jackson, S. Joseph Wright, Osvaldo Calderón, James M. Bullock, Tom H. Oliver, Sofia Gripenberg (2022). **Pre-dispersal seed predation could help explain premature fruit drop in a tropical forest.** *Journal of Ecology*, DOI: 10.1111/1365-2745.13867.

E.E.J., S.G. and S.J.W. conceived the idea for the study, which was developed following discussions with J.M.B. and T.H.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.H.O.; E.E.J. conducted formal analyses, visualisations and wrote the initial draft. All authors contributed to subsequent revisions.

Chapter 3

Eleanor E. Jackson, S. Joseph Wright, Osvaldo Calderón, James M. Bullock, Tom H. Oliver, Sofia Gripenberg. **Local density of fruiting conspecifics predicts premature fruit drop in a tropical forest.** *In preparation for submission.*

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Chapter 4

Eleanor E. Jackson, Patrick G. Cannon, Matthew P. Greenwell, Sofia Gripenberg. **Density-dependent pre-dispersal seed predation and fruit set in a tropical tree: spatial scaling of plant-insect interactions.** *In preparation for submission.*

E.E.J and S.G. conceived the idea for the study, which was developed following discussions with P.G.C. and M.P.G.; E.E.J., P.G.C. and M.P.G. collected the data; E.E.J. developed the statistical methodology, supported by S.G.; E.E.J. conducted formal analyses, visualisations and wrote the manuscript with revisions from S.G.

Chapter 5

Eleanor E. Jackson, Matthew P. Greenwell, James M. Bullock, Tom H. Oliver, Susie Topple, Christopher W. Foster, Sofia Gripenberg. **Density-dependent effects on the reproductive ecology of trees in a temperate woodland.** *In preparation for submission.*

E.E.J. and S.G. conceived the idea for the study, which was developed following discussions with J.M.B., T.H.O. and C.W.F.; M.P.G. collected the mapping data; E.E.J. collected the fruit drop and fruit set data with some assistance from S.T., C.F. and S.G.; E.E.J. developed the statistical methodology, supported by S.G.; E.E.J. conducted formal analyses, visualisations and wrote the manuscript with revisions from S.G.

Data availability

New data were collected for Chapters 4 and 5 and have been archived in Zenodo at DOI: 10.5281/zenodo.10599499 (Jackson *et al.* 2024a) and DOI: 10.5281/zenodo.10599207 (Jackson *et al.* 2024b).

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Chapter 1

General introduction

1.1 Seed production and seed survival — implications for plant population dynamics

The individual processes of birth and death are central to ecology (Begon *et al.* 2006). Demography controls the size and shape of populations, and interacting populations of different species in turn shape the structure and dynamics of ecological communities (Griffith *et al.* 2016). For plants, which generally produce many offspring, mortality events in early life cycle stages are particularly impactful in altering species relative abundances.

For long-lived plants such as trees, the seed stage is typically only a brief period relative to the total lifespan, yet it can have a disproportionate influence on population- and community-level dynamics (Levine & Murrell 2003; Poorter 2007). This is because few seeds ever become seedlings (Fenner & Thompson 2005) and seed survival is mediated by multiple non-random factors, which are partly a function of species identity (Harms *et al.* 2000; Green *et al.* 2014). Consequently, the transition of a plant from seed to established seedling is often characterised as a 'bottleneck' for the recruitment of individuals to a population (Grubb 1977; Green *et al.* 2014). Yet a dispersed seed has already overcome several potential hurdles during its production and maturation while still attached to its parent. The production of a viable seed involves successful flowering, pollination and seed-set (Grubb 1977). The proportion of flowers which produce viable seeds can vary widely between species (Wiens 1984; Sutherland 1986) and both flowers and developing fruits can be aborted by the parent tree (Stephenson 1981). Where plant populations are seed limited at the site of dispersal, seed production and pre-dispersal seed mortality can influence species abundances (Figure 1.1) (Ehrlén *et al.* 2006). Seed limitation is often demonstrated by seed addition experiments where additional seeds increase recruitment

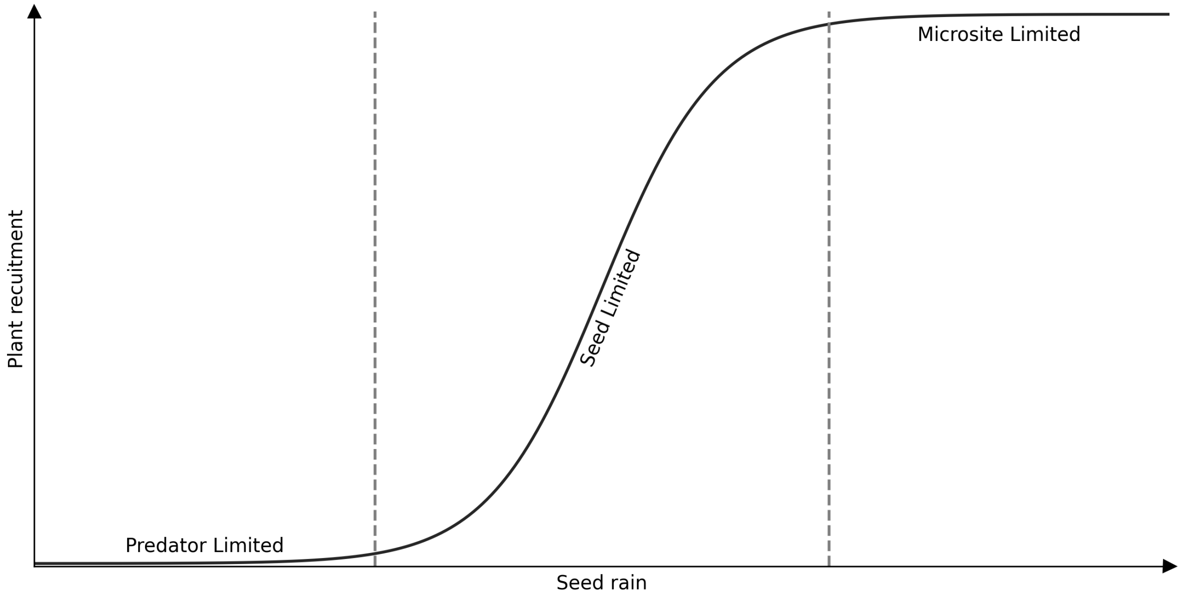

Figure 1.1: A schematic model of recruitment limitation in plants, adapted from Crawley (2000). Where seed rain per unit area is low, post-dispersal seed predators may consume all the dispersed seeds preventing any recruitment into the adult population. As seed rain increases, recruitment becomes proportional to seed density. It is in this region where reduced seed rain due to pre-dispersal seed predators could limit plant recruitment. At very high seed densities predators may be satiated and recruitment becomes limited by the availability of suitable microsites for germination.

and the survivorship of seedlings (Turnbull *et al.* 2000, e.g. Rother *et al.* 2013). The frequency with which seed production, rather than seedling establishment, limits plant recruitment is not well understood (Levine & Murrell 2003; Ashman *et al.* 2004; Clark *et al.* 2007), but mortality events earlier in the life cycle are likely to have knock-on effects at later stages of plant development (Crawley 2000; Kolb *et al.* 2007, e.g. Crawley & Long 1995; Grass *et al.* 2018).

1.2 The role of insects in the reproductive success of plants

Ecologists have long targeted plant-insect interactions when exploring how some species can influence the distribution and abundance of others (Maron & Crone 2006; Forrister *et al.* 2019). Plants interact with a diverse range of insects, some of which have life long associations with their host plant (Kennedy & Southwood 1984; Basset *et al.* 1996). Insects provide services which are essential to plant reproduction such as pollination and seed dispersal, but can also consume and damage reproductive plant parts (Schoonhoven *et al.* 2005). The reproductive success of plants is often determined by the joint outcome of these mutualistic and antagonistic plant–insect interactions (Grass *et al.* 2018).

1.2.1 Pollination

Globally, over 80% of flowering plants rely on pollinators for reproduction and the majority of animal pollinators are insects (Ollerton *et al.* 2011). In nature, plants frequently produce fewer seeds compared to what would have been possible with the receipt of additional pollen. Such pollen limitation often reduces the reproductive success of plants (Knight *et al.* 2005). Pollinators can limit seed set in two ways: through reduced pollen quantity, whereby an insufficient number of pollen grains are delivered to maximise ovule fertilisation, and through reduced pollen quality, for example where pollen grains are too genetically similar to the plant receiving them, causing seeds to die during development (Aizen & Harder 2007). The foraging behaviours, diversity and abundance of insect pollinators can all influence the degree of pollination success (Gómez *et al.* 2010; Gagic *et al.* 2021). Although the majority of pollinators within a community tend to be generalists to some degree, visiting a variety of plant species (Vázquez & Aizen 2004), shifts in the composition of flowering plants between seasons and years can generate functional specialisms whereby the majority of pollinators are visiting only a small subset or even a single plant species (Alarcón *et al.* 2008; Petanidou *et al.* 2008).

1.2.2 Predation

While herbivores typically do not kill their plant hosts, some herbivores which feed on the reproductive parts of a plant are known as plant predators, as they are a direct source of mortality to young individuals (seeds) in the population (Janzen 1970). The reproductive structures of plants provide a food resource which is qualitatively different to other vegetative plant parts. Seeds in particular are nutritionally dense presenting a high quality resource for consumers, however they are only present on the plant for a short time, can have high levels of structural and chemical defences (e.g. Fricke & Wright 2016; Gripenberg *et al.* 2018), and their numbers are often highly variable and unpredictable across years (Crawley 2000; Wright *et al.* 2005b). To adapt to these constraints, plant predators which attack developing seeds are often specialised to feed on one or a few plant species (Janzen 1971b; Pacala & Crawley 1992; Hulme & Benkman 2002; Gripenberg *et al.* 2019a). Specialist pre-dispersal seed predators must synchronise their life cycles to the ephemeral availability of seeds on their host plant. Insects have been able to exploit this, perhaps due to their fast generation times allowing for evolutionary flexibility (Hulme & Benkman 2002, e.g. Harman 1999; Rouault *et al.* 2004). Consequently, the majority of pre-dispersal animal seed predators are specialist insects, which often develop inside the seed (Crawley 2000).

Pre-dispersal herbivory on reproductive plant parts can impact the fitness of individuals in several ways. Consumption of the entire seed will kill the embryo and partial damage to the endosperm can remove the resources required for germination (Lesieur *et al.* 2014). Insect attacks that don't involve direct consumption of the seed can nevertheless reduce its chances of survival by triggering early abscission (abortion) of reproductive structures (Stephenson 1981), introducing pathogens (Luchi *et al.* 2012), and preventing seed dispersal (Manzur & Courtney 1984; García *et al.* 1999).

1.3 Spatial dynamics of plant-insect interactions

The movements and foraging decisions of pollinators, herbivores, and plant predators are often influenced by spatial variation in resource densities and this can result in spatial variation in the reproductive ecology of plants (Maron & Harrison 1997; Gripenberg *et al.* 2014; Wetzel *et al.* 2023). The density of reproductive structures such as flowers or seeds can be heterogeneous both within and between plants in a population (Bonal *et al.* 2007; Trad *et al.* 2013) and between populations at the wider landscape level (Campbell 1987). At the intra-plant scale, the size of seeds can be important for determining oviposition decisions of seed predators (Campbell 2002; Cope & Fox 2003), sometimes generating a trade-off for plants between producing many small seeds and fewer large seeds in an effort to satiate predators (Mack 1998; Bonal *et al.* 2007). At the population scale, host plants can be conceptualised as islands of suitable habitat to specialist insects (Janzen 1968, 1973). The attractiveness of a particular 'island' to a foraging insect can depend on the density and apparency of the resource and its distance from the insects' current location (Gripenberg & Roslin 2005; Castagneyrol *et al.* 2013; Pérez-Barrales *et al.* 2013). Patterns of foraging are likely limited by the typical dispersal range of individual insects (Delnevo *et al.* 2020). Whilst the movements of pollinators are often well characterised thanks to techniques which can identify the parentage of dispersed pollen (e.g. Nason *et al.* 1996; Kamm *et al.* 2009; O'Connell *et al.* 2018), we know relatively little of the dispersal ranges of seed predators.

1.4 Plant-insect interactions as a mechanism for plant species coexistence

Ecologists' interest in species coexistence is as old as the discipline itself (Kingsland 1991). The fundamental problem of how species can coexist in ecological communities when some are better competitors than others has been the subject of much hypothesising. It is now understood that species interact with the environment and with other species in different ways, and individual species are therefore limited by unique factors (Chesson 2000). In the case of tropical tree communities, where over 450 species can coexist within a single hectare of forest (Valencia *et al.* 1994; De Oliveira & Mori 1999), interactions with natural enemies such as insects are thought to be particularly important in maintaining diversity by promoting species coexistence (Wright 2002).

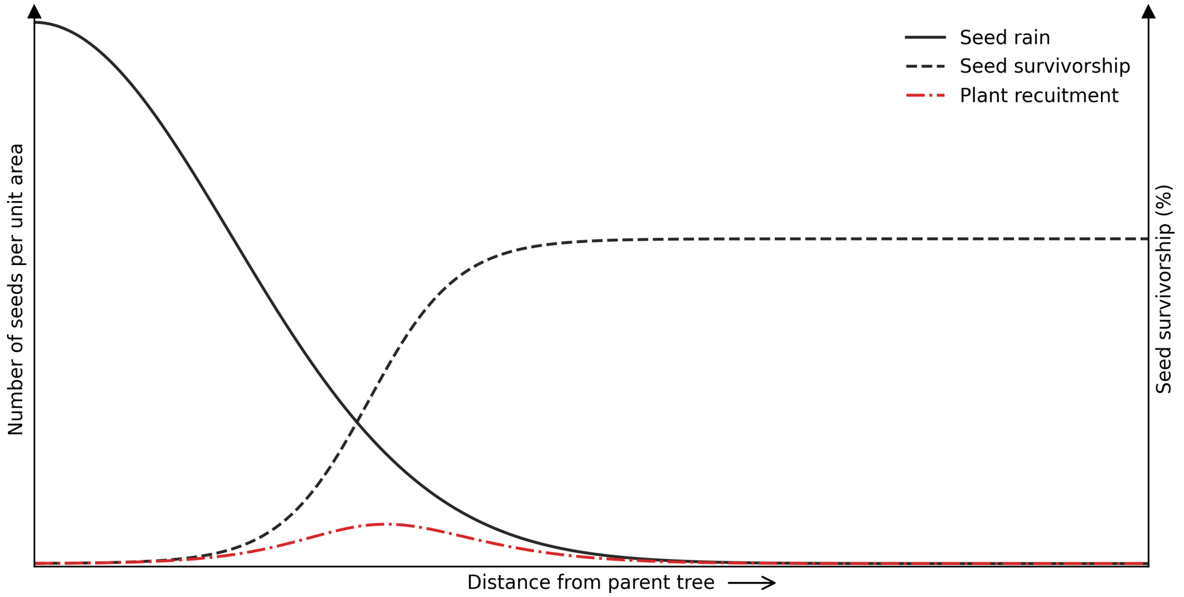

Figure 1.2: The Janzen-Connell model of plant population recruitment adapted from Janzen (1970). As the distance from the parent tree increases, the number of dispersed seeds per unit area decreases (solid black line), but survival of dispersed seeds is hypothesised to increase due to reduced enemy attack (dashed black line). The product of these two curves generates a plant population recruitment curve (in red) where a new conspecific adult is most likely to appear. In most systems the seed survivorship curve will not reach 100% due to mortality factors independent of distance and density.

As a tree species becomes more abundant, so too do its specialised enemies, and its offspring are therefore subject to higher rates of attack and mortality (Gillett 1962). The Janzen-Connell hypothesis incorporates a spatial aspect of plant-insect interactions into this mechanism, proposing that coexistence of tree species could be partly explained by patterns resulting from two processes: (1) the number of seeds reaching any given point decreases with distance from the parent plant, and (2) there is an increased rate of predation by host-specific natural enemies where prey are abundant (Janzen 1970; Connell 1971). These two processes result in a population recruitment curve that peaks where probability of recruitment into the population is highest — a point that is some distance away from the parent plant (Figure 1.2). As a result, the space immediately surrounding a reproductive tree individual is more likely to be colonised by seeds of other plant species, despite most of the tree's own seeds falling in that area. This results in density- and distance-dependent patterns of plant mortality within species, which can enhance diversity at the community level. Since its proposal, the hypothesis has received much attention, with many studies finding support for its predictions (Comita *et al.* 2014). Strong patterns of negative distance- and density-dependent mortality have been reported for seedlings (Packer & Clay 2000; Hille Ris Lambers *et al.* 2002) and have been shown to increase diversity at the community level (Harms *et al.* 2000; Bagchi *et al.* 2014).

Whilst Janzen's 1970 paper highlighted that mortality at any stage from developing seed to recruitment could have implications for diversity (Janzen 1970), the scientific literature published to date overwhelmingly focuses on enemies attacking seeds after their dispersal from the parent plant (Gripenberg 2018). Pre-dispersal insect seed predators can cause substantial mortality of developing seeds (Janzen 1971a; Nakagawa *et al.* 2005; Hosaka *et al.* 2011; Xu *et al.* 2015; Hirayama *et al.* 2017) and have high levels of host specificity (Novotny & Basset 2005; Gripenberg *et al.* 2019a), traits which are prerequisites for the Janzen–Connell mechanism to contribute to diversity maintenance (Sedio & Ostling 2013; Stump & Chesson 2015). Reduced seed production due to attack by pre-dispersal enemies could lower the curve of seed rain (i.e. reduce the number of dispersed seeds per unit area) (Figure 1.2). As noted by Janzen (1970), reduced seed rain could shift the population recruitment curve closer to the parent tree, implying that pre-dispersal seed predators might in fact *erode* plant diversity. Whilst evidence is accumulating of the role of seed predation in plant community dynamics (Maron & Crone 2006), ecologists rarely consider the seed production and pre-dispersal development stages when investigating spatial patterns of recruitment in the context of the Janzen-Connell hypothesis.

1.5 Mutualistic and antagonistic density effects

Plant reproductive success is the outcome of both mutualistic and antagonistic plant-insect interactions which are resource-mediated and often density-dependent (Grass *et al.* 2018). A high resource offering to pollinators may increase pollination success (Grindeland *et al.* 2005; Ballarin *et al.* 2022) resulting in a positively density-dependent pattern in seed set (Severns 2003; Dauber *et al.* 2010). Increased seed set would in turn be more attractive to seed predators and could result in greater seed mortality (Jones & Comita 2010). In the few studies which have examined positive and negative density dependence concurrently, the net effect of density on seed production has varied between systems (Platt *et al.* 1974; Jones & Comita 2010; Ballarin *et al.* 2022). If host-specific antagonists can maintain plant diversity via Janzen-Connell effects, we might expect that host-specific mutualists decrease diversity via 'reverse Janzen-Connell effects' (Zahra *et al.* 2021). Such patterns of conspecific positive density dependence enhancing species local abundance have been reported for plants associated with mutualistic and host-specific ectomycorrhizal fungi (Corrales *et al.* 2016; Delavaux *et al.* 2023). While pollinators generally have broader patterns of host use (Vázquez & Aizen 2004) suggesting they might be unlikely to respond to *conspecific* densities, differing flowering phenology between host species could still generate functional specialisms, counterbalancing any Janzen-Connell effects caused by antagonists such as seed predators.

1.6 Thesis outline

In this thesis I explore the impacts of plant-insect interactions on seed production and pre-dispersal seed development with the aim of furthering our understanding of the potential role of these understudied interactions in plant community dynamics. Using existing and newly collected data from two well-studied forest systems, Barro Colorado Island in Panama (Muller-Landau & Wright In press) and Wytham Woods in the UK (Savill *et al.* 2011), I investigate the density dependence of fruit set and premature fruit drop within and between plant species across multiple spatial scales.

Chapter 2: Pre-dispersal seed predation could help explain premature fruit drop in a tropical forest

Trees often abort a portion of their seeds prematurely, but this phenomenon — including its causes and potential consequences for plant dynamics — has rarely been studied in tropical forests. In this chapter, I use a large data set of seed rain collected over a period of 31 years to quantify interspecific variation in rates of premature fruit drop for a community of tropical forest trees. I investigate to what extent this variation can be explained by attributes hypothesised to be associated with high levels of enemy attack. Additionally, I test whether premature fruit drop is more common in plant species known to be attacked by pre-dispersal insect seed predators, as would be predicted if these enemies trigger some premature fruit abscission.

Chapter 3: Local density of fruiting conspecifics predicts premature fruit drop in a tropical forest

The Janzen-Connell hypothesis for species coexistence predicts that seed mortality due to natural enemies will be highest closest to adult plants of the same species and in areas of high conspecific density (Janzen 1970; Connell 1971). If specialist pre-dispersal seed enemies contribute to premature fruit drop (Jackson *et al.* 2022; Chapter 2), we might therefore expect fruit abscission rates to be highest in parts of the forest where the density of conspecific tree individuals is highest. In this chapter, I use the same data set as in the previous chapter to explore the relationship between premature fruit drop and the density and identity (conspecific versus heterospecific) of neighbouring trees, testing the hypothesis that more fruits are aborted prematurely in areas of high conspecific fruit density.

Chapter 4: Density-dependent pre-dispersal seed predation and fruit set in a tropical tree: spatial scaling of plant-insect interactions

Jacaranda copaia is a tropical canopy tree species which has a known relationship with a pre-dispersal host specific seed predator on Barro Colorado Island, causing premature abscission of infested fruits. A previous study (Jones & Comita 2010) found that the seed predator caused higher levels of pre-dispersal seed mortality in areas of high conspecific density, although this negative density dependence was still outweighed by increased fruit set (likely due to higher pollination success) in areas where reproductive conspecifics were abundant. In this chapter, I apply a similar approach to a spatial area 30 times greater than the original study to determine if previously documented patterns of density dependence hold across a much wider range of conspecific densities.

Chapter 5: Density-dependent effects on the reproductive ecology of trees in a temperate woodland

While tree reproduction is the joint outcome of both mutualistic and antagonistic insect-plant interactions, the conspecific density dependence of these interactions are rarely studied in parallel. In this chapter, I quantify rates of fruit set and fruit drop in a common temperate tree (*Crataegus monogyna*) in Wytham Woods and relate these to tree size and the local density of conspecifics to determine how their joint impact may contribute to spatial patterns of tree fecundity.

The thesis concludes with a general discussion chapter (Chapter 6), in which I discuss the broader implications of my findings.

Chapter 2

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

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

2.2 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 (Turnbull *et al.* 2000; Maron & Crone 2006; Clark *et al.* 2007; Green *et al.* 2014). 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 (Roughgarden *et al.* 1988; Turnbull *et al.* 2000; Fenner & Thompson 2005; James *et al.* 2011; Rother *et al.* 2013). A number of processes contribute to the success or failure of a developing seed, including nutrient availability (Bertamini & Nedunchezhian 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 (Steffan-Dewenter *et al.* 2001; Karron *et al.* 2006). 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, i.e., 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 (Pérez-Pérez *et al.* 2008; Nussbaumer *et al.* 2020; Reichardt *et al.* 2020), can trigger premature fruit drop due to competition for resources among fruits (Stephenson 1981; Bawa & Webb 1984; Goubitz *et al.* 2002). Developmental or genetic abnormalities (Kraus 1915; Bradbury 1929; Forino *et al.* 1987), 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 (Boucher & Sork 1979; Planes *et al.* 2014; Akinsanmi *et al.* 2016). 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 wide-spread 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 co-existence 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. Holl & Lulow 1997; Comita *et al.* 2014; 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; Janzen 1970; Gripenberg 2018), 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: (1) plant phylogeny, (2) plant traits and population attributes hypothesised to be associated with high levels of enemy attack and (3) previously documented patterns of attack by one enemy-group (insect seed predators) known to trigger premature fruit drop in other settings (Tzanakakis *et al.* 1997; Follett 2002). 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 (Janzen 1968; Castagneyrol *et al.* 2013; Gripenberg *et al.* 2019a).
3. **Negative relationship between investment in mechanical seed defences and the proportion of seeds prematurely abscised.** Species that in-

vest 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 1976b).
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 (Toy 1991; Toy *et al.* 1992; Kelly 1994).
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 (Pacala & Crawley 1992; Hanski 2001).

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).

2.3 Methods

Barro Colorado Island (BCI; 9°9’N, 79°51’W) is a 16 km^2 island situated in Gatun Lake in the Panama Canal, which supports semideciduous 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 & Calderón 1995; Wright *et al.* 1999, 2003, 2005b). A 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 m^2 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), 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 to 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; unpublished data) and added to the number of seeds. For each species, the weekly counts ($n = 1615$ 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 5,295 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 Introduction 2.2) 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 (Wright *et al.* 2010; Gripenberg *et al.* 2019a,b). Information on how plant traits and population attributes were estimated, and their original sources are provided in Table 2.1.

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 us-

Table 2.1: 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 (Gripenberg *et al.* 2019a,b).

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 is 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 material was oven dried at 60°C for at least 72 hours 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 $\mathrm{CV}_{\mathrm{year}}$ in (Wright *et al.* 2005b) 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 to 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 ($\mathrm{DBH}_{\mathrm{max}}$) was extracted and individuals with a DBH larger than $0.5 \times \mathrm{DBH}_{\mathrm{max}}$ (the known size threshold for tree reproduction (Visser *et al.* 2016)) were counted.

ing the `lme4` package (Bates *et al.* 2015). 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 2.1) 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.* 2017) 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 if 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 (Gripenberg *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 2020). The `contMap` function was used to visualise phylogenetic signal in mean premature seed abscission as a continuous trait mapped onto the phylogenetic tree.

2.4 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 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 2.1).

Correlations between the explanatory variables were relatively weak (Figure A.1). Of

867 species × 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 2.3, Table A.1).

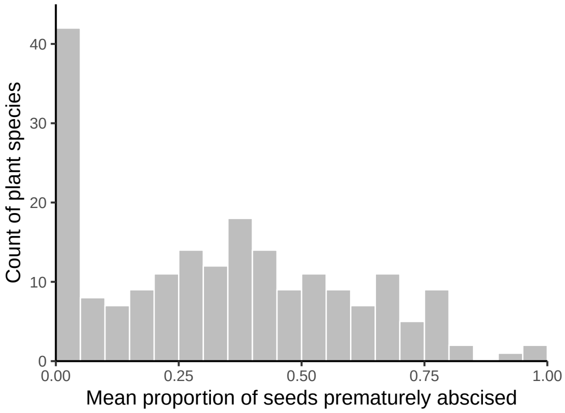

Figure 2.1: Average rates of premature seed abscission for 201 woody plant species on Barro Colorado Island. The proportion of seeds prematurely abscised per year for each plant species is averaged across 31 years to give the means presented here.

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 2.2).

2.5 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 (Gripenberg 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 an-

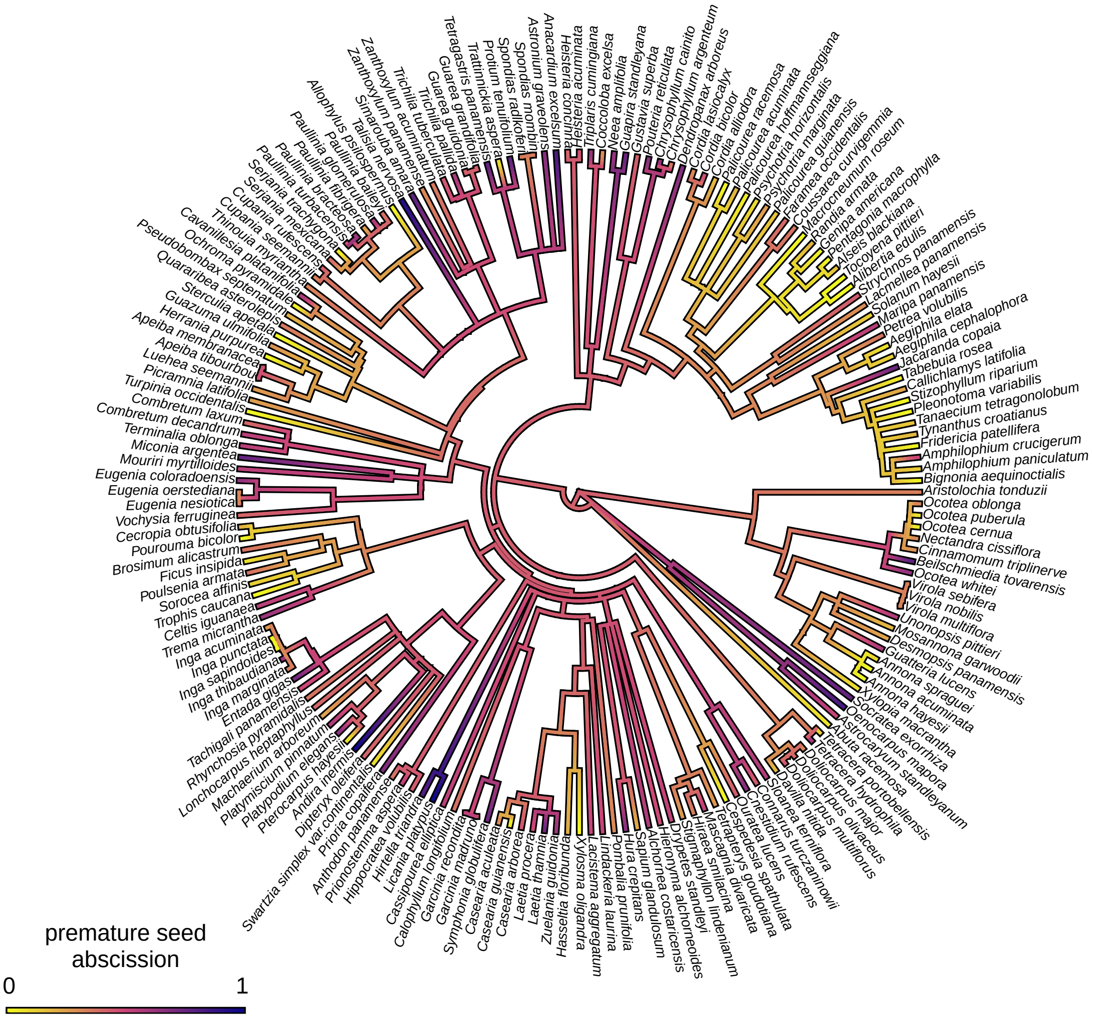

Figure 2.2: Reconstructed evolution of premature seed abscission rates for 184 woody plant species on Barro Colorado Island, Panama, using continuous character mapping. Based on the mean proportion of seeds prematurely abscised ($n = 31$ years), where yellow = lower proportion of seeds prematurely abscised, and purple = higher proportion of seeds prematurely abscised.

cestry can only explain a small amount of the variation observed across plant species.

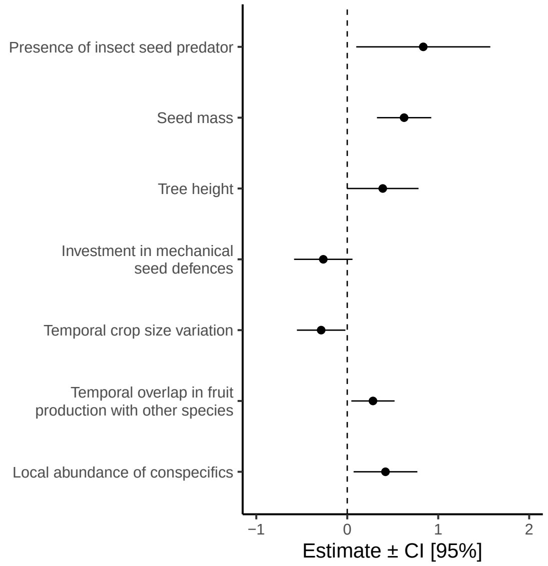

Figure 2.3: Relationships between premature seed abscission rates and plant attributes hypothesised to reflect likelihood of attack by seed enemies. Positive estimates represent increased premature seed abscission rates with increased attribute values, and the opposite for negative effects. Points are coefficient estimates from generalised linear mixed effects models. Error bars denote 95% confidence intervals.

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.

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 (Coley 1983, 1988; Schuldt *et al.* 2012; Cárdenas *et al.* 2014). 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 (Pacala & Crawley 1992; Hanski 2001). 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 understory trees and shrubs (Janzen 1968; Castagneyrol *et al.* 2013). 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 (Gripenberg *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 A.2). 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 (Janzen 1970; Connell 1971). 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 Gripenberg 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-fertilized. In the context of tropical forest trees, Ghazoul & Satake (2009) 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. 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.

Chapter 3

Local density of fruiting conspecifics predicts premature fruit drop in a tropical forest

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3.1 Abstract

Host specific pre-dispersal seed predators have the potential to cause the premature abscission of developing seeds. If these plant enemies cause greater seed mortality in areas where conspecific seeds are abundant they could alter patterns of seed rain in a way that promotes plant species coexistence. We used 29 years of fruit drop data for 46 woody plant species in a 50-ha mapped forest plot in Panama, to determine if spatial patterns of seed mortality associated with premature fruit drop are dependent on the densities of conspecific plants, fruiting conspecifics and fruiting heterospecifics. We found that seed mortality increased with conspecific density and was driven by fruiting conspecifics, but this positive relationship was dampened at the highest densities of conspecifics, suggesting predator satiation. We found a weak negative relationship between heterospecific density and seed mortality. Our results are consistent with the idea that host-specific pre-dispersal plant enemies can influence the reproductive success of trees in ways that are dependent on the density and identity of surrounding plants.

3.2 Introduction

The high levels of plant diversity found in many tropical forests have long been puzzling ecologists: highly diverse tropical forests should not exist under Gause's law (Hardin 1960) where competition between species limits its diversity. Explaining species coexistence remains a central question in tropical forest ecology (Comita & Stump 2020; Terborgh 2020), and in community ecology more broadly (e.g. Heinen *et al.* 2020; Quimbayo *et al.* 2020). A wealth of mechanisms have been proposed to prevent competitive exclusion (Chesson 2000; Wright 2002). Of these mechanisms, conspecific negative density dependence has received particular attention in the context of tropical forest plant communities (Harms *et al.* 2000; Peters 2003; Metz *et al.* 2010). It is a phenomenon whereby individuals surrounded by many members of their own species are at a fitness disadvantage in comparison to more isolated individuals. Such density dependence can result from a variety of ecological processes that make individuals perform worse when surrounded by conspecifics rather than by heterospecifics (Chesson 2000).

An idea first suggested by Gillett (1962), and later formalised by Janzen (1970) and Connell (1971), natural enemies of plants are thought to be key drivers of conspecific negative density dependence in tropical forest plants. If enemies are highly specific in their choice of host plant (e.g. feed on one or only a few species of plant), they are more likely to find, and predate upon, plants growing close to members of their own species. Isolated plants, or plants growing in areas of lower overall conspecific density, are more likely to escape enemy attack. Many studies have found support for these types of Janzen-Connell effects (reviewed in Carson *et al.* 2008; Comita *et al.* 2014; Comita & Stump 2020; Terborgh 2020). However, the majority of studies have focused on the survival of seedlings or seeds that have already dispersed from the mother plant. Although Janzen himself (Janzen 1970) noted that pre-dispersal seed enemies could contribute to diversity maintenance through conspecific negative density dependence, this possibility has received little attention in the ecological literature.

Levels of pre-dispersal seed mortality in tropical trees can be high but are rarely studied as a source of plant mortality. For example, in a recent study (Jackson *et al.* 2022; Chapter 2) we found that in the well-studied tropical forest of Barro Colorado Island (BCI) in Panama, across 201 woody plant species, 39% of seeds were likely to die because of premature fruit drop. Such premature fruit drop can be triggered by a variety of factors, including seed predation by insects (Stephenson 1981). Insect seed predators are a group of plant enemies which often exhibit high levels of host-specificity in tropical forests (e.g. Basset *et al.* 2021), including on BCI (Gripenberg *et al.* 2019a). An interesting finding of our study of interspecific patterns of premature fruit drop (Jackson *et al.* 2022; Chapter 2) was that plant species that are abundant in the woody plant community of BCI suffered from higher levels of seed mortality through premature fruit drop than species that are locally rare. This suggests that premature fruit drop, possibly triggered by host-specific insect seed predators, might be a mechanism contributing to the coexistence of tree species in the plant community of BCI. The question remains whether similar density dependence in pre-dispersal seed mortality rates also exists within species, as envisaged by Janzen (1971a).

Few studies have explored the conspecific density dependence of premature fruit drop in tropical forests. Working in the 50-ha ForestGEO plot on BCI, Jones and Comita (2010) assessed spatial patterns of premature fruit abscission (likely caused by a Hymenopteran seed predator) in the canopy tree *Jacaranda copaia*. In line with Janzen's and Connell's predictions, fruit abscission rates increased with increasing densities of conspecific neighbours. However, this increase was not large enough to cancel out the positive density dependence of fruit set, which — in the studied system — was likely a result of pollen limitation in areas of low conspecific density. Positive density dependence can also be promoted via predator satiation at high conspecific densities (Janzen 1971a; Kelly 1994; Kelly & Sork 2002). Since positive conspecific density dependence has the potential to erode diversity (Zahra *et al.* 2021), the effect of pre-dispersal seed enemies must have a net negative effect of density on fruit set for us to see the diversity-enhancing pattern that Gillett (1962) and Janzen (1970) predicted at the community level.

The scarcity of studies on the density dependence of pre-dispersal seed mortality may be due, in part, to logistical challenges. Comparison of pre-dispersal seed mortality for individuals in areas of varying conspecific density requires information on the spatial distribution of individuals of the focal plant species over relatively large areas. Mapping tree distributions across large areas of tropical forest is a vast logistical challenge, requiring time and effort that is outside the scope of many projects. In this context, the larger plots within the ForestGEO network of forest dynamics plots (Anderson-Teixeira *et al.* 2015) provide an opportunity to investigate conspecific density dependence over spatial scales largely unexplored for natural enemies of tropical forest trees. In these plots (which are typically between 0.25 and 0.5 km^2), the location, size, and species identity of all woody stems >1 cm DBH (diameter at breast height) are recorded every 5 years, providing an excellent resource for testing the extent to which plant mortality relates to the density of conspecific individuals in the neighbourhood.

Here, we used data from a long-term study on seed and fruit fall in the 50-ha ForestGEO plot on Barro Colorado Island to assess if, and how, seed mortality through premature fruit drop varies with the local densities of conspecifics (all size classes), reproductive-sized conspecifics, and reproductive-sized heterospecific individuals across 46 tree species. Following predictions by Gillett (1962) and Janzen (1970), we expect that premature fruit drop will increase with increasing density of reproductive-sized conspecifics if pre-dispersal seed predators are a major driver in causing trees to drop fruits prematurely (Jackson *et al.* 2022; Chapter 2).

3.3 Methods

Study site

This study was conducted using data collected from the permanent 50-ha ForestGEO forest dynamics plot on Barro Colorado Island, Panama (BCI; 9°9'N, 79°51'W) (Anderson-Teixeira *et al.* 2015). BCI is a 16 km^2 island situated in the Panama Canal, which supports a lowland, moist tropical forest with a 35 m tall canopy. The forest dynamics plot is a 1 km × 0.5 km section of old growth forest located on a plateau in the centre of the island (Figure 3.1 a). In the plot census conducted in 2015, 221,527 free-standing woody plant individuals (trees and shrubs) belonging to 328 species were recorded (Condit *et al.* 2019).

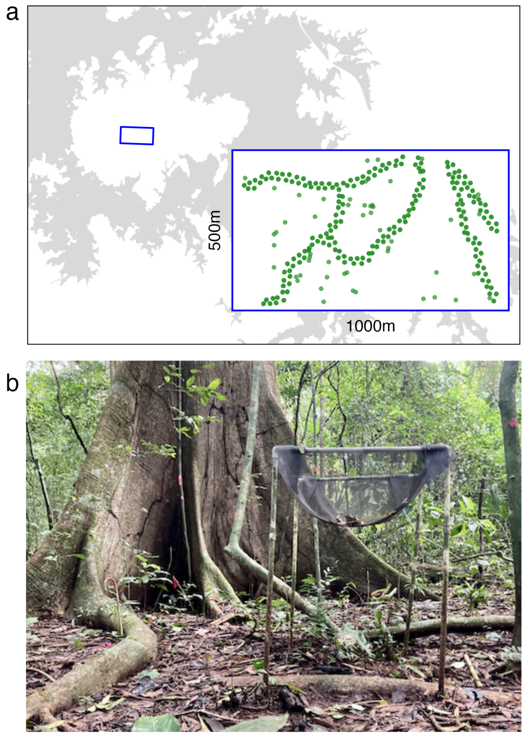

Figure 3.1: (a) A map showing the location of the 50-ha ForestGEO plot on BCI. The inset map shows the location of 450 seed traps within the plot, which are marked with green points. Map tiles by Stamen Design, under CC BY 3.0. (b) A seed trap in the ForestGEO plot on BCI. Photo: E.E. Jackson.

Assessing premature fruit abscission

Since 1987, seed and fruit production by trees, shrubs and lianas has been monitored in the ForestGEO plot through a network of seed traps. 200 seed traps were established in 1987 and have been continuously monitored. These traps are located at 13.5 m intervals on alternating sides 4-10 m from trails along a 2.7 km network of pre-existing trails within the forest dynamics plot (Figure 3.1 a). Between June 2002 and June 2004, 50 traps were added in naturally occurring tree fall gaps within the plot and have been monitored since. In March 2011, 200 traps were added 2 m away from each of the original 200 traps and were monitored for 23 months (Figure 3.1 a). Each seed trap consists of a mesh sheet (1 mm mesh size) attached to a 0.5m^2 PVC frame. The mesh is suspended 80 - 100 cm above the ground by PVC posts (Figure 3.1 b). Seeds, fruits and other reproductive material that fall in the traps are collected on a weekly basis, counted and identified to species. Seeds and fruits are categorised as mature (endosperm of seeds is fully developed) or immature (endosperm is not fully developed) (Wright *et al.* 1999). For some animal dispersed species, the number of 'capsules' are also recorded. Here, capsules are defined as a part of the fruit which is not eaten by animals and is dropped from the canopy as the fruit is being consumed. Botanically, capsules could refer to a capsule, pedicel or bract and each count of a capsule corresponds to a single fruit count (i.e. if a fruit has three capsule parts, three capsule parts from that species would be counted as one capsule). From dropped capsules we can estimate the number of mature fruits consumed by vertebrates, since in Panama, animal dispersal agents are not likely to eat unripe fruits and usually consume the fruit at the location where it is found (e.g. capuchins Rowell & Mitchell 1991).

To assess premature fruit abscission rates for each species in each trap, we extracted the total sums of immature and mature seeds in each trap for each year, using data from 1988 to 2017 inclusive. Seed counts equal the sum of individual seeds plus seeds inside fruits collected in the traps, the latter was obtained by multiplying fruit counts by known species-specific seed-to-fruit ratios. Seed-to-fruit ratios were calculated as the means obtained from dissections of five mature fruits from five individuals of each species (n = 25 fruits per species; S. J. Wright, unpublished data). For species for which it was possible to estimate the number of mature fruits consumed by seed dispersers based on capsules in the seed traps, either the number of capsules or the number of individual seeds was added to the count of mature seeds from within fruits, whichever was larger. This approach was taken to avoid double counting, since some of the individual seeds may have originated from the same fruit as the capsule. Premature fruit abscission rates at the location of the seed trap were approximated as the proportion of the total number of seeds found in the trap that were immature. We removed animal dispersed species for which we were not able to reconstruct mature fruit counts based on capsules from the data set. We also excluded dioecious species, since we did not have information on which individuals in the ForestGEO plot were fruit-bearing females. This resulted in a data set of 46 species (Table B.1). Across these species, a total of 1,293,846 seeds (individual seeds, or seeds inside dropped fruits) were recorded in the traps during the 29 year time period. For the species included in the analyses, we assume that the probability of a seed or fruit falling into the trap once detached from the parent tree is the same for mature and immature fruits and seeds. Data points were omitted from the dataset if the sum of fruits plus individual seeds collected in a trap was less than three for a particular species in a given year. We deemed that less than three counts would give an unreliable estimate of proportion abscised.

Estimating local tree densities

To determine the local densities of tree species included in our study, we used data from tree censuses of the forest dynamics plot conducted every 5 years from 1990 to 2015 (Condit 1998; Condit *et al.* 2019). In each census, the species identity, coordinates (accurate to 0.5 m), and diameter at breast height (DBH, measured at 1.3 m above the ground) were recorded for all free-standing woody plants larger than 1 cm in DBH (Condit 1998).

For years in the seed trap data in which no census of trees took place, we used tree distribution data from the most recent census year when assessing the densities of individuals in the forest dynamics plot. In other words, we assumed individual trees remained alive and had no notable change in DBH for two years either side of each census. For example, seed fall data from 2013, 2014, 2015, 2016 and 2017 were matched to 2015 plot survey data. The rate of tree mortality on BCI is approximately 2% per year (Condit *et al.* 1995), so our estimates of local tree densities matched to the trap data are likely to be accurate.

We used a spatial connectivity index to assess the density of individual trees at the location of each seed trap. The connectivity index proposed by Hanski (1994) accounts for both the size of, and distance to, conspecific individuals within the forest dynamics plot. Connectivity is additive and decays with distance, providing more biological realism than simpler models (Smith 2022). Similar indices have been used in previous studies to estimate habitat connectivity from the perspective of plant enemies (e.g. Comita *et al.* 2010). We calculated connectivity at the location of each seed trap in every year and for each plant species as

$$S_i = \sum exp(-\alpha dist_{ji}) A_j^b \qquad (3.1)$$

, where S_i is the connectivity of trap i, A_j is the DBH (in mm) of tree j and $dist_{ji}$ the distance (in m) from tree j to the seed trap i. α is a measure of the hypothesised dispersal ability (1/average dispersal distance in m) of host-specific enemies associated with seeds of the focal tree species. DBH has been shown to scale linearly with fruit production in tropical trees (Chapman *et al.* 1992) and is therefore a suitable parameter to describe the 'size' of the habitat patch, A_j, from the perspective of a pre-dispersal seed enemy. We chose the scaling parameter for emigration, b, at 0.5 according to the assumptions of Moilanen & Nieminen (2002), who suggested that the ratio of patch edge to patch size decreases with $A^{0.5}$. Dispersal distances of tropical seed predators are unknown; we therefore fit eight models covering a range of α values, corresponding to average dispersal distances of 5, 10, 20, 30, 40, 50, 60 and 70 m. We compared the predictive accuracy of each model using approximate leave-one-out cross-validation in the `R` package `loo` (Vehtari *et al.* 2017; Yao *et al.* 2018; Vehtari *et al.* 2023). The models with connectivity calculated assuming an average migration distance of 20 m and 10 m had the highest expected log predictive density and the difference in predictive accuracy between the two models was negligible (Figure B.1). We chose to use the model where the average migration distance is 20 m, corresponding to α = 0.05. Distance decay parameters similar to α have been estimated at BCI previously as 0.2 (5 m) (Comita *et al.* 2010) and 0.07 (15 m) (Hubbell *et al.* 2001). Although tree-associated insects are likely to vary in their dispersal abilities, the exact choice of α has been shown to have a relatively small impact on S_i (Moilanen & Nieminen 2002), and comparisons of parameter estimates from our eight fitted models show that our choice of α had little effect on our results (Figure B.2). We removed traps from the dataset if they were closer than the average migration distance (20 m) from the edge of the plot since we could not accurately predict connectivity with missing data.

We calculated three different connectivity estimates. The first included all reproductive-sized conspecifics and was used to assess the effect of conspecific fruit density on premature fruit drop. The second included all conspecifics regardless of size, but with DBH >3 cm, since there were many very small (<3 cm DBH) individuals in the dataset which made the computational load challenging. Connectivity to all conspecifics was calculated to ascertain if any effects were due to the density of conspecific trees *per se* rather than the density of fruits (such effects could indicate that agents causing premature fruit drop respond to other, species-specific cues than the fruits themselves). Finally, we calculated a connectivity estimate which included all reproductive-sized heterospecifics in the data set to determine if any effect on premature fruit drop was due to fruit densities regardless of species, as would be expected if generalist seed predators were causing premature fruit drop.

Reproductive-sized trees were identified based on known relationships between DBH and the onset of reproduction. For tree species at BCI, 81% of interspecific variation in reproductive size thresholds can be explained by

$$R_{50} = \frac{1}{2} D_{max} \qquad (3.2)$$

, where R_{50} gives the size at which individuals have a 50% probability of being reproductive and D_{max} is the maximum diameter of each species (Visser *et al.* 2016), calculated as the mean DBH of the largest six individuals recorded in the forest dynamics plot censuses. In the context of our analyses, individuals with a DBH lower than the size at which they have a 50% probability of being reproductive (R_{50}) were classed as non-reproductive.

Modelling the relationship between connectivity and premature fruit abscission

We used three separate Bayesian hierarchical models to assess the relationships between premature fruit abscission and density of reproductive-sized conspecifics, all conspecifics and reproductive-sized heterospecifics. All models were structured identically with only the type of connectivity index differing between the three models. In each model, the proportion of seeds prematurely abscised due to premature fruit drop was modelled as a function of connectivity (a population-level effect). To account for non-independence of observations within the data, year, trap and quadrat (a 50m × 50m subplot within the forest dynamics plot within which a trap was located) were modelled using group-level ('random') intercepts while the slope of the relationship between premature fruit abscission and connectivity was allowed to vary between species (intercept and slope). Our response data are bounded at zero and one, and inflated at zero, where seeds within a trap can be all immature (1) or all mature (0). We decided to model these values explicitly with a Zero One Inflated Beta (ZOIB) model, as its assumptions better match observed features of the data than other approaches (Ospina & Ferrari 2008, 2012). ZOIB models use a beta distribution for responses within the closed (0, 1) interval, and a Bernoulli distribution for the binary 0, 1 responses. Under this type of model, predictors can affect either or both the continuous responses (in terms of their spread) and binary responses (in terms of proportions) (Ospina & Ferrari 2012). We fitted the models using the Hamiltonian Monte Carlo (HMC) sampler `Stan` (Carpenter *et al.* 2017), interfaced through the `R` package `brms` (Bürkner 2017, 2018) with four chains and 5,000 iterations with an additional 2,000 as a warmup. For all parameters we used prior distributions that are the default setting in the `brm` function; uninformative priors for population-level effects and a half student-t prior with a location of zero, three degrees of freedom and scale parameter of 2.5 for the population-level intercept and the group-level effects. We characterised the goodness-of-fit of models by conducting posterior predictive checks (Figures B.3 a, B.4 a, B.5 a). We verified that the Gelman–Rubin convergence statistic ($\hat{R}$) <1.1 for all models, indicating good mixing of the four HMC chains (Gelman & Rubin 1992; Figures B.3 b, B.4 b, B.5 b). Visual inspection of the chains showed convergence to a common target and there were no divergent transitions after warm-up (Figures B.3 c, B.4 c, B.5 c).

3.4 Results

81% of trap × year × species combinations contained only mature seeds, and 6% contained only immature seeds. Excluding these zero and one values, the median proportion of immature seeds in a trap across the 46 species was 50%. Estimated connectivity values varied 197-fold for reproductive-sized conspecifics, 651-fold for all conspecifics and 288-fold for reproductive heterospecifics, indicating that the greatest range of densities was seen when including all conspecifics regardless of size.

The proportion of immature seeds found in the traps increased with the traps' connectivity to reproductive-sized conspecific trees, but only to some extent. At highly connected traps (connectivity greater than 50), the proportion of prematurely abscised seeds plateaued at around 40-50% (Figure 3.2 a). A similar relationship was found between the rate of seed abscission and a trap's connectivity to all conspecifics (reproductive and non-reproductive

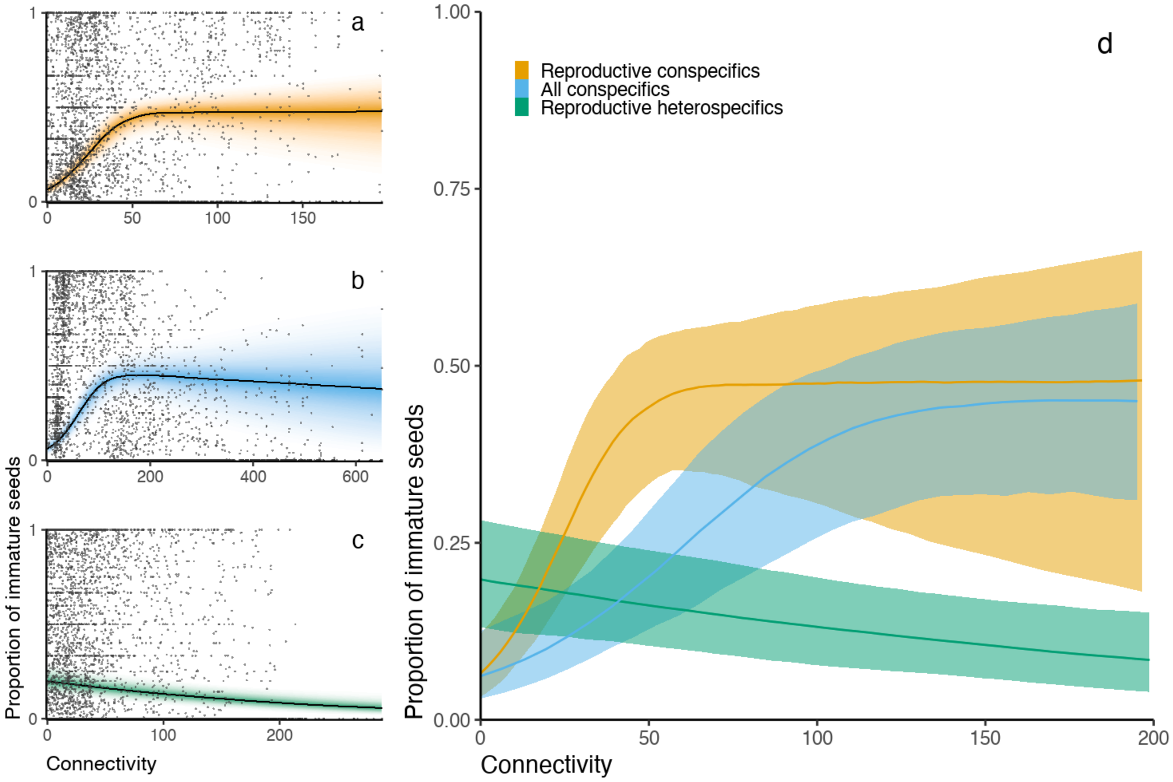

Figure 3.2: The relationship between the proportion of immature seeds in a trap and the density of reproductive-sized conspecifics (orange), all conspecifics (blue), and reproductive-sized heterospecifics (green) at that location. In the left-hand side panels (a - c), each black point corresponds to a unique trap × year × species combination. The solid line represents the median of 1000 draws from the expectation of the posterior predictive distribution with transparency corresponding to the density of draws. In the larger right-hand side panel (d) each of the models has been used to predict immature seed proportions for the same range of connectivity values. The solid lines represent the median of 1,000 draws from the expectation of the posterior predictive distribution and the transparent area represents the 95% confidence interval.

individuals larger than 3 cm DBH) (Figure 3.2 b). The initial rate of increase in the proportion of immature seeds with overall connectivity was weaker than for reproductive conspecifics. The relationship between the rate of premature seed abscission and connectivity to reproductive-sized heterospecifics was different in both direction and shape to conspecific connectivity, with a weak negative relationship across the observed range of connectivities (Figure 3.2 c).

3.5 Discussion

Our analysis of a large data set on patterns of seed and fruit fall in a community of tropical forest plants demonstrates that conspecific density-dependent seed mortality can, as predicted by Janzen (Janzen 1970), operate before seeds are dispersed from their parent tree. The proportion of seeds that were prematurely dropped increased sharply with increasing connectivity to conspecific adult individuals before levelling off. The rate of premature seed abscission showed a weak negative relationship with connectivity to reproductive-sized heterospecific individuals. Whilst we cannot confirm that immature seeds and fruits were dropped due to the action of host-specific plant enemies (Jackson *et al.* 2022; Chapter 2), the pattern of conspecific density dependence in seed mortality revealed by our study supports this theory.

Our findings agree with many other studies, some of them conducted on BCI, which have found positive relationships between conspecific densities and the mortality of dispersed seeds or seedlings (Hubbell *et al.* 2001; Comita *et al.* 2010; Comita *et al.* 2014). Our results differ from the majority of these studies in the shape of the response, with seed mortality levelling off at high conspecific densities. While most empirical studies predict a general increase in survival with conspecific density, enemies are unlikely to respond linearly to resource densities (Bachelot *et al.* 2016). The role of predator satiation in determining patterns of seed survival through reduced predation at high densities was mentioned in Janzen's seminal paper (1970). Satiation is most often explored in terms of its temporal aspect, where the synchronous reproduction of individuals in a population can enable a larger proportion of seeds to escape attack from specialist enemies (Kelly 1994; Kelly & Sork 2002). However, satiation can also occur without masting, across a spatial gradient of density (Augspurger & Kitajima 1992; Hammond & Brown 1998). Although the Janzen-Connell and predator satiation hypotheses are sometimes held in opposition (e.g. Xiao *et al.* 2017), they are not mutually exclusive and could explain the patterns of seed mortality seen in our study.

The relationship between seed mortality and connectivity to all conspecific trees (regardless of whether the trees were in the reproductive size range) was similar to the relationship based on connectivity of reproductive-sized conspecifics only. It is worth noting that the two types of connectivity measures are not independent of each other: reproductive-sized individuals are included in the calculations of total connectivity and the correlation between the two connectivity measures is strong and positive (Pearson's correlation coefficient, $r = 0.72$). Given that reproductive-sized individuals are the largest individuals in the population they will likely be driving patterns of total connectivity, and the relationship between seed mortality and connectivity to all conspecific trees is therefore plausibly explained by host-specific seed enemies which are attracted to reproductive-sized trees specifically. That being said, there are other mechanisms which could cause similar patterns. Foliar herbivory can trigger premature fruit drop by reducing the amount of resources available to the plant (Stephenson 1980, 1981; Mehouachi *et al.* 1995; Petzold *et al.* 2009). Where host-specific herbivores respond to local host-densities (e.g. Blundell & Peart 1998; Norghauer *et al.* 2006), foliar herbivory could potentially lead to patterns of premature fruit drop such as those documented in this study. To understand the exact mechanisms causing documented patterns of density dependence, detailed studies focusing explicitly on patterns of enemy attack are ultimately needed (e.g. Jones & Comita 2010; Chapter 4).

The observation that pre-dispersal seed mortality decreased with connectivity to reproductive-sized heterospecific trees could potentially result from a negative relationship between the connectivity of conspecific and heterospecific individuals: in parts of the forest where reproductive-sized conspecifics are common, there might be fewer reproductive-sized heterospecifics. The lack of correlation between the two sets of connectivity values (Pearson's correlation coefficient, r = -0.06) suggests that alternative mechanisms are needed to explain the relationship between pre-dispersal seed mortality and the connectivity of reproductive-sized heterospecifics. One possible explanation could involve the foraging behaviours of specialist plant enemies (e.g. seed predators and leaf herbivores that trigger premature fruit abscission). The probability of a plant being found by herbivores is known as plant apparency (Feeny 1976), and unapparent plants might therefore suffer fewer attacks (Endara & Coley 2011). Herbivores locate host plants via a range of visual and chemical cues. Surrounding non-host plants can sometimes interfere with host location, essentially 'hiding' the plant individual from foraging insects (Floater & Zalucki 2000; McNair *et al.* 2000; Jactel *et al.* 2011; Dulaurent *et al.* 2012). Tree individuals surrounded by many large heterospecifics may therefore be less apparent to host-specific enemies, resulting in reduced premature fruit drop in areas with high densities of heterospecifics.

While we tried to include as many species as possible in our analyses, various biological and methodological considerations meant that only a subset (14%) of the species that occur in the ForestGEO plot were included. One bias of our study is the overall focus on species that are relatively common in the plot: rare species and species which generally produce few fruits and seeds are likely under-represented, since the chance of them falling into a seed trap is lower. The strength of conspecific negative density dependence can depend on the relative abundance of a species, with rarer species sometimes showing stronger patterns of conspecific negative density dependence (Comita *et al.* 2010 data reanalysed by Detto *et al.* 2019; Johnson *et al.* 2012). If this is the case for pre-dispersal seed mortality, we might expect the documented patterns of conspecific negative density dependence to have been even stronger if rarer species had been better sampled. While it would have been interesting to explore the relationship between species abundances and the strength of density dependence in our data set, preliminary analyses suggested that it would be difficult to generate accurate species-specific predictions with the available data.

In summary, the results of our study demonstrate a net negative, non-linear pattern of conspecific density dependence in pre-dispersal seed mortality. In one of the first studies assessing density dependence of pre-dispersal seed mortality, we show that patterns are consistent with both the Janzen-Connell and predator satiation hypotheses. Conspecific density-dependent patterns of seed survival acting at the pre-dispersal stage can directly influence the distribution of dispersed seeds on the forest floor (Janzen 1970), with potential implications for post-dispersal patterns of seed survival and ultimately plant recruitment (Crawley & Long 1995; Crawley 2000; Kolb *et al.* 2007; Sunyer *et al.* 2015). To build a comprehensive understanding of the processes determining spatial patterns of plant recruitment and species diversity maintenance, pre-dispersal seed mortality in tropical forests merits further investigation.

Chapter 4

Density-dependent pre-dispersal seed predation and fruit set in a tropical tree: spatial scaling of plant-insect interactions

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4.1 Abstract

Conspecific density-dependent processes acting at early stages in the life of a tree are thought to play an important role in determining spatial patterns of plant recruitment, and ultimately community structure. High densities of flowers and fruits attached to adult trees can attract both pollinators and pre-dispersal seed predators, resulting in contrasting density-dependent effects on seed production and survival. We studied the density dependence of fruit set and pre-dispersal seed mortality caused by an insect seed predator in the canopy tree *Jacaranda copaia* ($n = 90$) across a 15.6 km^2 island of tropical forest in Panama. We did not find any relationships between individual fruit set or fruit size and the local density of conspecific adult trees. On average, 16% of seeds were dropped prematurely due to insect attack. Premature fruit drop rates varied across the population with highly fecund individuals suffering higher levels of insect attack. At the wider population level this pattern was reversed, with seed predation showing a negative relationship with the local density of conspecific trees, potentially indicating satiation of predators at the population scale. Our results, which differ from those from a similar study carried out at a smaller spatial scale, caution against the assumption that density-dependent processes detected at one spatial scale will hold if investigated at other spatial scales.

4.2 Introduction

Of the many mechanisms proposed to promote plant species coexistence in diverse tropical forests, conspecific negative density dependence (CNDD) — i.e. the idea that individuals fare worse when surrounded by members of the same species — has received substantial attention (Wright 2002). The reduced survival of seeds and seedlings at high conspecific densities is now well documented (Harms *et al.* 2000; Peters 2003; Metz *et al.* 2010; LaManna *et al.* 2022) and evidence is accumulating that host-specific plant enemies, such as pathogens and insects which congregate where their hosts are abundant, can drive these patterns (Bagchi *et al.* 2014; Comita *et al.* 2014).

Although diversity-promoting CNDD driven by specialist enemies (often referred to as Janzen-Connell effects, Janzen 1970; Connell 1971) can happen at any stage of the plant life cycle, the scientific literature is dominated by studies assessing conspecific density dependence in the mortality of saplings, seedlings, and seeds that have already dispersed from the mother plant (Packer & Clay 2000; Hille Ris Lambers *et al.* 2002). The scarcity of studies on pre-dispersal seed mortality is somewhat surprising given that Gillett, who first raised the possibility of specialist enemies contributing to diversity-enhancing CNDD, used a system involving a pre-dispersal insect seed predator to illustrate his idea (Gillett 1962). While Janzen in his seminal paper (1970) also discussed the potential diversity-enhancing effects of pre-dispersal seed predators, tropical forest ecologists have paid much less attention to pre-dispersal seed mortality compared to post-dispersal mortality (Gripenberg 2018).

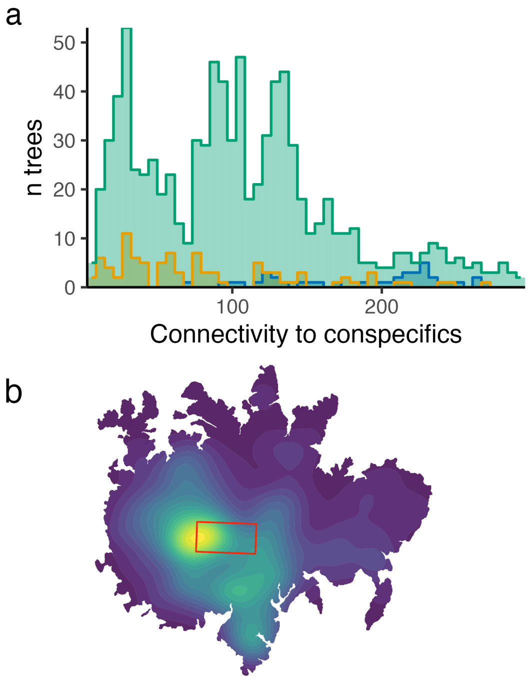

Figure 4.1: Conspecific density of adult *Jacaranda copaia* on Barro Colorado Island. Panel (a) is a histogram of calculated connectivity values for individual reproductive *J. copaia*: in the 50-ha forest dynamics plot, $n = 39$ (blue), sampled in this study, $n = 90$ (orange), and all other adult *J. copaia* across the island, $n = 884$ (green). Panel (b) is a map of Barro Colorado Island coloured by density of *J. copaia* individuals, with lighter (yellow) colours indicating high density and darker (purple) colours indicating low density. The rectangle outlined in red indicates the location of the 50-ha plot.

In one of the few studies to have investigated the density dependence of pre-dispersal seed mortality, Jones & Comita (2010) examined density dependence in fruit set and insect-mediated premature fruit drop in *Jacaranda copaia* in 50 hectares of lowland tropical forest in Panama (the 50-ha ForestGEO plot on Barro Colorado Island; Anderson-Teixeira *et al.* 2015). They found that although pre-dispersal seed predators increased seed mortality in a density-dependent pattern consistent with the predictions of the Janzen-Connell hypothesis, this effect was not large enough to counteract increased fruit set in areas of high conspecific density. This resulted in a net positive density-dependent pattern in realised reproductive output (i.e. the production of healthy seeds). The authors attributed the positive density-dependent pattern in fruit set to increased pollination success, whereby pollinators are attracted to high density areas. Such 'reverse Janzen-Connell effects', where host-specific mutualists increase the abundance or performance of plant species where they are common, could theoretically reduce community diversity (Zahra *et al.* 2021).

While the study by Jones & Comita did not reveal any clear evidence suggesting that host-specific insect seed predators are likely to play a major role in suppressing reproductive output of *J. copaia* at high densities, it would be premature to conclude that density-dependent patterns of insect-inflicted seed mortality with potential effects on tree diversity maintenance do not operate in other contexts or at other spatial scales. Many ecological processes are scale dependent, and patterns documented at one scale might not hold across other spatial scales (Wiens 1989; Levin 1992; Chave 2013). In the context of insect-plant interactions, the scale at which any density-dependent patterns will be apparent is likely to be dependent on the dispersal abilities and foraging decisions of insects in response to spatial variation in resource densities (Gripenberg *et al.* 2014). Moreover, if host abundances vary across the landscape, the range of host densities captured in a small-scale study might not reflect the wider range of host densities that enemies might experience.

In this study we investigated whether the patterns of pre-dispersal seed predation and fruit set previously documented by Jones & Comita (2010) hold when expanding the spatial scale to an area over 30 times larger (15.6 km^2) than the original study area (the entirety of Barro Colorado Island), and encompassing a much wider range of *Jacaranda copaia* densities than can be found in the 50-ha ForestGEO plot (Figure 4.1). We quantified pre-dispersal seed predation and fruit set for 90 individuals across the island using protocols identical to the study conducted by Jones & Comita (2010). We used maps created from island-wide high resolution aerial imagery to quantify local densities of reproductive *J. copaia* across the study area. Given the wider range of conspecific densities in the surrounding of our focal trees, and the potential for metapopulation-level processes to drive patterns of insect attack at this larger spatial scale (Gripenberg & Roslin 2005), we predicted that any effects of conspecific density on insect attack would be more pronounced than in the original study by Jones & Comita (2010).

4.3 Methods

Site and species description

We conducted field surveys for our study in October and November of 2022 on Barro Colorado Island (BCI), Panama. The 15.6 km^2 island is situated in Gatun Lake in the Panama Canal and is a protected area of lowland tropical rainforest with a long history of ecological research (Muller-Landau & Wright In press). Receiving an average of 2,600 mm of rainfall per year, BCI has a pronounced dry season between late December and June (Windsor 1990), in which many canopy tree species flower.

Figure 4.2: Aerial images of BCI from February 2023 provided by H. C. Muller-Landau and collected by drone pilot Milton Garcia. Reproductive *J. copaia* can be identified by conspicuous blue-purple flowers.

Jacaranda copaia (Bignoniaceae) is a pioneer tree species reaching a height of up to 45 m and a typical trunk diameter (DBH) of up to 50 cm (Croat 1978). It is common across the Neotropics and on BCI, with 309 individuals (≥1 cm DBH) recorded within the island's 50-ha forest dynamics plot in 2015 (Condit *et al.* 2019). Seedlings exhibit strong canopy gap dependence and *J. copaia* is one of the most light-demanding species on BCI (Brokaw 1987; Wright *et al.* 2003). Only upon reaching the upper canopy of the forest, at a size of approximately 20 cm DBH (Wright *et al.* 2005a), will individuals attempt reproduction. The *J. copaia* population on BCI produces a conspicuous blue-purple floral display between February and May (Figure 4.2), at the peak of the dry season. Flowering among individuals is synchronised only as to season (Gentry 1974). *Jacaranda copaia* employs a 'cornucopia' pollination strategy whereby individuals produce many flowers each day over several weeks, primarily attracting medium-sized solitary bees (Gentry 1974; Maués *et al.* 2008). *Jacaranda copaia* is self-incompatible, as is typical among tropical Bignoniaceae, and can be strongly pollen limited (Jones & Comita 2008; Maués *et al.* 2008). On BCI the fruits mature from July to September. The mature fruit is a bivalved dehiscent capsule (Figure 4.3 a) which opens in the canopy to release 200-300 flat winged seeds per locule (unpublished data, S. J. Wright), the majority of which disperse within 1 km from the mother tree (Jones *et al.* 2005; Jones & Muller-Landau 2008; Wright *et al.* 2008). Approximately 70% of *J. copaia* fruits are aborted prematurely in BCI's 50-ha forest dynamics plot, but this figure can vary substantially between years (Jones & Comita 2008; Jackson *et al.* 2022; Chapter 2). Immature fruits are on average 50 mm smaller than mature fruits and do not dehisce (Figure 4.3 c; Figure C.2). The empty dehisced capsules and aborted immature fruit fall to the forest floor and can remain intact for up to one year (Jones & Comita 2010).

Figure 4.3: *Jacaranda copaia* capsules collected on Barro Colorado Island. (a) mature non-predated capsules, (b) capsules which have been predated by a Chalcid wasp (Hymenoptera: Chalcidiodea) and (c) capsules which have fallen from the parent tree when still immature. In predated capsules the septum is curved and locules are asymmetrical. The unit of measurement on the tape pictured at the top of the image is centimetres.

A Chalcid wasp (Hymenoptera: Chalcidiodea) is known to predate *J. copaia* seeds on BCI (Jones & Comita 2010). The wasp infests capsules in the canopy as the fruit is maturing. Between five and ten larvae consume the seeds and pupate within the capsule, causing infected locules to deform into a characteristic woody gall (Figure 4.3 b) (Jones & Comita 2010). Infected fruits do not dehisce but fall from the canopy prematurely in May and June (F. A. Jones *pers. comm.*). Predation of fruits by the Chalcid wasp results in the death of all seeds within the capsule either through direct consumption or premature abscission (Jones & Comita 2010).

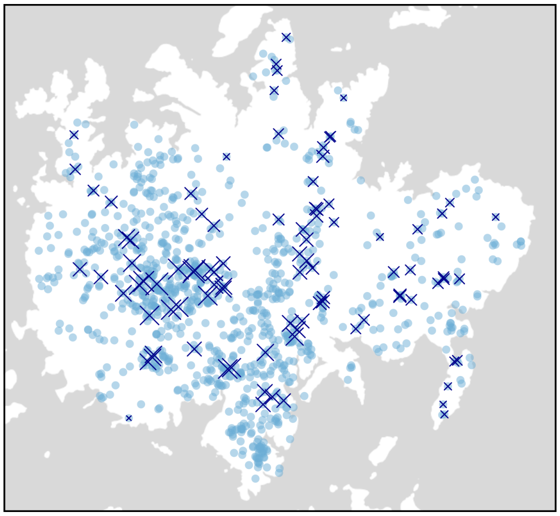

Figure 4.4: Map of adult *Jacaranda copaia* on Barro Colorado Island, Panama. Reproductive individuals are marked with points (n = 1,016). Trees which were selected for sampling are additionally marked with crosses ($n = 90$), where cross size is scaled with connectivity. Map tiles by Stamen Design, under CC BY 3.0.

Fecundity and predation estimation

We estimated the fecundity and levels of insect seed predation on *J. copaia* individuals distributed across BCI. We located potential survey trees from an estimated 1,016 reproductive sized *J. copaia* individuals on BCI (Garzon-Lopez *et al.* 2013) using two approaches: first, in late September and early October 2022, we walked the entire trail network of BCI, opportunistically looking for *J. copaia* individuals (*J. copaia* capsules on the ground, conspicuous canopies, distinctive bark). Through this approach, we located 62 easily accessible adult individuals (<20 m from a trail). To achieve a broader coverage of the island, and to ensure we included a sufficient number of the most isolated individuals, additional trees were located with the help of preexisting maps, constructed from aerial photographs by Garzon-Lopez *et al.* (2013). In total, 90 individuals were located and used in our study using these two approaches (Figure 4.4).

Between 29th October and 26th November 2022, we visited selected trees to assess fecundity (total count of capsules, regardless of their size and shape) and levels of attack by the Hymenopteran insect seed predator (proportion of galled capsules). Following methods in Jones & Comita (2010), we sampled fallen capsules along four transects, one in each cardinal compass direction from the centre of the tree's canopy to its edge. Since it was often difficult to see the extent of the canopy from the forest floor, we estimated canopy radius (m) as $r = 0.63 + (0.009 \times \text{DBH}\ /\text{mm})$ following known allometric relationships between crown radius and DBH for *J. copaia* on BCI (unpublished data, H. C. Muller-Landau; Figure C.1). Canopies of *J. copaia* do not overlap with conspecific or heterospecific canopies due to shade avoidance (Wright *et al.* 2005a). We placed a 0.5 × 0.5 m PVC quadrat at each metre along the transect and collected any *J. copaia* capsules within the quadrat. To assess whether the size of mature capsules depended on conspecific density, we measured collected capsules along the septum using callipers. In cases where the septum was not straight, we used string to follow its shape. We classified capsules as immature, predated by the Hymenopteran seed predator, or mature. Predated capsules were identified by having asymmetrical locules and a curved septum and/or a distorted shape with knobbly galls (Figure 4.3 b). Symmetrical fruits were categorised as immature if they were less than 55 mm long, otherwise they were classed as mature (Figure 4.3 a, c; Figure C.2). Classification of capsules into these groupings was confirmed as consistent with classifications used in Jones & Comita (2010) (F. A. Jones *pers. comm.*). To calculate an estimate of the total fruit set for each individual (individual fecundity), we first summed the number of capsules (mature, immature, and predated) sampled from beneath its canopy and divided this by area sampled. We then multiplied this figure by the total canopy area of the individual, estimated as $A = \pi r^2$. To estimate realised fecundity, we used the same process, but included only mature capsules. Single halves of capsules were included in summed counts as 0.5 of a capsule.

Conspecific density estimation

The location and individual crown area of fruiting *J. copaia* individuals on BCI was determined using pre-existing maps, derived from high-resolution aerial digital photographs as published by Garzon-Lopez *et al.* (2013) and described therein. The *J. copaia* crown maps were determined to have an accuracy of 76% (Garzon-Lopez *et al.* 2013). Photographs were taken in 2005 and 2006. The rate of tree mortality on BCI is approximately 2% per year (Condit *et al.* 1995). Although some mapped trees are likely dead at the time of sampling, the overall patterns of local *J. copaia* densities across the island are unlikely to have substantially changed.[1]

We used a connectivity index developed by Hanski (1994) to estimate how connected our focal trees were to conspecifics from the perspective of a seed predator or pollinator. Indices which take into account the size of the focal patch and the distances to and sizes of potential source patches are better at detecting neighbourhood effects than simpler nearest neighbour measures (Moilanen & Nieminen 2002). Additionally, if seed mortality increases with the local abundance of natural enemies that disperse from nearby conspecific trees, an 'additive-distance-decay' model (as described here) captures more biological realism than simpler non-additive or fixed distance models (Smith 2022). Connectivity was calculated as

$$S_i = \sum_{j \neq i} exp(-\alpha dist_{ji}) A_j^b \tag{4.1}$$

, where S_i is the connectivity of tree i, A_j is the crown area (in m^2) of conspecific tree j, and $dist_{ji}$ the distance (in m) from conspecific tree j, to the focal tree i. α is a measure of dispersal ability (1 / average migration distance in m) and b is a parameter, which scales the size of surrounding habitat patches. Crown area correlates with DBH in *J. copaia* (Figure C.1), and DBH scales linearly with fruit production in tropical trees (Chapman *et al.* 1992). Crown area is therefore a suitable parameter to describe the 'size' of the habitat patch, A_j, from the perspective of an insect associated with *J. copaia*. We selected $\alpha = 0.008$, which corresponds to an average migration distance of 120 m. We estimated α by comparing AIC for models fitted with different values of α (Figure C.3). We chose the scaling parameter for

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[1] New aerial imagery were collected in February and March 2023. Maps of *J. copaia* are currently being constructed by some of the authors of this study, but were not completed in time to be included in this thesis.

emigration, b, at 0.5 according to the assumptions of Moilanen & Nieminen (Moilanen & Nieminen 2002), who suggested that the ratio of patch edge to patch size decreases with $A^{0.5}$.

Fecundity and predation modelling

We analysed the effect of individual fecundity and connectivity on predation rate using a Bayesian logistic model with a zero-inflated binomial response distribution. The number of successes was equal to the number of predated fruits and the number of trials was equal to the total number of fruits. Individual tree fecundity, connectivity and their interaction were included as predictor variables. There was no evidence of spatial autocorrelation in predation rate (Figure C.4), so potential corrections for spatial non-independence of data points were not considered necessary.

To test whether pre-dispersal predation might negate a hypothesised positive effect of neighbours on fruit set (following Jones & Comita 2010), we investigated the effect of connectivity on individual fecundity (estimated total fruit set) and the effect of connectivity on realised fecundity (estimated number of mature capsules only). These two models were constructed as Bayesian models with negative binomial response distributions since the response data are discrete and overdispersed. As hypothesised by Jones & Comita (2010), if negative density-dependent predation is sufficiently strong to offset positive density-dependent fruit set, we expect any connectivity effect on the total number of capsules to no longer be positive when analysing only mature, non-predated capsules.

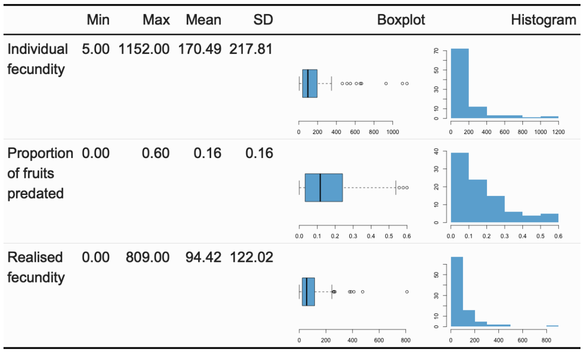
Finally, to examine whether greater connectedness to conspecifics resulted in the production of larger healthy fruits and whether fruit size correlated with individual fecundity, we modelled capsule length (of mature capsules only) as a function of connectivity, individual fecundity and their interaction, with tree individual as a random effect. We used a Bayesian model with a lognormal response distribution as the response data are continuous and non-negative.

To facilitate model convergence and interpretation of posterior parameter estimates, we scaled all predictor variables to a mean of zero and variance equal to one standard deviation in all models. The predictor variables were given weakly informative normal priors with a mean of zero and standard deviation of one. For the population-level intercept we used the default prior provided by the `brms` package: a half student-t prior with a location of zero, three degrees of freedom and scale parameter of 2.5.

All analyses were conducted in `R` (version 4.0.5, R Core Team 2021). The Bayesian models were implemented using the Hamiltonian Monte Carlo (HMC) sampler `Stan` (Stan Development Team 2022), interfaced through the `R` package `brms` (Bürkner 2017, 2018). We used posterior predictive checks to assess the global fit of the models to the data (Figures C.5 a, C.6 a, C.7 a, C.8 a). We ran four parallel chains for each model. The initial values for the chains were chosen at random within a reasonable range, as is default in `brms`. Each chain was run for 12,500 iterations with a burn-in phase of 500 iterations. We checked for convergence by visually inspecting the chains and verifying that $\hat{R}$ was below 1.01 for all parameters of the fitted models (Figures C.5 b, c, C.6 b, c, C.7 b, c, C.8 b, c). We present median estimates along with 95% confidence intervals (Highest Density Interval) for all estimates as measures of uncertainty.

4.4 Results

Jacaranda copaia trees sampled in this study produced an estimated average of 171 fruits (SD 218) per individual and with the exception of nine individuals which we estimated to have produced over 400 fruits, there was relatively little variation in reproductive output between trees (Figure 4.5). We saw greater variation in the rate of predispersal seed predation across the population with a mean of 16% (SD 16%) of sampled *J. copaia* capsules showing signs of predation (Figure 4.5).



	Min	Max	Mean	SD
Individual fecundity	5.00	1152.00	170.49	217.81
Proportion of fruits predated	0.00	0.60	0.16	0.16
Realised fecundity	0.00	809.00	94.42	122.02

Figure 4.5: Summary statistics for fruit set and pre-dispersal seed predation in *Jacaranda copaia* on Barro Colorado Island, Panama (n = 90 individual trees). Boxplots display the median value as a thickened line and the interquartile range as a box with whiskers extending to minimum and maximum values.

We found support for a clear positive relationship between the rate of pre-dispersal seed predation and individual fecundity (0.26 [0.17, 0.34]; Figure 4.6 a) and a negative relationship between the rate of pre-dispersal seed predation and connectivity to conspecific trees (-0.13 [-0.25, -0.01]; Figure 4.6 b). The interaction between individual fecundity and connectivity had a likely positive effect on rate of predispersal seed predation (0.19 [0.10, 0.28]).

Neither individual fecundity (-0.12 [-0.32, 0.09]; Figure 4.6 c) nor realised fecundity (-0.06 [-0.28, 0.18; Figure 4.6 d) had clear relationships with connectivity to conspecific trees. No relationships between the size of mature fruits and individual fecundity (-0.01 [-0.04, 0.02]; Figure 4.6 e), connectivity (0.02 [-0.01, 0.04]; Figure 4.6 f), or their interaction (0.00 [-0.03, 0.04]) were detected.

4.5 Discussion

A key motivation for our study was to test whether the density-dependent patterns of seed production and insect-inflicted seed mortality in *J. copaia* documented in a previous study covering a small part of BCI (Jones & Comita 2010) hold when density dependence is examined across the scale of the entire island. Like in the original study, we detected density-dependent seed predation, but specific patterns differed (Figure 4.7). In contrast with Jones & Comita (2010), we did not find support for any relationships between tree fecundity (a likely outcome of pollination success) and the density of conspecifics (Figure 4.7). Below we discuss our results and potential reasons for the contrasting findings.

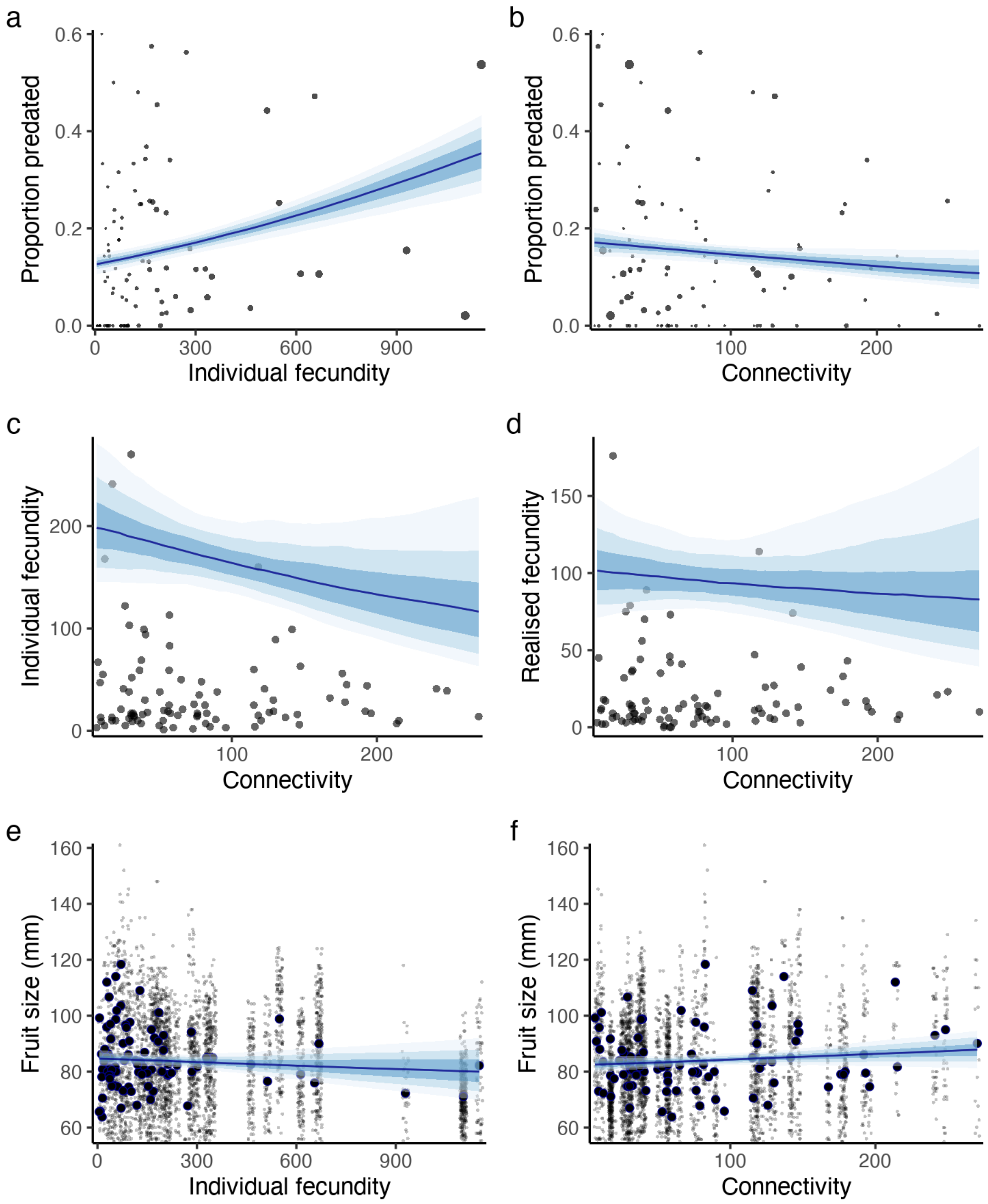


Figure 4.6: Conditional effects of connectivity, fruit set and tree size on the proportion of capsules predated and fruit counts. Since models depicted in panels (a), (b), (e), and (f) included interaction terms, these panels show conditional effects where predicted values of each response variable (y axis) are plotted across each predictor (x axis) whilst the other predictor is held at its mean. Panels (c) and (d) show model predictions for fitted data. The solid blue line is the median estimate with 50%, 80% and 95% credible intervals represented by bands in transparent shades of blue. In panels (a) and (b) the size of the points is scaled by total fruit count. In panels (e) and (f) the smaller points correspond to a single fruit size measurement, jittered on the x axis, and the larger points correspond to the median fruit size per individual tree to aid with visualisation.

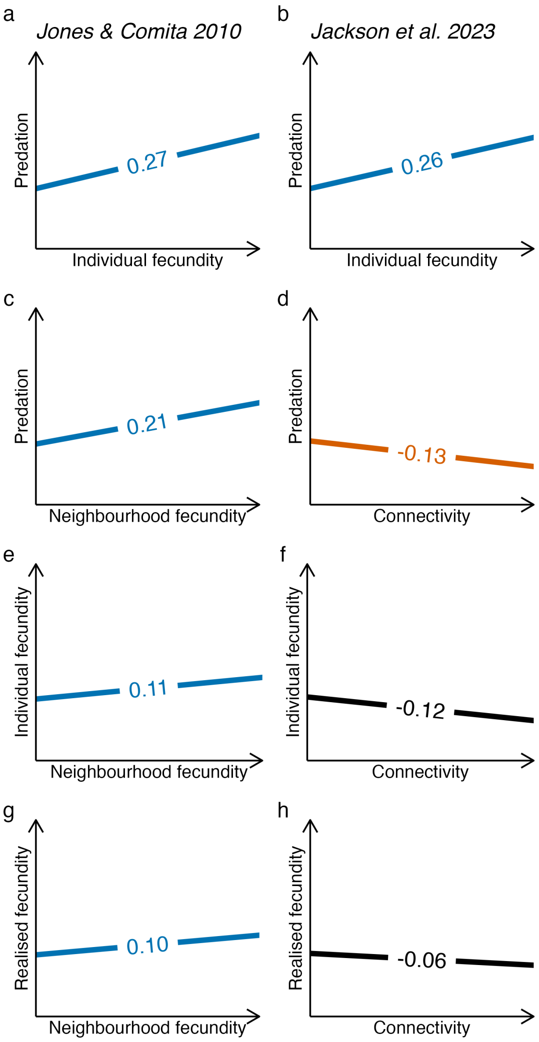


Figure 4.7: Schematic comparing effect sizes between this study and Jones & Comita (2010). Panels (a), (c), (e), (g) show results from (Jones & Comita 2010) and panels (b), (d), (f), (h) show results from the current study. Corresponding tests are aligned horizontally. Positive relationships are coloured blue, negative relationships are coloured red and relationships for which there wasn't strong support (95% credible intervals contained zero) are coloured black.

Seed predation

We found evidence for both negative and positive density-dependent pre-dispersal seed predation in the *J. copaia* population at BCI. Interestingly, the sign of the density-dependent effect was contingent on spatial scale: seed predation was positively related to the local abundance of fruits on individual trees, but showed a negative relationship with the density of reproductive-sized individuals in the neighbourhood (as defined by our measure of connectivity). The first result supports Janzen's (1970) hypothesis that the pre-dispersal predation of fruits by insects is likely to be highest in trees bearing many fruits. In terms of its strength, the positive relationship between predation and estimated fruit crop size was strikingly similar to that reported by Jones & Comita (2010; Figure 4.7 a, b). High predation in fecund trees suggests that the wasp predating on *J. copaia* seeds is attracted to trees in which resources are locally abundant. As noted by Jones & Comita (2010), if the same tree individuals tend to produce high numbers of fruit from one year to another, this could allow for large insect populations to build up close to highly fecund trees if infested fruits and emerging pupae remain close to the original tree.

In contrast to the results of Jones & Comita (2010), we found that the relationship between pre-dispersal seed predation and the density of conspecifics was negative when examined at a scale larger than the tree individual (Figure 4.7 c, d). Whilst we had tentatively predicted that the positive effects of conspecific density on insect attack might be more pronounced than in the original study given the wider range of conspecific densities sampled, this assumes that the responses of predators to small-scale variation in seed densities is predictive of their responses across scales up to several thousand metres. Although little is known of the movements of pre-dispersal predators, our result may indicate that the wasp seed predator does not respond to spatial variation in *J. copaia* seed densities through long-distance dispersal between habitat patches. At a relatively local scale, seed predators might be attracted to areas of high resource density, but at larger spatial scales, other mechanisms might come into play. For example, the most optimal foraging (or oviposition) strategy (Pyke 1984) of female seed predators in areas of low local host densities might be to lay their eggs on locally fecund trees rather than attempt to migrate large distances in search for patches of higher resource density. Such behaviours could contribute to the patterns documented in this study, where a high density of conspecifics appears to satiate predators, allowing more seeds to escape enemy attack.

Tree fecundity and fruit size

We found no evidence of the positive density-dependent pattern in individual fecundity reported by Jones & Comita (2008, 2010; Figure 4.7 e, f), and the pattern we found of reduced predation at high connectivities (Figure 4.7 d) did not translate to any change in realised fecundity with increasing connectivity (Figure 4.7 h). For insect-pollinated species, such as *J. copaia*, individual fecundity is likely to be associated with pollination success, and the responses of pollinators to the density and spatial distribution of flowering trees could result in density-dependent patterns of fruit set. Although insect pollinators in the tropics have been reported to disperse pollen >10 km, the majority of pollen dispersal typically occurs across local scales (<0.5 km Dick *et al.* 2008), especially when flowering individuals are unevenly distributed in space (Stacy *et al.* 1996). This could perhaps explain why we did not find a relationship between connectivity and individual fecundity in the present study.

We did not find any support for our prediction that fruit size might be related to local fruit crop size and connectivity. The number of seeds per fruit likely scales with fruit size in *J. copaia* (S. J. Wright *pers. comm.*) and we predicted increased pollinator attraction at high conspecific densities would improve fertilisation success and therefore increase seed set and fruit size. Since we found no evidence of a density-dependent pattern in individual fecundity, it follows that actual numbers of seeds produced (fruit size) did not depend on the local density of conspecifics. At the local scale, we might have expected a negative relationship between fruit size and individual fecundity if individuals have finite resources to allocate to reproduction, creating a trade-off between fruit abundance and size (e.g. Aliyu & Awopetu 2011; Dombroskie *et al.* 2016), but we found no evidence of this in our study population.

Methodological & contextual considerations

While the differences in results between our study and Jones & Comita (2010) could be due to biological processes operating differently across spatial scales and ranges of conspecific densities, some methodological and contextual differences could also contribute to the contrasting patterns of density dependence.

If spatial patterns of density dependence are linked to the overall abundance of resources, differences in overall seed abundance could depend on the year of the study. For example, predators might respond to high seed densities in years with low resource abundances, but could be satiated in years when resources are abundant. *Jacaranda copaia* exhibits substantial interannual variation in fruit production. In 2022 when we conducted our study, average *J. copaia* fruit production per individual was 171, which is consistent with a low reproductive year in the population and close to the range of average fruit production values recorded by Jones & Comita (2010) (299, 289 and 189 in each of the three years covered by the study). It should also be noted that the average rate of pre-dispersal predation experienced by trees in our study was 16%, which falls within the range of yearly predation rates (8% to 38%) documented by Jones & Comita (2010).

One key methodological difference between our study and Jones & Comita's study (2010) may have contributed to the differences between our results. Working across a small spatial area enabled Jones & Comita (2010) to estimate the individual fecundity of neighbouring trees by sampling fruits of every *J. copaia* individual in the 50-ha forest dynamics plot. In the present study it was not feasible to sample fruits from every *J. copaia* tree (∼ 1,000 individuals) across the island, hence when calculating our connectivity metric we assumed that non-focal trees of equivalent size produced the same amount of fruit. While this is a plausible assumption (Chapman *et al.* 1992), it likely introduces some error to our estimated connectivity values. For example, physiological decline in large, old trees can diminish fecundity (Qiu *et al.* 2021), suggesting that very large individuals could be over represented in our study. Before this chapter is submitted for publication in a journal, aerial imagery of flowering *J. copaia* crowns collected in 2023 will be combined with our fruit count data, allowing us to explore the relationship between tree size and fruit numbers in greater detail and assess the possibility of reproductive senescence introducing errors into our estimates of connectivity.

Conclusions

Our study adds to a body of literature suggesting that ecological processes act at a variety of spatial scales. While it is well known that fundamental operations at one scale can become entirely obscured when the system is examined on a different scale (Wiens 1989; Levin 1992; Chave 2013), the scale dependency of conspecific density dependence in processes affecting the reproduction and survival of tropical trees remains understudied (but see e.g. Schupp 1992; Xiao *et al.* 2017). In particular, studies covering spatial scales larger than the typical size of mapped forest plots such as those within the ForestGEO network (Anderson-Teixeira *et al.* 2015) are still scarce. The approach of mapping reproductive-sized tree individuals across larger landscapes using remote sensing techniques opens up possibilities for studies of conspecific density dependence at spatial scales that would be difficult to cover using ground-based mapping methods alone (e.g. Garzon-Lopez *et al.* 2015; Kellner & Hubbell 2018). To our knowledge, our study is one of the first to combine maps generated from remote sensing products with ground-based surveys of enemies to investigate density-dependent enemy attack on tropical trees.

Adopting an approach near identical to Jones & Comita (2010), we failed to find evidence of positive density dependence in fruit set and the rate of pre-dispersal predation when covering spatial area over 30 times larger than in the original study. Our results demonstrate that density-dependent effects at the scale of a few metres do not necessarily translate to larger landscapes, and that these effects can change direction depending on the scale being examined. To understand if and how interactions between plants and insects can facilitate species coexistence through Janzen-Connell effects, the larger spatial scale should not be ignored when investigating patterns of seed production and survival.

Chapter 5

Density-dependent effects on the reproductive ecology of trees in a temperate woodland

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In preparation for publication

5.1 Abstract

Interactions between plants and other organisms can have opposing effects on plant reproductive success and are often uneven in space. For example, while a high density of flowers can attract pollinators and improve seed set, a high density of seeds can attract enemies such as seed predators. It is the joint outcome of positive and negative density-dependent effects which will determine the spatial distribution of a population, yet they are rarely studied in parallel. We related two contrasting indicators of reproductive success (fruit set and pre-dispersal fruit drop) to the size and density of neighbouring conspecifics for 32 *Crataegus monogyna* (Rosaceae) individuals in a temperate woodland. Overall, we found that 24% of flowers set seed and 85% of initiated fruits were dropped, with considerable variation among trees. While there was no pattern of density dependence in fruit set, our results suggest that fruit drop increases with fruit density in this system, with potential implications for spatial patterns of seedling recruitment.

5.2 Introduction

Mutualistic and antagonistic interactions between plants and other organisms are important determinants of plant fitness, and can ultimately influence plant demography and community structure (Harms *et al.* 2000; Frederickson & Gordon 2007; Rother *et al.* 2013). These interactions might be particularly important at the very earliest stages in the life of a plant, when interactions between flowers and pollinators are often crucial for successful reproduction (Steffan-Dewenter *et al.* 2001; Karron *et al.* 2006) and an encounter with a herbivore can be fatal for developing seeds (Janzen 1976a).

Interactions between plants, their pollinators, and plant enemies are rarely uniform in space (Dupont *et al.* 2014; Wetzel *et al.* 2023). Large and dense areas of flowers, whether due to a high local abundance of flowering plants or the large floral display of a single plant, tend to attract pollinators (Sih & Baltus 1987; Smithson & Macnair 1997). More visits from pollinators benefit the fitness of plants when pollen is limiting, resulting in a positively density-dependent pattern in seed set (Severns 2003; Dauber *et al.* 2010). Higher densities of a plant species can additionally improve seed set by increasing outcrossing due to reduced genetic similarity to nearby conspecifics (Ågren 1996). However, a high density of developing fruits can also attract plant enemies such as flower and seed predators, especially if they are host specific (Östergård & Ehrlén 2005). Such pre-dispersal attack can result in mortality directly through seed predation or indirectly through premature abscission of damaged fruits (Boucher & Sork 1979; Stephenson 1981; Meyer *et al.* 2014; Planes *et al.* 2014; Jackson *et al.* 2022; Chapter 2; Chapter 4).

The effects of conspecific density on plant reproduction and fitness have received considerable attention in the context of forest trees. Insect pollinated trees and shrubs in isolated forest fragments have been shown to receive less pollen and experience lower levels of outcrossing than individuals in continuous forests, resulting in reduced fruit set for self-incompatible species (Cunningham 2000; Ghazoul & McLeish 2001; Chacoff *et al.* 2008) and a loss of genetic diversity in the population (Vranckx *et al.* 2012). Fewer studies have examined pollen limitation in woody plants within continuous forests (but see e.g. Maycock *et al.* 2005; Jones & Comita 2008; Aoyagi *et al.* 2023; Chapter 4). Although the scale of conspecific isolation between trees within forests is typically smaller than between forest fragments, we know that insect pollinators will often remain foraging in areas of high flower density rather than travel the full distances they are capable of (Smithson & Macnair 1997; Goverde *et al.* 2002), suggesting that low density areas within forests could still be neglected or less favoured by pollinators.

Reduced plant fitness and reproductive success in areas of high conspecific density has also been widely documented in a range of forest systems (Hille Ris Lambers *et al.* 2002). A well studied example is the Janzen-Connell hypothesis, which proposes that host-specific plant enemies reduce plant recruitment and survival in areas of high conspecific density (Janzen 1970; Connell 1971). To date, most studies investigating the effects of conspecific density on tree performance have focused on the survival of post-dispersal seeds, seedlings, and saplings, with relatively few studies having assessed patterns of conspecific density dependence in the period between successful pollination and seed dispersal (but see Jones & Comita 2010; Ballarin *et al.* 2022; Chapter 3; Chapter 4).

In this study, we investigated spatial variation in two elements influencing the reproductive success of *Crataegus monogyna* (hawthorn), initial fruit set (the proportion of flowers turning into immature fruits) and fruit drop (the proportion of fruits dropped from the tree when protected from avian dispersers). We quantified fruit set and fruit drop on 32 trees distributed across Wytham Woods, a 4.2 km^2 woodland in Oxfordshire, UK, and related these processes to tree size and connectivity metrics reflecting the local density of reproductive and non-reproductive hawthorn individuals in the neighbourhood. Since both pollinators and enemies associated with developing fruits might be attracted to areas of high hawthorn abundance, we expected larger trees and trees with high connectivity to reproductive conspecifics to experience both higher initial fruit set and greater fruit drop.

5.3 Methods

Site and species description

We conducted our study between 2021 and 2023 in Wytham Woods, Oxfordshire, UK. The area covers 4.2 km^2 and houses a mixture of ancient and secondary woodland alongside plantations from the nineteenth and twentieth centuries (Morecroft *et al.* 2008).

Crataegus monogyna (hawthorn; Rosaceae) is a deciduous small tree or shrub which is common throughout Wytham Woods and across much of Europe (Sorensen 1981; Fichtner & Wissemann 2021). In 2008, 1,308 *C. monogyna* individuals (≥1 cm DBH) were recorded in the 18-ha ForestGEO permanent forest dynamics plot in Wytham Woods (Butt *et al.* 2009) and local densities of *C. monogyna* vary throughout the woodland (Kirby *et al.* 2014). *Crataegus monogyna* is characteristically thorny and densely branched, reaching a height of between 2 and 10 m, with stems of up to ~ 30 cm in diameter (Fichtner & Wissemann 2021). From April to May adult *C. monogyna* produce many thousands of white flowers. Immature green fruits appear in June and ripen from August through September, turning red (Fichtner & Wissemann 2021). Only one seed is produced per fruit. Mature fruits can remain on the plant for over nine months until they are dispersed by vertebrates (usually birds) (Sorensen 1981; Guitián & Fuentes 1992). The species has self-incompatible gametes (Raspé & Kohn 2002) and the majority of studies agree that insects are important for pollination in this species (Guitián & Fuentes 1992; Chacoff *et al.* 2008; Jacobs *et al.* 2009; Fichtner & Wissemann 2021; but see Gyan & Woodell 1987b). The white flowers of hawthorn attract a range of flower visitors, predominantly Diptera but also various Hymenoptera and Coleoptera (Fichtner & Wissemann 2021). Many herbivorous invertebrates are associated with *C. monogyna* in the UK, including host specific insects which target the reproductive parts of the plant such as flower weevils (*Anthonomus pedicularius* and *Anthonomus bituberculatus*), Lepidopteran and Dipteran larvae which consume the fleshy pulp of the fruit (*Blastodacna hellerella* and *Anomoia purmunda*), and *Torymus varians*, a Hymenopteran seed predator of hawthorn and apple (Fichtner & Wissemann 2021).

Focal tree selection and estimation of connectivity to conspecifics

To select *C. monogyna* individuals for our study we walked the entire trail network of Wytham Woods in July 2021, opportunistically marking 32 focal study individuals which were easily accessible, reproductive and at least ~ 50 m apart from each other (Figure 5.1). From May 2022 to September 2022 we mapped all hawthorn individuals within a 50 m radius of each of the focal trees using a differential global positioning system (dGPS, Emlid Reach RS2+) (see detailed protocol in Appendix D). The hawthorn individuals surrounding one of the focal trees were mapped later, in April 2023. In addition to coordinates, we recorded the DBH (diameter at breast height) and reproductive status (whether the individual had flowers or fruits at the time of recording) of each individual.

We used the connectivity index proposed by Hanski (1994) to estimate how connected our focal trees were to conspecifics from the perspective of pollinators or seed predators visiting *C. monogyna*. Connectivity was calculated as

$$S_i = \sum_{j \neq i} exp(-\alpha dist_{ji}) A_j^b \tag{5.1}$$

, where S_i is the connectivity of tree i, A_j is the DBH (in mm) of conspecific tree j, and $dist_{ji}$ the distance (in m) from conspecific tree j, to the focal tree i. α is a measure of dispersal propensity (1/average migration distance in m) of a pollinator or seed predator and b is a parameter which scales the size of surrounding trees. Plant size correlates closely with fruit production in *C. monogyna* (Sallabanks 1992) and DBH is therefore a suitable parameter to describe the 'size' of the habitat patch, A_j, from the perspective of an insect associated with *C. monogyna*. We chose $\alpha = 0.02$, which corresponds to an average migration distance of 50 m. Since the dispersal distances of insects associated with *C. monogyna* are unknown and likely to vary across species, we chose this value based on empirical data on the average dispersal distance of a leaf mining moth associated with oak trees (Gripenberg & Roslin 2005). The maximum possible value of average migration distance was limited by our study design (we only mapped trees within a 50 m radius of our focal trees), but to test if the average migration distance could be less than 50 m we compared AIC for models fitted with values ranging from 5 to 50 m (Figure D.1). It is worth noting that the exact choice of α has a relatively small impact on Hanski's connectivity index (Moilanen & Nieminen 2002). We chose the scaling parameter for emigration, b, at 0.5 according to the assumptions of Moilanen & Nieminen (2002), who suggested that the ratio of patch edge to patch size decreases with $A^{0.5}$. The connectivity of each focal tree was calculated separately to include all conspecific individuals within 50 m and including reproductive conspecifics only. We refer to these as *total connectivity* and *reproductive connectivity*, respectively.

Estimation of fruit set and fruit drop

On 31st May 2023 we recorded flower abundance on three to six marked branches of focal trees (if a marked branch had less than 20 flowers, and an additional flowering branch was in reach, it was also surveyed). This resulted in 20,514 flowers surveyed across 101 branches from 32 trees. On 26th and 29th June 2023 we recorded initial fruit abundance for each surveyed branch. At this stage fruits were green and not attractive to avian dispersers.

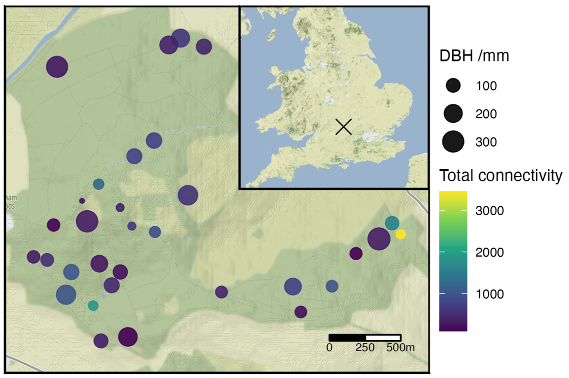


Figure 5.1: Map of focal *C. monogyna* trees in Wytham Woods. Shaded circles show locations of focal trees with colour denoting total connectivity and size scaled by DBH ($n = 32$). The inset map shows the location of Wytham Woods in the UK. Map tiles by Stamen Design, under CC BY 3.0 and map data by OpenStreetMap under ODbL.

On 5th August 2021 we recorded fruit abundance on six marked branches of each of the 32 focal trees and repeated this approximately every four weeks until 7th March 2022, comprising eight surveys in total. If the branches surveyed in 2021 for fruit drop produced flowers in 2023, they were also selected to be surveyed for fruit set. To protect fruits from vertebrate removal, three of the six marked branches of each tree were encased in wire mesh (13 mm mesh size) before fruits started to ripen (Figure D.2 a). The wire mesh should exclude most vertebrate seed consumers but allow entry to all in-vertebrate seed predators. Only the branches protected with mesh cages were used to estimate premature fruit drop. In total 4,718 fruits were surveyed across 90 branches. Fruit dropped per branch was calculated as the fruit abundance in the first survey minus the fruit abundance in the final survey. While fruits may have been exposed to insects for longer than if vertebrates were not excluded from branches, insect activity is likely diminished during the colder months. Additionally, our aim is to assess spatial patterns of insect attack rather than absolute levels of damage.

Statistical analysis

We analysed the effect of tree size (DBH) and connectivity (reproductive and total) on fruit set (the proportion of flowers turning into immature fruits) using two Bayesian mixed-effects models with a binomial response distribution estimated using MCMC sampling. The number of trials was equal to the number of flowers and the number of successes was equal to the total number of green fruits on a branch. Reproductive or total connectivity, DBH, and their interaction were included as predictor variables. Tree ID was included as a group-level (‘random’) effect to account for non-independence of branches within trees.

The effect of tree size (DBH) and connectivity (reproductive and total) on fruit drop was modelled using the same method as for fruit set, with the same predictors and where the number of successes was equal to the number of dropped fruits and the number of trials was equal to the initial total number of fruits.

Before model fitting, we assessed spatial autocorrelation in fruit set and fruit drop using variograms created with the `R` package `gstat` (Pebesma 2004; Gräler *et al.* 2016) (Figure D.3). To facilitate model convergence and interpretation of posterior parameter estimates, we scaled all predictor variables to a mean of zero and variance equal to one standard deviation in all models. The population-level effects were given weakly informative normal priors with a mean of zero and standard deviation of one. For the population-level intercept and the group-level effect of tree ID we used the default priors provided by the `R` package `brms` (Bürkner 2017, 2018): a half student-t prior with a location of zero, three degrees of freedom and scale parameter of 2.5.

All analyses were conducted in `R` (version 4.2.3) (R Core Team 2023). The Bayesian models were implemented in `Stan` (Carpenter *et al.* 2017) and run in `R` through the package `brms` (version 2.19.0) (Bürkner 2017, 2018). We ran four parallel chains for each model. The initial values for the chains were chosen at random within a reasonable range, as is default in `brms`. Each chain was run for 2,000 iterations with a burn-in phase of 1,000 iterations. We checked for convergence by visually inspecting the chains (Figure D.4) and verifying that $\hat{R}$ was below 1.01 for all parameters of the fitted model (Table D.1).

We used posterior predictive checks to assess the global fit of the model to the data (Figure D.5). We present median estimates along with 95% credible intervals (Highest Density Interval) for all estimates as measures of uncertainty.

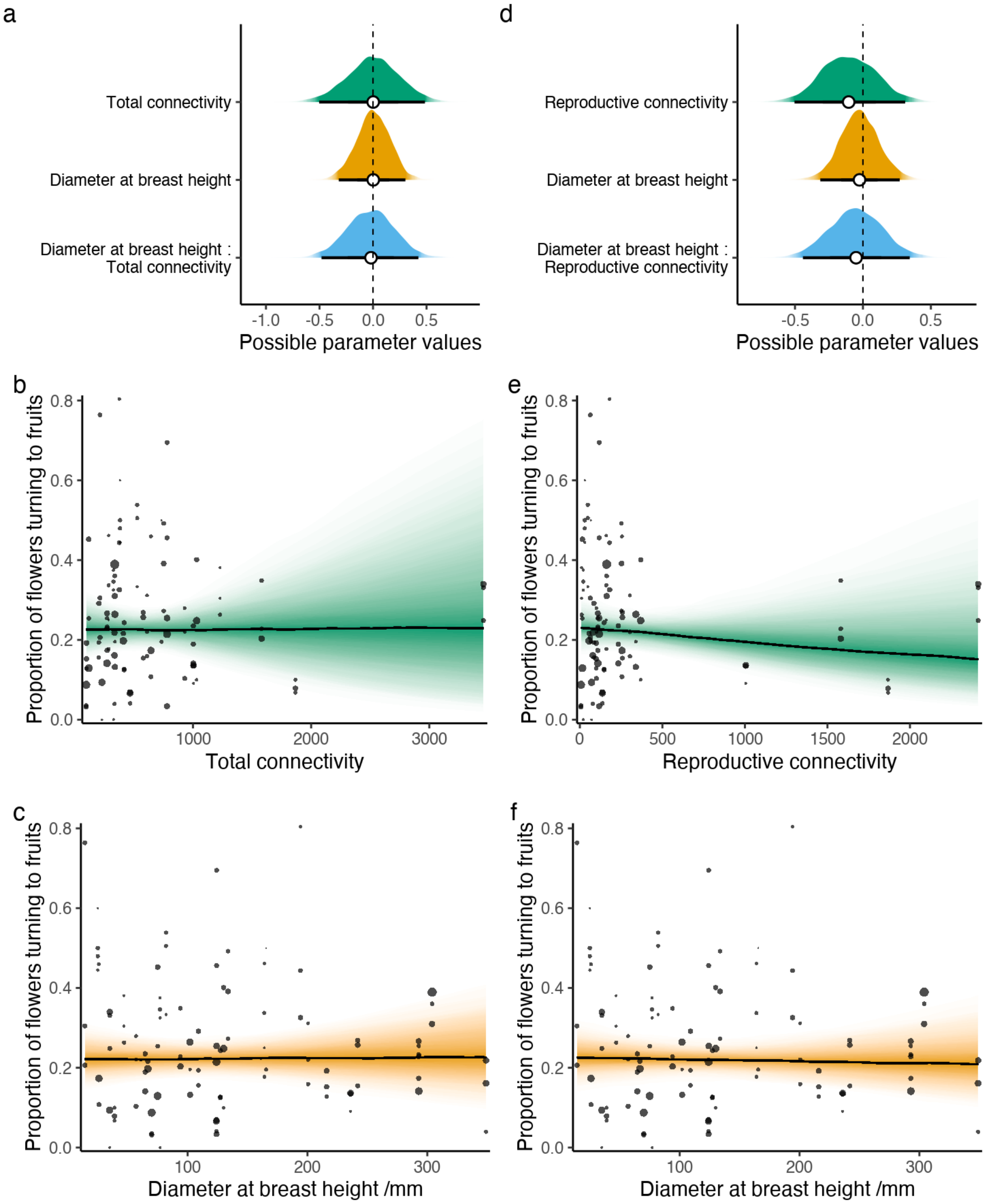


Figure 5.2: Effects of connectivity and plant size on fruit set (the proportion of flowers turning into fruits). Panels (a - c) correspond to the model which included total connectivity as a predictor and panels (d - f) correspond to the model which included reproductive connectivity as a predictor. Panels (a, d) show the posterior parameter distributions with white points depicting posterior medians and lines 95% credible intervals. Panels (b, e) show conditional effects of connectivity and panels (c, f) show conditional effects of tree size (DBH) on fruit set. Predicted values of fruit set are plotted across each predictor whilst the other predictor is held at its mean. Each point corresponds to a single branch with point size scaled by the original number of flowers. The solid line represents the median of 500 draws from the expected value of the posterior predictive distribution with transparency corresponding to the density of draws.

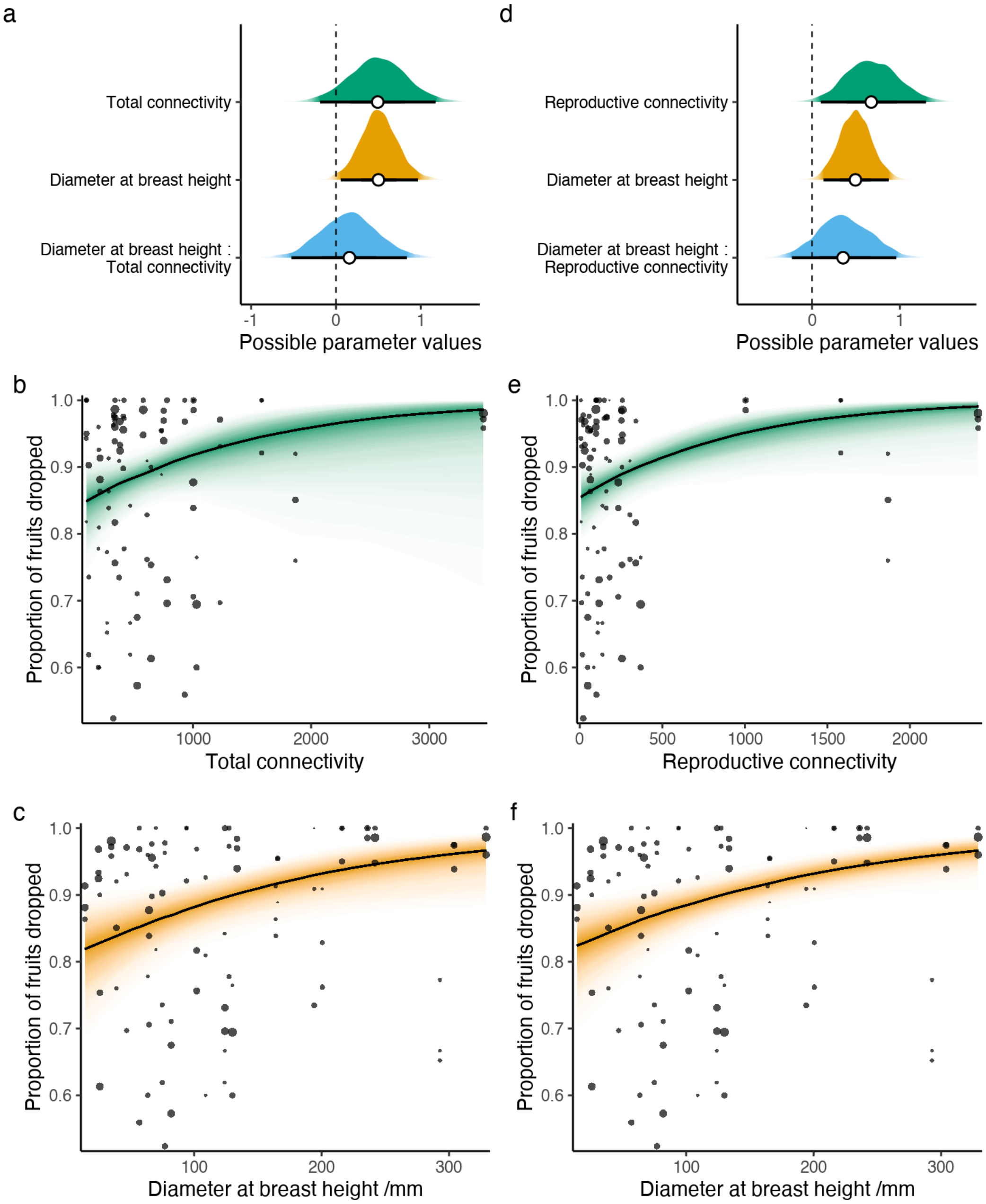
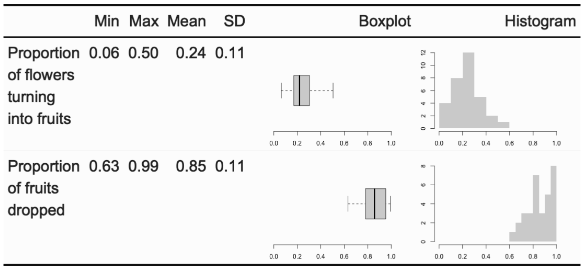


Figure 5.3: Effects of connectivity and plant size on the proportion of fruits dropped. Panels (a - c) correspond to the model which included total connectivity as a predictor and panels (d - f) correspond to the model which included reproductive connectivity as a predictor. Panels (a, d) show the posterior parameter distributions with white points depicting posterior medians and lines to 95% credible intervals. Panels (b, e) show conditional effects of reproductive connectivity and panels (c, f) show conditional effects of tree size (DBH) on the proportion of fruits dropped. Predicted values of the rate of fruit drop are plotted across each predictor whilst the other predictor is held at its mean. Each point corresponds to a single tree branch with point size scaled by the maximum fruit count. The solid lines represent the median of 500 draws from the expected value of the posterior predictive distribution with transparency corresponding to the density of draws.

5.4 Results

On average, 24% of sampled flowers turned into green fruits and 85% of fruits were dropped without being dispersed (Figure 5.4). There was considerable variation among individual trees in rates of both fruit set and fruit drop (Figure 5.4) and this appears larger than variation among branches within trees (Figure 5.2; Figure 5.3). We found no evidence of spatial autocorrelation in fruit set or fruit drop (Figure D.3).



	Min	Max	Mean	SD	Boxplot	Histogram
Proportion of flowers turning into fruits	0.06	0.50	0.24	0.11		
Proportion of fruits dropped	0.63	0.99	0.85	0.11		

Figure 5.4: Summary statistics for fruit drop and fruit set in *C. monogyna*. Boxplots display the median value as a thickened line and the interquartile range as a grey box with whiskers extending to minimum and maximum values, $n = 32$.

The proportion of flowers turning into fruits (fruit set) did not depend on tree size and there was also no relationship between fruit set and total or reproductive connectivity (Figure 5.2; Table D.1).

There was no evidence to support a relationship between total connectivity and fruit drop (Figure 5.3 a, b; Table D.1), but the proportion of fruit dropped showed a positive relationship with both reproductive connectivity (Figure 5.3 d, e; Table D.1) and tree size (Figure 5.3 d, f; Table D.1). The interaction effect between connectivity and tree size was not significantly different from zero (Figure 5.3 d; Table D.1).

5.5 Discussion

Our study of the reproductive ecology of hawthorn in Wytham Woods did not yield any clear evidence to support our hypothesis that flower to fruit transition would be positively density-dependent. In line with our predictions, we did find that initiated fruits in larger trees and in trees in areas with a high local hawthorn density were less likely to reach the stage at which they would typically be dispersed from the mother tree. Below we discuss some potential explanations for and implications of these findings.

No evidence of density dependence in fruit set

A relatively small proportion of flowers resulted in immature fruits. On average, we found that 24% of an individual's flowers resulted in green immature fruits, most of which are likely to have matured into red fruits later in the season. Abortion of green immature fruits soon after flowering, which is common in some other systems (e.g. Jackson *et al.* 2022; Chapter 2), does not seem to happen in hawthorn (*pers. obs.*). A flower to fruit conversion rate of 24% agrees with reported rates of fruit set from hawthorn populations in northern Spain, which vary between 20% and 50% under natural conditions (Guitián & Fuentes 1992; Chacoff *et al.* 2008).

While the flower-to-fruit transition rates varied considerably across the surveyed trees, this variation could not be explained by the size of the trees and their location in respect to the density of conspecifics in the neighbourhood.

The lack of density dependence in fruit set contrasts with a previous study on hawthorn populations (García & Chacoff 2007) and a number of studies conducted in other systems (Augspurger 1980; Sih & Baltus 1987; Ghazoul 2005; Grindeland *et al.* 2005; Aizen & Harder 2007; Ballarin *et al.* 2022) which have shown that pollinators might be attracted to large plants or highly fecund individuals and to areas in which there are many flowering individuals.

Whilst we included individuals from across the extent of Wytham Woods, it is possible that the scale of density covered is not relevant from the perspective of pollinators. Garcia & Chacoff's (2007) study which found density-dependent fruit set in hawthorn was conducted across similar spatial scales (20 - 100 m) as our study, but was assessing populations fragmented by pasture and heathland. Forest patches surrounded by matrix habitat presumably present a less attractive resource to pollinators than an equally valuable resource at a similar distance away connected by continuous forest habitat. We surveyed only a few trees which were highly connected to reproductive conspecifics (reproductive connectivity >500) due to their rarity in the woodland. It is possible that the scale of conspecific hawthorn densities present within continuous forests does not elicit density-dependent foraging patterns in pollinators, but this would need to be confirmed with targeted surveys of highly connected trees.

It could perhaps be argued that the broad patterns of host use shown by many pollinators in the UK (e.g. Memmott 1999) will make it unlikely to pick up conspecific density effects. However, many of the insects visiting hawthorn flowers could be considered functional specialists. Hawthorn flowers in early spring when insects are scarce and at Wytham Woods it is likely to be the most abundant floral resource at the time of flowering (Gyan & Woodell 1987a,b). *Prunus spinosa* (Rosaceae) shares a similar flower morphology and is attractive to a similar range of pollinators as hawthorn, but the two species have sharply differentiated flowering phenology (Gyan & Woodell 1987b).

Some evidence of density dependence in fruit drop

Fruit drop can be triggered by damage to the fruit or seed (caused by enemy attack or abiotic factors), or through selective abscission of undamaged fruits by the parent tree (Stephenson 1981). Selective abscission is often due to limiting resources or pollination failure, and usually happens soon after flowering (Tromp & Wertheim 2005; Jackson 2010). Although resource availability and pollination success are likely to vary across space, it is unlikely that fruit drop due to these factors was captured in our study, since we began monitoring fruits as they were beginning to ripen. Abiotic damage to fruits, while a potential cause of fruit drop, is unlikely to occur in density-dependent patterns. Whilst we did not quantify enemy attack, it seems likely that some fruit drop was caused by insect fruit and seed predators. Adult *Anomoia purmunda* (Diptera: Tephritidae), a hawthorn specific fruit predator, was observed at focal trees and we found many fruits infested with Dipteran and Lepidopteran larvae (likely hawthorn specific *Blastodacna hellerella* as reported by Manzur & Courtney (1984)). Other studies in Europe have measured infestation of *Anomoia purmunda* in hawthorn fruits at 52% and 40% (Guitián & Fuentes 1992; Teodoru *et al.* 2015), Lepidopteran larvae infestation at 22% (Guitián & Fuentes 1992), and overall insect damage at 37% (Manzur & Courtney 1984). Tephritid flies have been reported to cause fruit drop in many agriculturally important crops (e.g. Stonehouse *et al.* 2002; Dutta *et al.* 2022), so it seems plausible that some of the fruit drop observed in our study could indeed have been triggered by Tephritidae. Whilst fruits dropped due to insect attack could still contain viable seeds, the probability that they will germinate and mature is low. Birds often reject insect infested hawthorn fruits making dispersal unlikely (Manzur & Courtney 1984) and seeds which remain under the canopy of their parent tree may experience increased rates of attack from enemies and higher intraspecific competition if they were to successfully germinate (Howe 1989; Murphy *et al.* 2017).

Conclusions

In this study we aimed to understand the spatial density dependence of mutualistic and antagonistic interactions associated with tree reproduction in a temperate woodland. Despite reproductive success being a function of these opposing processes they are rarely studied in parallel. While it was not possible to follow the same cohorts of flowers and fruits through to maturation in this study, our results point towards a pattern of net negative conspecific density dependence in the pre-dispersal reproductive success of hawthorn trees, with individuals in areas with few reproductive conspecifics at an advantage. Although it would be premature to hypothesise on the broader implications of the patterns documented in our study, they align with predictions from the Janzen-Connell hypothesis whereby specialist plant enemies promote plant species coexistence through conspecific density dependence (Janzen 1970; Connell 1971). While the joint outcome of positive and negative density-dependent processes is what will ultimately influence species' distributions in space, understanding how different components (e.g. enhanced pollination versus higher pressure from enemies under high local densities) shape patterns of recruitment will give us a better understanding of diversity maintenance in plant communities and the likely implications of potential perturbations in these interactions.

Chapter 6

General discussion

The pre-dispersal stages of seed production and development are perhaps the most hazardous periods in the life cycle of a plant, as in many species only a very small proportion of ovules eventually mature into viable seeds (Fenner & Thompson 2005). Interactions with insects — as pollinators, herbivores and predators — can play an important role in determining the fate of an ovule. These interactions can vary with the density of flowers, fruits and seeds, potentially causing spatial patterns in the number of mature seeds available for dispersal from the mother plant (Crawley 2000; Dauber *et al.* 2010). If patterns of seed production and pre-dispersal seed survival are conspecifically density-dependent, they could have important implications for plant community dynamics and species coexistence (Gillett 1962; Janzen 1970). Yet, the conspecific density dependence of pre-dispersal seed production and seed survival remains critically understudied in comparison to post-dispersal processes (Gripenberg 2018).

The main aim of this thesis was to explore patterns of density dependence in seed production and pre-dispersal seed development to further our understanding of the potential role plant-insect interactions play in plant community dynamics. The majority of the thesis focuses on trees in tropical forests — a habitat in which host-specific plant enemies have been hypothesised to play a particularly important role in promoting the high local diversity of tree species (Janzen 1970; Connell 1971). In Chapter 2 (Jackson *et al.* 2022), I analysed a unique long-term data set of seed rain to investigate the poorly studied phenomenon of premature fruit drop in a community of tropical forest trees. The proportion of fruits dropped prematurely was a significant cause of seed mortality and varied substantially between species. Species known to be attacked by pre-dispersal insect seed predators and species which were locally abundant in the community had higher rates of premature fruit drop. In Chapter 3, I utilised the same data set to investigate spatial variation in premature fruit drop. In line with predictions, my analyses revealed clear positive conspecific density dependence in premature fruit drop, but this positive relationship levelled off at high conspecific densities. Through field based studies targeting single species in a tropical (*Jacaranda copaia*, Chapter 4) and a temperate (*Crataegus monogyna*, Chapter 5) tree, I then explored conspecific density dependence in the parallel processes of fruit set and fruit drop. In both systems, I found conspecific density-dependent patterns of fruit drop but no evidence to suggest that fruit set varied with conspecific density.

In the following sections I synthesise the results of these studies and explore the wider implications of my findings before highlighting some priorities for further research.

6.1 Discussion of main findings

6.1.1 Premature fruit drop is widespread and might be caused by enemies

Premature fruit drop is a phenomenon reported in many plant species which has the potential to cause significant mortality of developing seeds (reviewed in Stephenson 1981). While fruit abscission can be triggered through several means, including resource limitation (Bawa & Webb 1984; Goubitz *et al.* 2002), genetic or developmental abnormalities in the fruit (Kraus 1915; Bradbury 1929; Forino *et al.* 1987) and damage caused by abiotic factors (Rodrigo 2000; Rodrigo *et al.* 2006; Tagliasacchi *et al.* 2006), abscission triggered by enemy attack is of particular interest to the study of mechanisms promoting plant species coexistence (e.g. Boucher & Sork 1979; Planes *et al.* 2014; Akinsanmi *et al.* 2016). Premature fruit drop has rarely been studied in the context of tropical forest plants (but see Bawa & Webb 1984; Jones & Comita 2010; Aoyagi *et al.* 2023), and never before in the context of entire woody plant communities.

Results from Chapter 2 demonstrated that premature fruit drop is a widespread phenomenon in the forest of Barro Colorado Island and that the rates of associated seed mortality can be very high, with an estimated average of 40% across species. While the specific causes of the documented premature fruit drop remain unknown, the observed link between species-specific fruit drop rates and previously documented patterns of attack by pre-dispersal seed predators suggests that insects likely contribute to at least some of the premature fruit drop. Further studies (e.g. experimental exclusion of pre-dispersal seed predators) would be needed to fully establish whether the phenomenon of enemy-triggered premature fruit drop observed in *Jacaranda copaia* (Chapter 4) is likely to be more widespread. Given that Chapter 2 has shown rates of premature fruit drop to be nonrandom across the community of tree species and a large source of mortality, premature fruit drop has the potential to alter the relative abundance of species where populations are seed limited (Green *et al.* 2014), meriting further study as a contributor to plant community dynamics.

6.1.2 Premature fruit drop is density-dependent both within and among species

If premature fruit drop is indeed caused by host-specific enemies (Chapters 2 & 4, Jackson *et al.* 2022) and if enemies are more abundant where their food resources are locally abundant (Janzen 1970; Connell 1971), we might expect rates of premature fruit drop to be density-dependent both within and across species. Findings from Chapter 2 suggested that locally common plant species in the community exhibit higher levels of premature fruit drop than rare species. If high rates of premature fruit drop translate to population growth rates being lower for common species than for rare species, this would imply that pre-dispersal seed mortality is a stabilising force for species coexistence (Chesson 2000).

Chapters 3, 4 and 5 provided evidence for spatial density dependence in premature fruit drop within tree species, with the rate of premature fruit drop increasing (Chapters 3 & 5) or decreasing (Chapter 4) with the local density of conspecific trees. Fruit drop was also related to the fecundity (Chapter 4) or size (Chapter 5) of individual trees, with highly fecund trees and large trees dropping a larger proportion of their fruits. These results add to the large body of literature which has demonstrated conspecific density dependence in post-dispersal seed survival and the survival of seedlings, often in tropical forest systems (e.g. Hille Ris Lambers *et al.* 2002; Comita *et al.* 2014).

Implications of the documented conspecific density-dependent patterns of fruit drop on species coexistence are still unknown. Conspecific negative density-dependent patterns of seedling recruitment have been demonstrated to increase plant diversity (Harms *et al.* 2000; Bagchi *et al.* 2014), but whether similar processes operate for pre-dispersal seed survivorship remains open to speculation. Substantial levels of enemy-inflicted seed mortality at the pre-dispersal stage has the potential to suppress the number of seeds dispersed per unit area (Janzen 1970, 1971b; Crawley 2000; Hulme & Benkman 2002). Whilst it might seem logical that a reduced number of dispersed seeds would reduce the number of seedlings recruited to the population, lower densities of dispersed seeds could reduce intraspecific competition (Paine *et al.* 2008) and post-dispersal enemy attack (e.g. Bell *et al.* 2006) theoretically increasing recruitment. While the longer term effects are unknown, it seems likely that patterns of density-dependent survival at the pre-dispersal stage will have a non-negligible effect on plant recruitment and should not be ignored when investigating mechanisms for the maintenance of species coexistence.

6.1.3 Pre-dispersal seed mortality shows conspecific density dependence at multiple scales

Most existing studies of distance and density dependence in the survival of seeds and seedlings have been conducted at small spatial scales of a few metres (e.g. Harms *et al.* 2000; Comita *et al.* 2010; Metz *et al.* 2010; Bagchi *et al.* 2014). This is problematic, because species coexistence plays out at a landscape scale ($>\text{km}^2$), relevant to understanding forest-level patterns of diversity. Since ecological processes have often been shown to be scale-dependent (Wiens 1989; Levin 1992; Chave 2013), patterns and processes observed at one spatial scale should not be uncritically assumed to hold at other spatial scales. In this thesis, effects of density on pre-dispersal seed mortality were evident across scales, from the fruits of an individual tree (Chapters 4 & 5) to the densities of conspecific trees across landscapes measuring 0.5 km^2 (Chapter 3), 4.2 km^2 (Chapter 5) and 15.6 km^2 (Chapter 4).

I found that density dependence in pre-dispersal seed mortality was not uniform across spatial scales, becoming weaker or even changing direction across areas involving a larger range of densities (Chapters 3 & 4). These findings highlight that density-dependent patterns of survival on the scale of a few metres need not translate into density-dependent survival on the scale of a larger population. The exact reasons behind scale-dependent patterns in seed mortality remain unknown, but may be linked to processes driving the behaviours of individual enemies or factors structuring the enemy populations as a whole. Little is known about the typical foraging patterns of enemies associated with seeds of trees in natural forest systems. It seems likely that over small spatial scales enemies might actively be attracted to areas of high resource densities, whereas at larger spatial scales populations of plant enemies may instead be governed by other processes (Schupp 1992; Hanski 1998).

6.1.4 Density dependence of antagonistic and mutualistic plant-insect interactions can differ

Whilst the reproductive success of plants is determined by both antagonistic and mutualistic density-dependent interactions with insects (Grass *et al.* 2018), they are rarely studied in parallel (but see Maycock *et al.* 2005; Jones & Comita 2010; Ballarin *et al.* 2022; Aoyagi *et al.* 2023). The findings of this thesis consistently demonstrate support for conspecific density dependence in premature fruit drop (Chapters 2, 3, 4 & 5) which is, to some degree, likely caused by antagonistic interactions with insects (Chapters 2 & 4). However, in the two populations in which we assessed mutualistic plant-insect interactions (measured as successful fruit set in the study species, which are both insect-pollinated), we failed to find any evidence for density-dependent effects (Chapters 4 & 5). The reasons behind the lack of density dependence in fruit set can only be speculated on. Since populations of both *Jacaranda copaia* and *Crataegus monogyna* produce large, synchronous floral displays (Croat 1978; Fichtner & Wissemann 2021), one possibility is that pollinators may be satiated at the large spatial scales under study ($>\text{km}^2$). Additionally, pollinators tend to be less specialised than pre-dispersal seed predators, perhaps indicating that conspecific density dependence is not as common in plant-pollinator interactions. Although in this thesis density dependence in mutualistic plant-insect interactions was not detected, it seems possible that mutualistic and antagonistic interactions might be acting across different scales of resource density, especially given that flower abundance can be more than double the abundance of immature fruits produced by the same tree (Chapters 4 & 5). As mutualistic and antagonistic interactions jointly determine reproductive success it is important to consider them concurrently when thinking about how patterns of density dependence might translate to plant recruitment.

6.2 Future research priorities

In the space of a PhD project it is not possible to generate a complete understanding of the role of pre-dispersal plant-insect interactions in plant community dynamics and there are many questions remaining which would benefit from further study. One of these concerns a critical assessment of the population-level consequences of premature fruit drop on plant recruitment. As demonstrated in this thesis, and has been reported elsewhere (Stephenson 1981), the proportion of fruits dropped prematurely can often be high. Yet this does not necessarily translate into reduced population growth rates. A reduction in the number of dispersed mature seeds might only influence population growth rates where recruitment is seed-limited (Turnbull *et al.* 2000), and this is likely to be context-dependent, differing among sites and species (Crawley 2000). A growing number of studies suggest a potential role of pre-dispersal seed predation on plant population dynamics (Kolb *et al.* 2007) and while seed limitation has been demonstrated for several species on Barro Colorado Island (Svenning & Wright 2005), experiments in which levels of seed addition are informed by known levels of insect-triggered premature fruit drop could be informative for assessing the longer-term consequences of pre-dispersal seed mortality in plant populations.

In this thesis I have frequently noted how patterns of density dependence in seed production and pre-dispersal seed survival can be dependent on spatial scale. A key component to understanding the scales at which the effects of insects on plant recruitment might be apparent rests on understanding the movements and foraging behaviours of plant-associated insects in response to the spatial distribution and densities of resources (Lewis & Gripenberg 2008). Assessing the dispersal distances and movements of insects associated with seeds in the canopy presents a challenge as, for trees, these structures are difficult to observe and manipulate. This makes it logistically challenging to adopt methods successfully used to study dispersal distances of post-dispersal seed predators using sentinel seeds (e.g. Wright 1983). As an alternative, recent advances in monitoring insect movement through the use of radiotelemetry (Růžičková & Elek 2023) or fluorophore tags (Hagler *et al.* 2021) could potentially be leveraged to assess the distances predators travel from an infested host tree. Additionally, further exploration of density dependence in seed production and seed survival across different spatial scales, as touched upon in this thesis, will be of value in identifying the scales at which enemies such as insect seed predators might contribute to plant species coexistence. Remote sensing techniques used to identify conspicuous canopy trees (e.g. Garzon-Lopez *et al.* 2013; Kellner & Hubbell 2017) could be extended to spatial scales even larger than those assessed in this thesis.

Finally, I would recommend that researchers take a more comprehensive approach when investigating the role of density-dependent plant-insect interactions in driving plant population and community dynamics in tropical forests and more widely. The majority of studies focus on patterns of mortality at the post-dispersal seed to seedling stage and the action of specific groups of plant enemies (Gripenberg 2018). In this thesis I have focused on interactions occurring at the pre-dispersal stage. However, the interplay between these two stages is rarely studied (but see Crawley & Long 1995; Sunyer *et al.* 2015; Aoyagi *et al.* 2023) and could be central to determining the limitation or promotion of plant recruitment (Kolb *et al.* 2007). Exploring patterns of density dependence across multiple life stages of a tree (from pollination to adult recruitment) has the potential to provide important insights into the relative importance of processes operating at each stage and the ways in which they are interconnected.

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Appendix A

Supporting information for Chapter 2

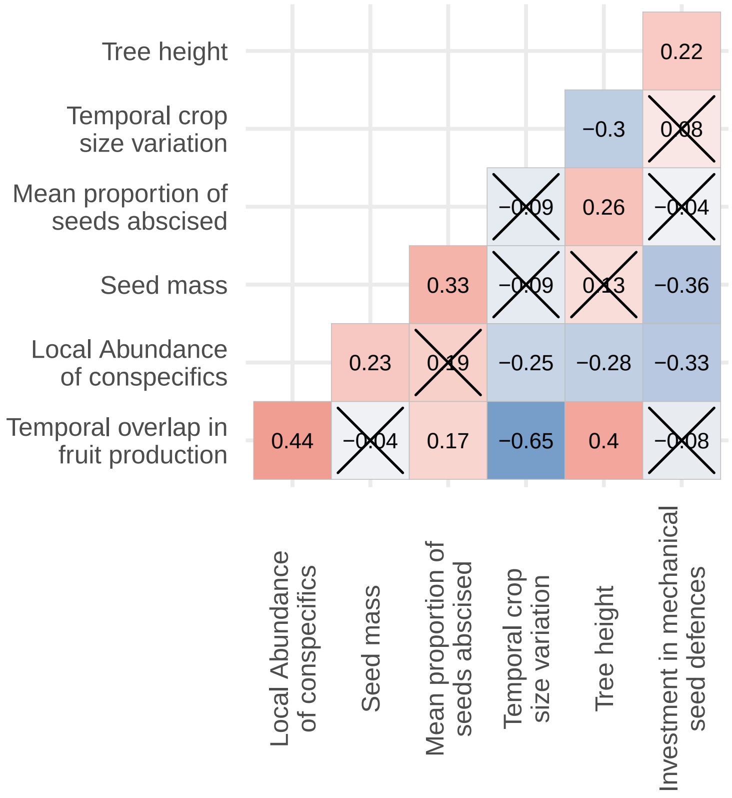


Figure A.1: Pairwise correlations between plant population attributes. Numbers and colours show Spearman's rank correlation coefficient (red = positive, blue = negative), tiles which are crossed indicate correlations for which p <0.05.

Table A.1: Results from seven generalised linear mixed effects models. Each model assesses the relationship between premature seed abscission rates and a single plant population attribute, where year and trap are random effects. Shown are the coefficient estimates and their 95% confidence intervals for the fixed effects. The estimates correspond to the number of units of change in seed abscission rates for one unit change in the plant population attribute. For each plant population attribute, data were only available for a subset of plant species and so sample size differs between models where n = the number of unique species × year combinations.

Plant population attribute	n	**Estimate**	± **CI [95%]**	z	p
Investment in mechanical seed defences	2660	-0.26	(-0.58, 0.06)	-1.61	0.11
Local abundance of conspecifics	2039	0.42	(0.07, 0.77)	2.35	0.02
Presence of insect seed predator	2726	0.84	(0.12, 1.55)	2.22	0.02
Seed mass	2657	0.62	(0.33, 0.92)	4.10	<0.01
Temporal crop size variation	2609	-0.29	(-0.55, -0.02)	-2.11	0.03
Temporal overlap in fruit production by other species	2704	0.28	(0.04, 0.52)	2.33	0.02
Tree height	2036	0.39	(0.00, 0.78)	1.94	0.05

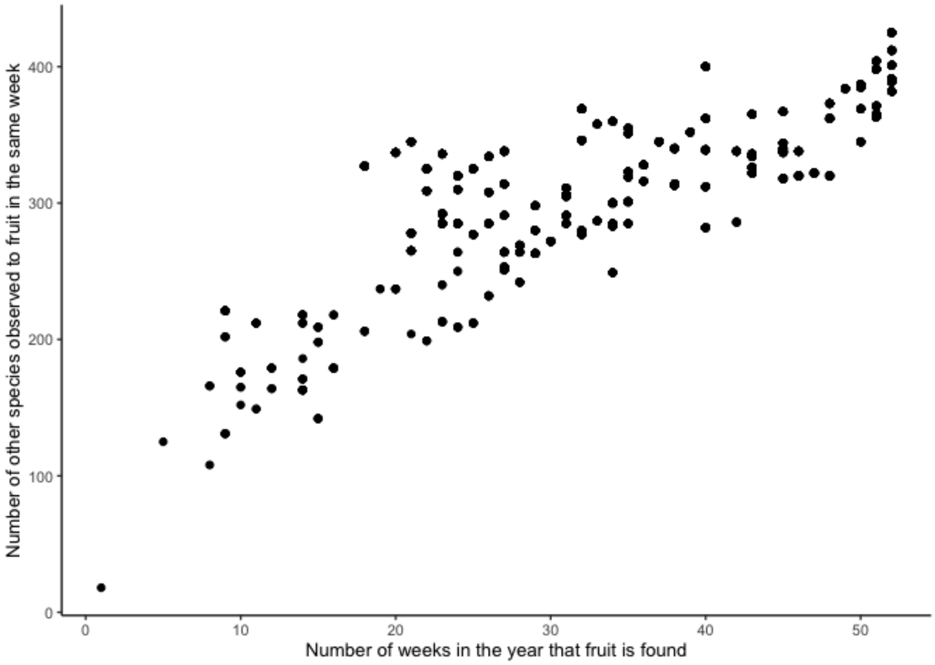


Figure A.2: The relationship between temporal overlap in fruit production and fruiting season duration. Each data point corresponds to a specific plant species.

Appendix B

Supporting information for Chapter 3

Table B.1: A list of the 64 species included in the study. Abundance is the median count of reproductive-sized individuals in the 50-ha plot across 30 years of ForestGEO survey data.

Family	**Genus**	**Species**	**Abundance**
Achariaceae	*Lindackeria*	*laurina*	27
Annonaceae	*Xylopia*	*macrantha*	64
Apocynaceae	*Aspidosperma*	*spruceanum*	13.5
Apocynaceae	*Tabernaemontana*	*arborea*	107.5
Arecaceae	*Astrocaryum*	*standleyanum*	174.5
Arecaceae	*Attalea*	*butyracea*	32.5
Arecaceae	*Oenocarpus*	*mapora*	1476
Arecaceae	*Socratea*	*exorrhiza*	311.5
Bignoniaceae	*Jacaranda*	*copaia*	87
Bignoniaceae	*Tabebuia*	*rosea*	15.5
Boraginaceae	*Cordia*	*alliodora*	19.5
Capparaceae	*Morisonia*	*frondosa*	371
Clusiaceae	*Chrysochlamys*	*eclipes*	67.5
Combretaceae	*Terminalia*	*oblonga*	23.5
Elaeocarpaceae	*Sloanea*	*terniflora*	7
Euphorbiaceae	*Hura*	*crepitans*	23.5
Euphorbiaceae	*Sapium*	*glandulosum*	7.5

Continued on next page

Table B.1: A list of the 64 species included in the study. Abundance is the median count of reproductive-sized individuals in the 50-ha plot across 30 years of ForestGEO survey data. (Continued)

Fabaceae	*Dipteryx*	*oleifera*	19
Fabaceae	*Erythrina*	*costaricensis*	32.5
Fabaceae	*Inga*	*marginata*	43
Fabaceae	*Inga*	*acuminata*	25
Fabaceae	*Inga*	*ruiziana*	4.5
Fabaceae	*Inga*	*sapindoides*	32
Fabaceae	*Inga*	*thibaudiana*	22.5
Fabaceae	*Lonchocarpus*	*heptaphyllus*	31.5
Fabaceae	*Platymiscium*	*pinnatum*	26
Fabaceae	*Platypodium*	*elegans*	12.5
Fabaceae	*Pterocarpus*	*rohrii*	4
Fabaceae	*Tachigali*	*versicolor*	10.5
Lauraceae	*Aiouea*	*montana*	8
Lauraceae	*Nectandra*	*cissiflora*	12.5
Lythraceae	*Lafoensia*	*punicifolia*	3
Malvaceae	*Cavanillesia*	*platanifolia*	11
Malvaceae	*Ochroma*	*pyramidale*	3.5
Malvaceae	*Pachira*	*sessilis*	5
Malvaceae	*Sterculia*	*apetala*	7
Meliaceae	*Cedrela*	*odorata*	2.5
Rubiaceae	*Alseis*	*blackiana*	90
Rubiaceae	*Macrocnemum*	*roseum*	10
Salicaceae	*Casearia*	*guianensis*	9.5
Salicaceae	*Laetia*	*procera*	5.5
Salicaceae	*Laetia*	*thamnia*	38.5
Sapindaceae	*Cupania*	*rufescens*	3.5
Sapindaceae	*Cupania*	*seemannii*	63.5
Violaceae	*Pombalia*	*prunifolia*	915.5
Vochysiaceae	*Vochysia*	*ferruginea*	4

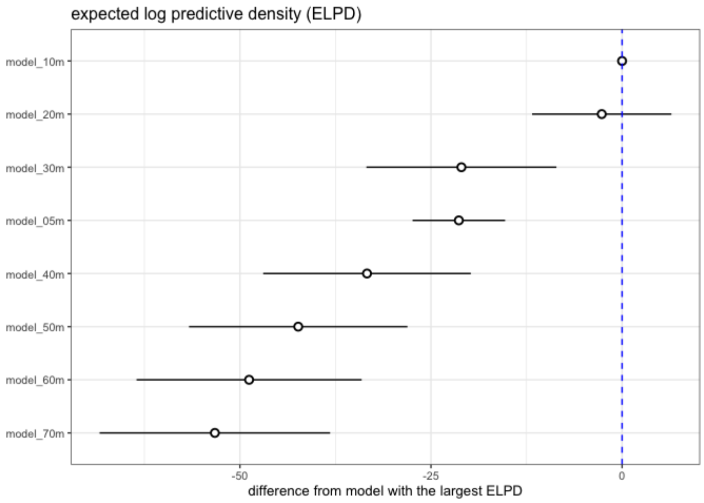


Figure B.1: Comparison of models with differing values for the average dispersal distance of a hypothetical seed predator. Connectivity was calculated including reproductive-sized conspecifics only and with varying values of α ($\alpha = 1$ / average dispersal distance, see Section 3.3). Models were compared using approximate Leave-one-out cross-validation (LOO-CV). The Expected Log Predictive Density (ELPD) is higher when new observations are well-accounted for by the posterior predictive distribution. Points indicate the difference in ELPD from the model with the largest ELPD (model_10m) and lines depict the standard error.

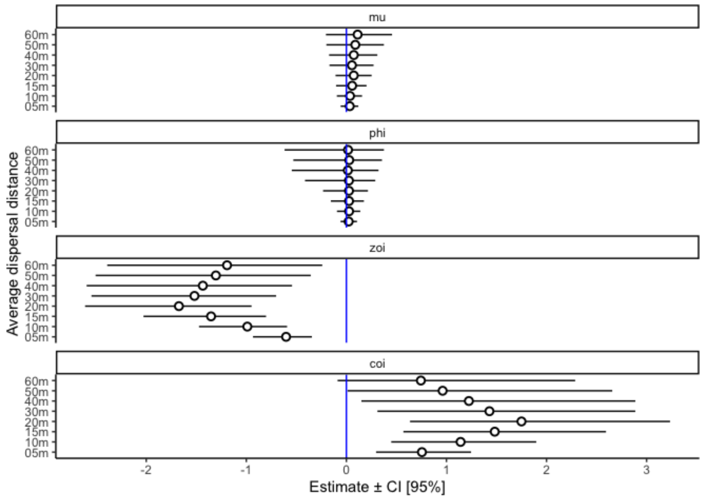
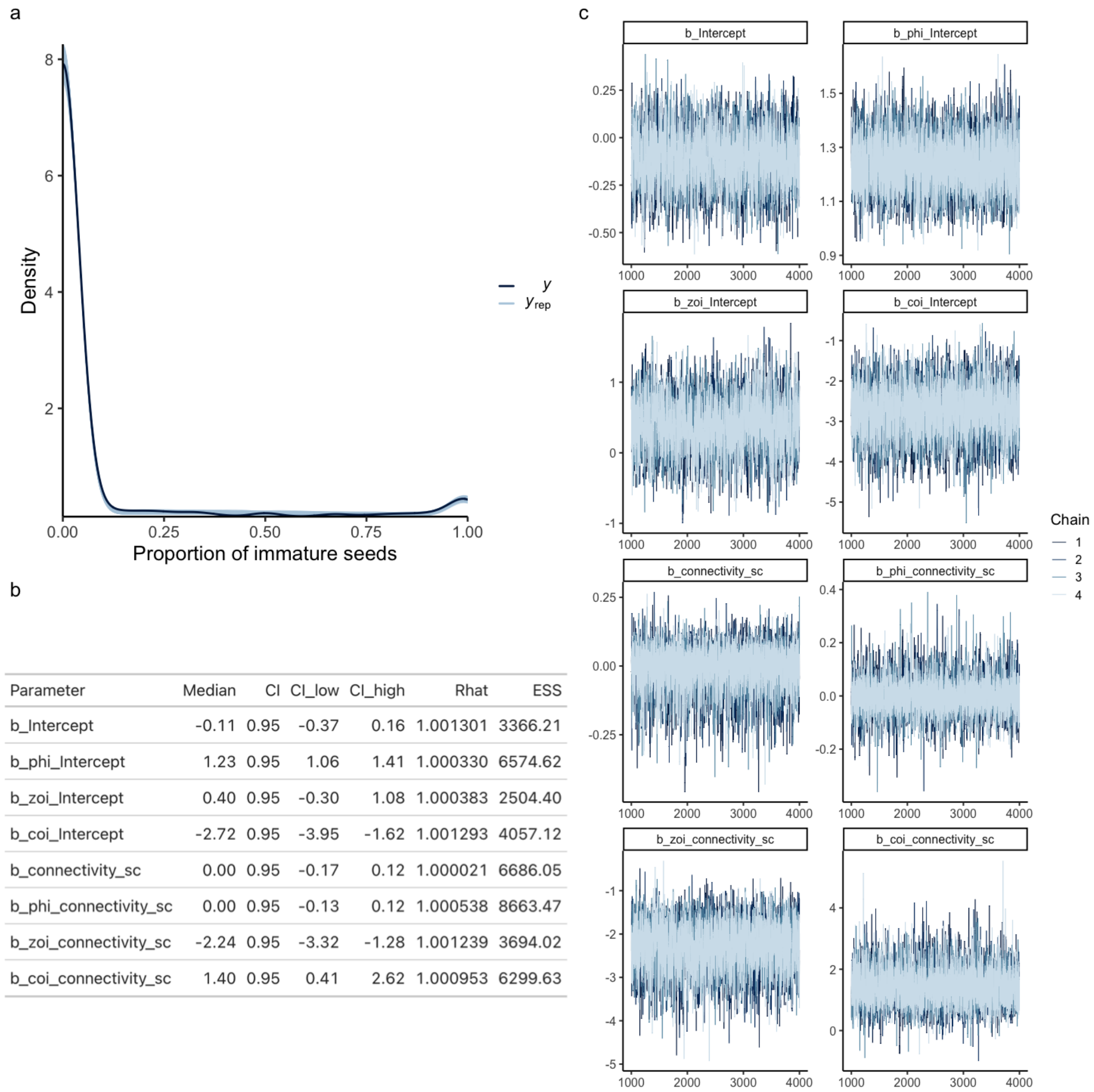
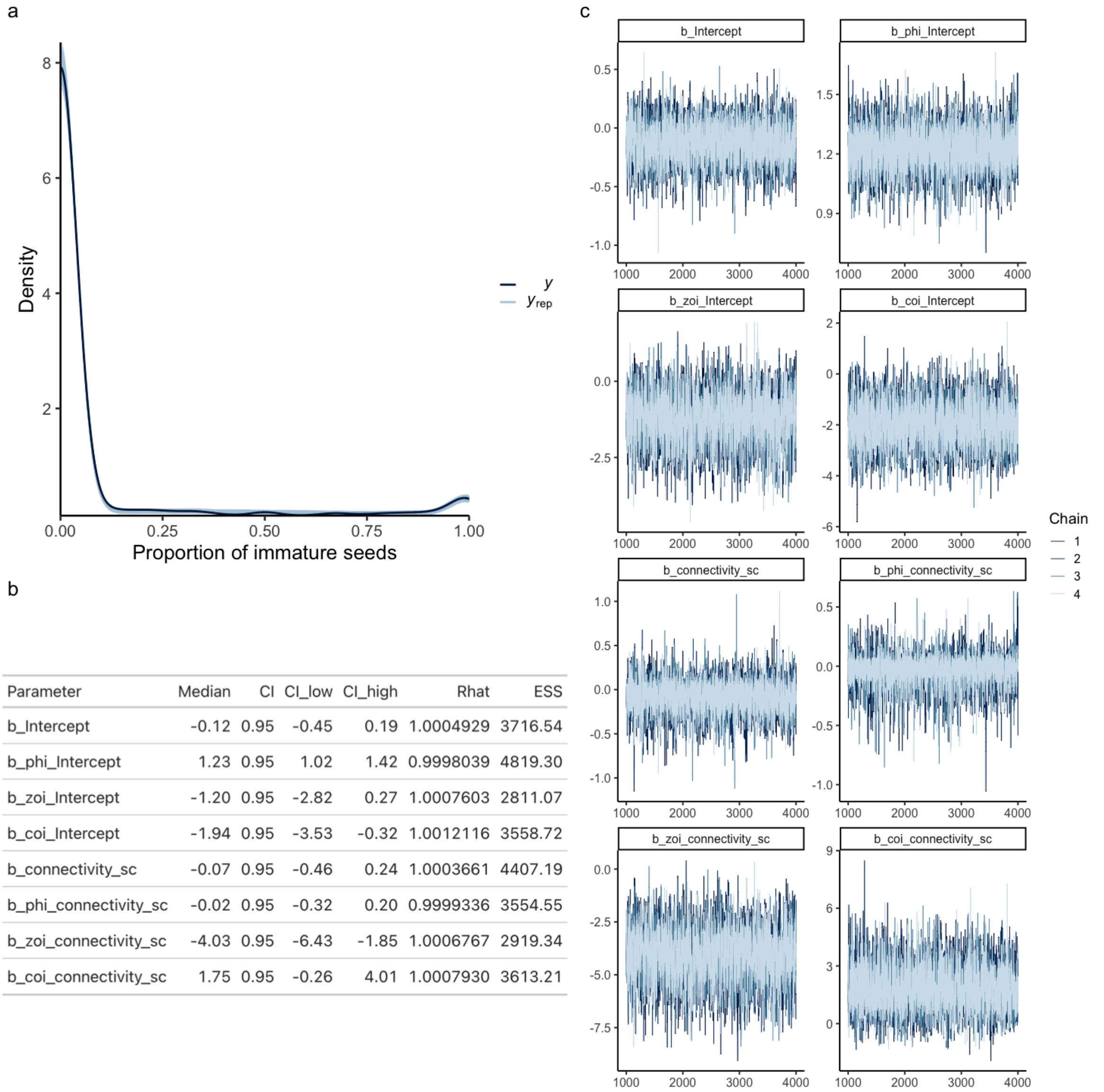


Figure B.2: Posterior parameters estimated by models with differing values for the average dispersal distance of a hypothetical seed predator. Connectivity was calculated including reproductive conspecifics only and with varying values of α ($\alpha = 1$ / average dispersal distance, see Section 3.3). Points indicate posterior medians and lines are 95% credible intervals. 'mu' is the mean of the beta distribution, 'phi' is the beta distribution's precision, 'zoi' refers to the probability of being a zero or a one and 'coi' refers to the conditional probability of being a one (given an observation is a zero or a one).



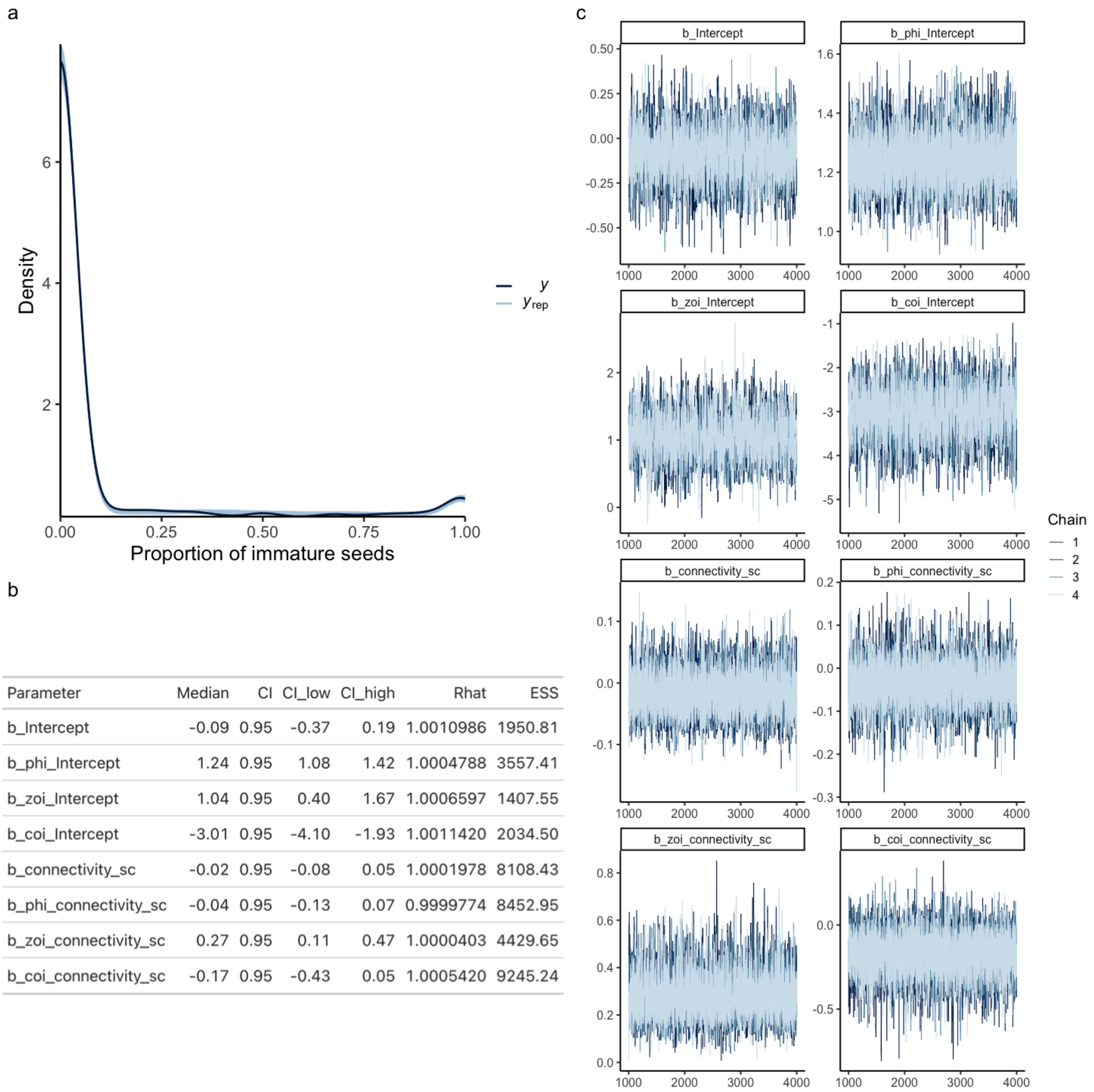
Parameter	Median	CI	CI_low	CI_high	Rhat	ESS
b_Intercept	-0.11	0.95	-0.37	0.16	1.001301	3366.21
b_phi_Intercept	1.23	0.95	1.06	1.41	1.000330	6574.62
b_zoi_Intercept	0.40	0.95	-0.30	1.08	1.000383	2504.40
b_coi_Intercept	-2.72	0.95	-3.95	-1.62	1.001293	4057.12
b_connectivity_sc	0.00	0.95	-0.17	0.12	1.000021	6686.05
b_phi_connectivity_sc	0.00	0.95	-0.13	0.12	1.000538	8663.47
b_zoi_connectivity_sc	-2.24	0.95	-3.32	-1.28	1.001239	3694.02
b_coi_connectivity_sc	1.40	0.95	0.41	2.62	1.000953	6299.63

Figure B.3: Output for the model where the predictors included connectivity to **reproductive-sized conspecifics only**. Panel (a) is a posterior predictive check where the observed data is in dark blue (y) and simulated samples from the posterior distribution are in light blue (y_{rep}, 500 draws). Panel (b) is a table of model output which includes: posterior medians, 95% credible intervals, $\hat{R}$ and Effective Sample Size (ESS) for population-level parameters in the model. Parameter names starting with 'b' indicate population-level parameters and 'sc' indicates variables which were centred with a mean of zero. 'zoi' refers to the probability of being a zero or a one, 'coi' refers to the conditional probability of being a one (given an observation is a zero or a one), and 'phi' is the precision parameter of zero-one inflated beta distribution. Panel (c) shows trace plots of MCMC draws for population level parameters.



Parameter	Median	CI	CI_low	CI_high	Rhat	ESS
b_Intercept	-0.12	0.95	-0.45	0.19	1.0004929	3716.54
b_phi_Intercept	1.23	0.95	1.02	1.42	0.9998039	4819.30
b_zoi_Intercept	-1.20	0.95	-2.82	0.27	1.0007603	2811.07
b_coi_Intercept	-1.94	0.95	-3.53	-0.32	1.0012116	3558.72
b_connectivity_sc	-0.07	0.95	-0.46	0.24	1.0003661	4407.19
b_phi_connectivity_sc	-0.02	0.95	-0.32	0.20	0.9999336	3554.55
b_zoi_connectivity_sc	-4.03	0.95	-6.43	-1.85	1.0006767	2919.34
b_coi_connectivity_sc	1.75	0.95	-0.26	4.01	1.0007930	3613.21

Figure B.4: Output for the model where the predictors included connectivity to **all conspecifics**. Panel (a) is a posterior predictive check where the observed data is in dark blue (y) and simulated samples from the posterior distribution are in light blue (y_{rep}, 500 draws). Panel (b) is a table of model output which includes: posterior medians, 95% credible intervals, $\hat{R}$ and Effective Sample Size (ESS) for population-level parameters in the model. Parameter names starting with 'b' indicate population-level parameters and 'sc' indicates variables which were centred with a mean of zero. 'zoi' refers to the probability of being a zero or a one, 'coi' refers to the conditional probability of being a one (given an observation is a zero or a one), and 'phi' is the precision parameter of zero-one inflated beta distribution. Panel (c) shows trace plots of MCMC draws for population level parameters.



Parameter	Median	CI	CI_low	CI_high	Rhat	ESS
b_Intercept	-0.09	0.95	-0.37	0.19	1.0010986	1950.81
b_phi_Intercept	1.24	0.95	1.08	1.42	1.0004788	3557.41
b_zoi_Intercept	1.04	0.95	0.40	1.67	1.0006597	1407.55
b_coi_Intercept	-3.01	0.95	-4.10	-1.93	1.0011420	2034.50
b_connectivity_sc	-0.02	0.95	-0.08	0.05	1.0001978	8108.43
b_phi_connectivity_sc	-0.04	0.95	-0.13	0.07	0.9999774	8452.95
b_zoi_connectivity_sc	0.27	0.95	0.11	0.47	1.0000403	4429.65
b_coi_connectivity_sc	-0.17	0.95	-0.43	0.05	1.0005420	9245.24

Figure B.5: Output for the model where the predictors included connectivity to **reproductive-sized heterospecifics only**. Panel (a) is a posterior predictive check where the observed data is in dark blue (y) and simulated samples from the posterior distribution are in light blue (y_{rep}, 500 draws). Panel (b) is a table of model output which includes: posterior medians, 95% credible intervals, $\hat{R}$ and Effective Sample Size (ESS) for population-level parameters in the model. Parameter names starting with ‘b’ indicate population-level parameters and ‘sc’ indicates variables which were centred with a mean of zero. ‘zoi’ refers to the probability of being a zero or a one, ‘coi’ refers to the conditional probability of being a one (given an observation is a zero or a one), and ‘phi’ is the precision parameter of zero-one inflated beta distribution. Panel (c) shows trace plots of MCMC draws for population level parameters.

Appendix C

Supporting information for Chapter 4

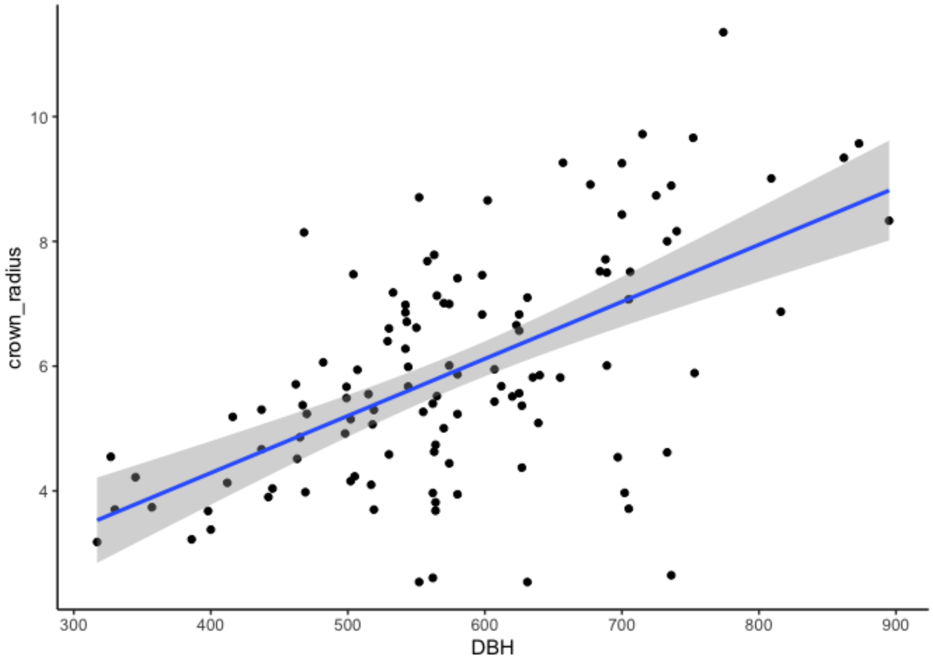


Figure C.1: The relationship between crown radius and DBH for *Jacaranda copaia* on Barro Colorado Island. Data is diameter at breast height (DBH /mm) and crown radius /m of 115 adult *J. copaia* provided by H. C. Muller-Landau. Grey area denotes the 95% confidence interval. (Linear model, slope estimate = 0.009, intercept estimate = 0.630, p = 8.41e-12).

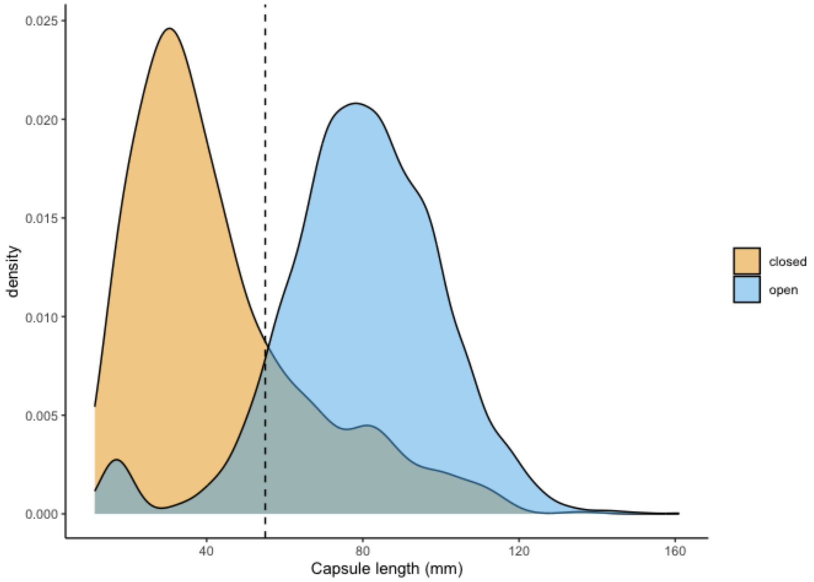


Figure C.2: Distribution of *J. copaia* non-predated capsule lengths. n = 4,598 non-predated capsules sampled across all trees. Capsules which were found open on the forest floor are in blue and capsules which were closed are in orange. There are a small number of capsules that are open but are comparatively small, causing the open capsules to have a bimodal distribution. These are probably immature capsules that opened on the forest floor. We used these data to determine a cut-off point for when capsules were classed as immature (<55mm indicated by dotted line, this is the median value between the two peaks).

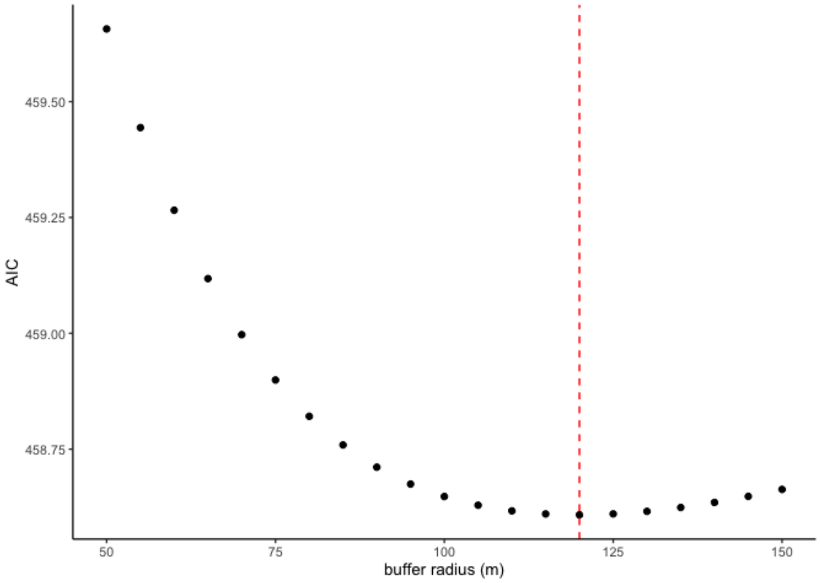


Figure C.3: AIC values for models fit with different buffer radii, r ($r = 1/\alpha$). Models were binomial general linear models fit using the `R` package `lme4`. The number of successes was equal to the number of predated fruits and the number of trials was equal to the total number of fruits. The predictor was connectivity. The dotted red line indicates the buffer radius used in the model with the lowest AIC.

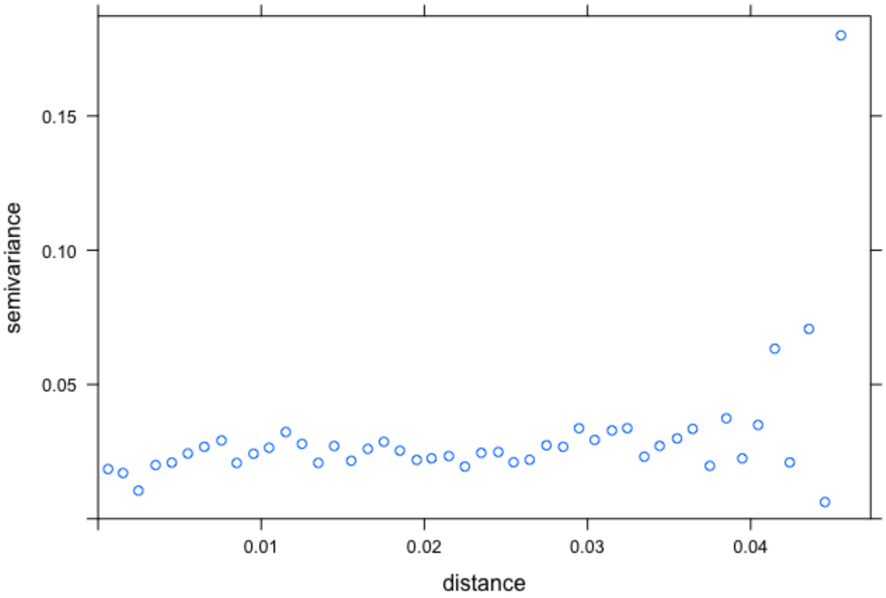
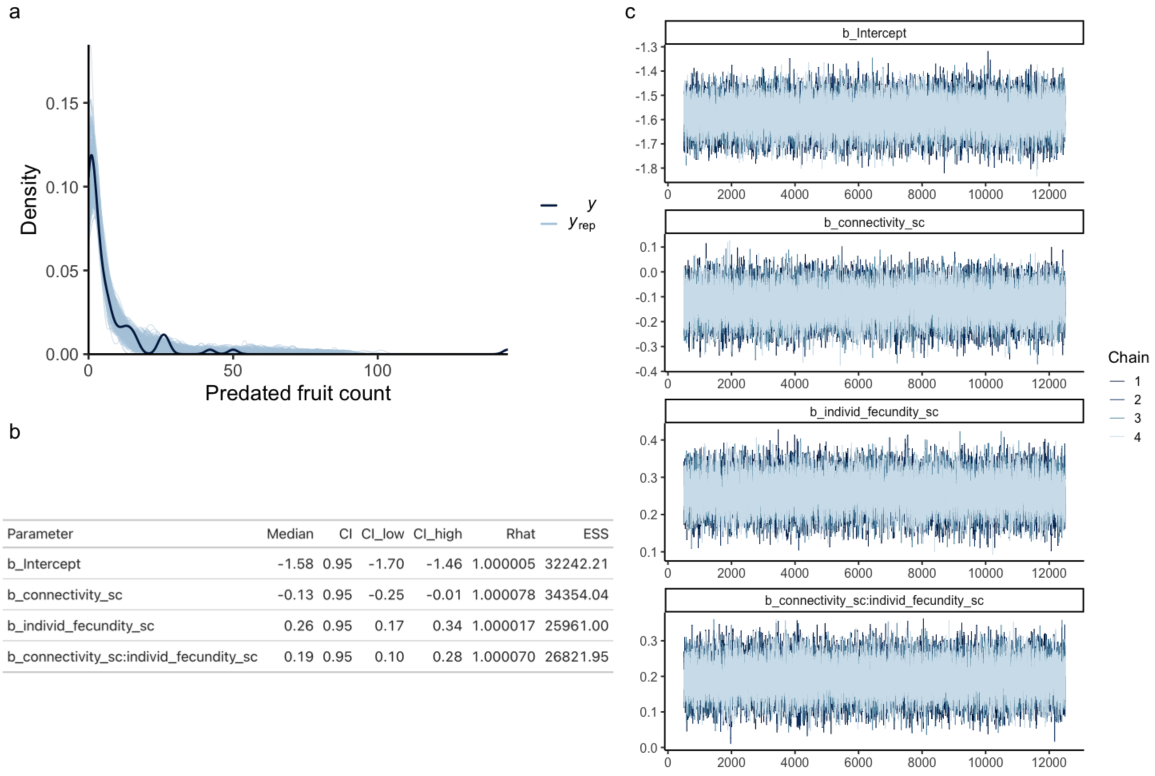
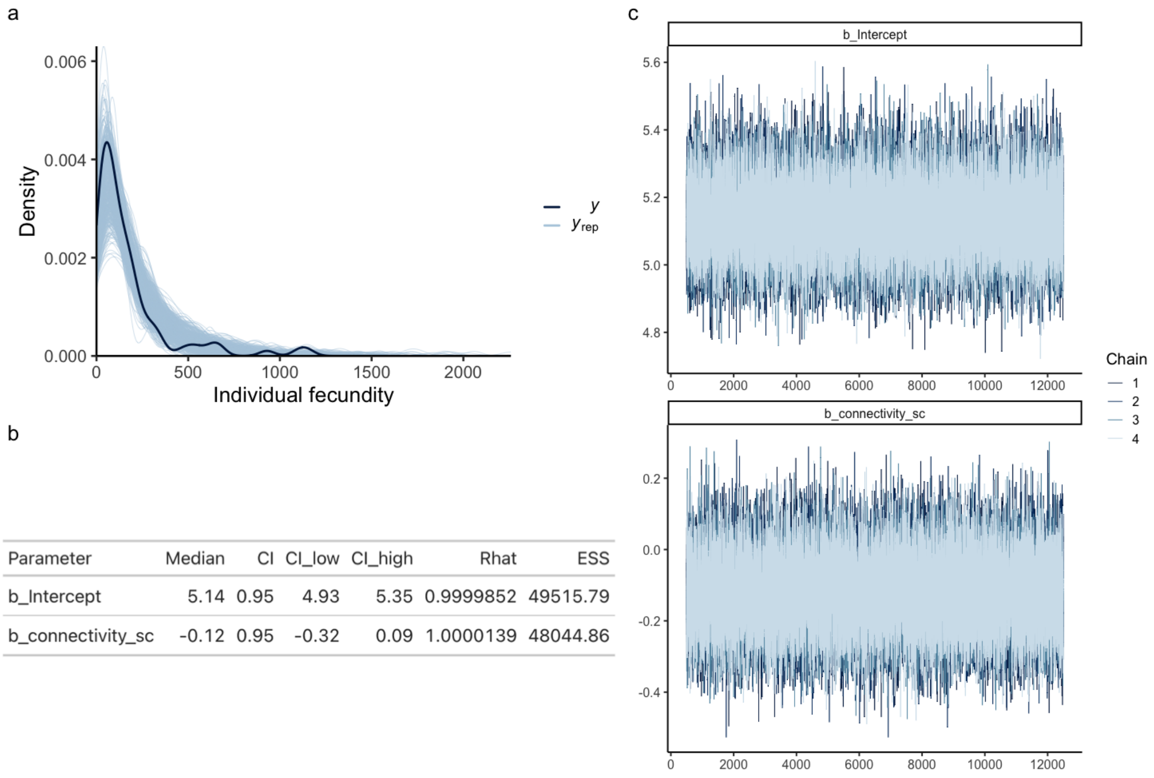


Figure C.4: Variogram of predation rate. The x axis represents the distance between trees (km) and each point represents a pair of observations. The semivariance stays flat indicating that spatial autocorrelation does not occur at the measured distances used in the experiment.



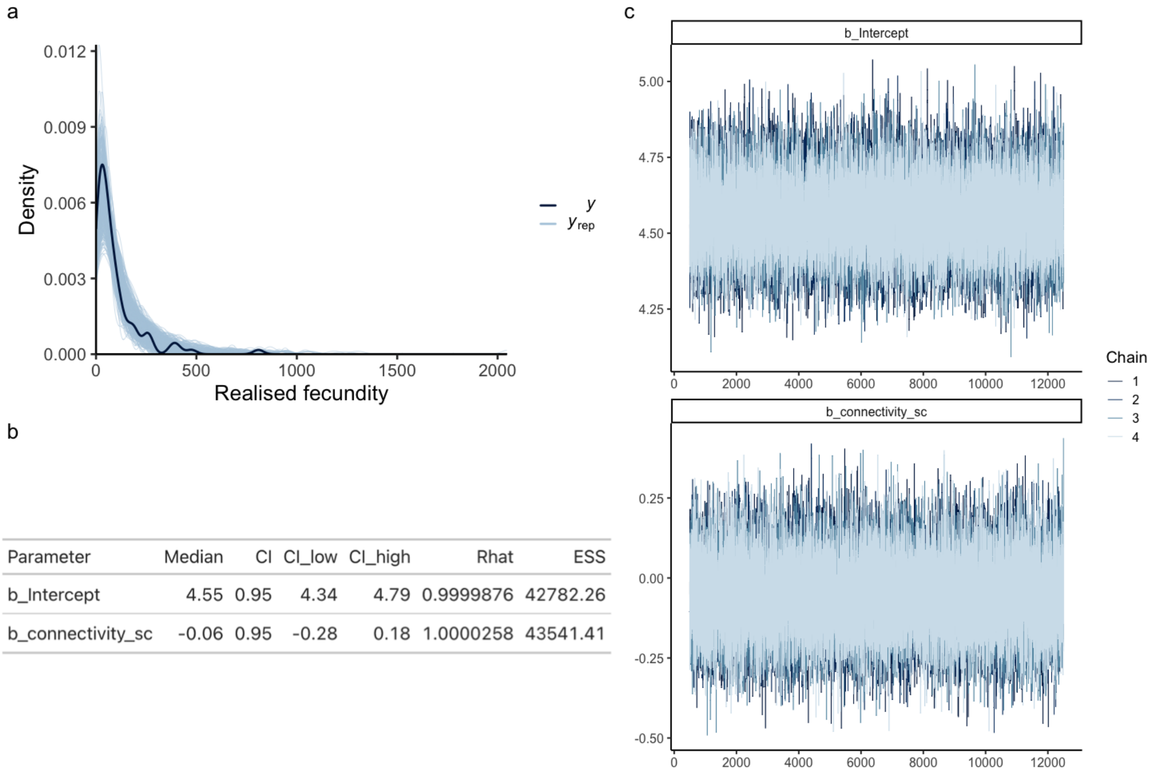
Parameter	Median	CI	CI_low	CI_high	Rhat	ESS
b_Intercept	-1.58	0.95	-1.70	-1.46	1.000005	32242.21
b_connectivity_sc	-0.13	0.95	-0.25	-0.01	1.000078	34354.04
b_individ_fecundity_sc	0.26	0.95	0.17	0.34	1.000017	25961.00
b_connectivity_sc:individ_fecundity_sc	0.19	0.95	0.10	0.28	1.000070	26821.95

Figure C.5: Output for the model predicting predated fruit count. Panel (a) is a posterior predictive check where the observed data is in dark blue (y) and simulated samples from the posterior distribution are in light blue (y_{rep}, 500 draws). Panel (b) is a table of model output which includes: posterior medians, 95% credible intervals, $\hat{R}$ and Effective Sample Size (ESS) for population-level parameters in the model. Names starting with ‘b’ indicate population-level parameters and ‘sc’ indicates variables which were centred with a mean of zero and scaled with variance equal to one standard deviation. Panel (c) shows trace plots of MCMC draws for population level parameters.



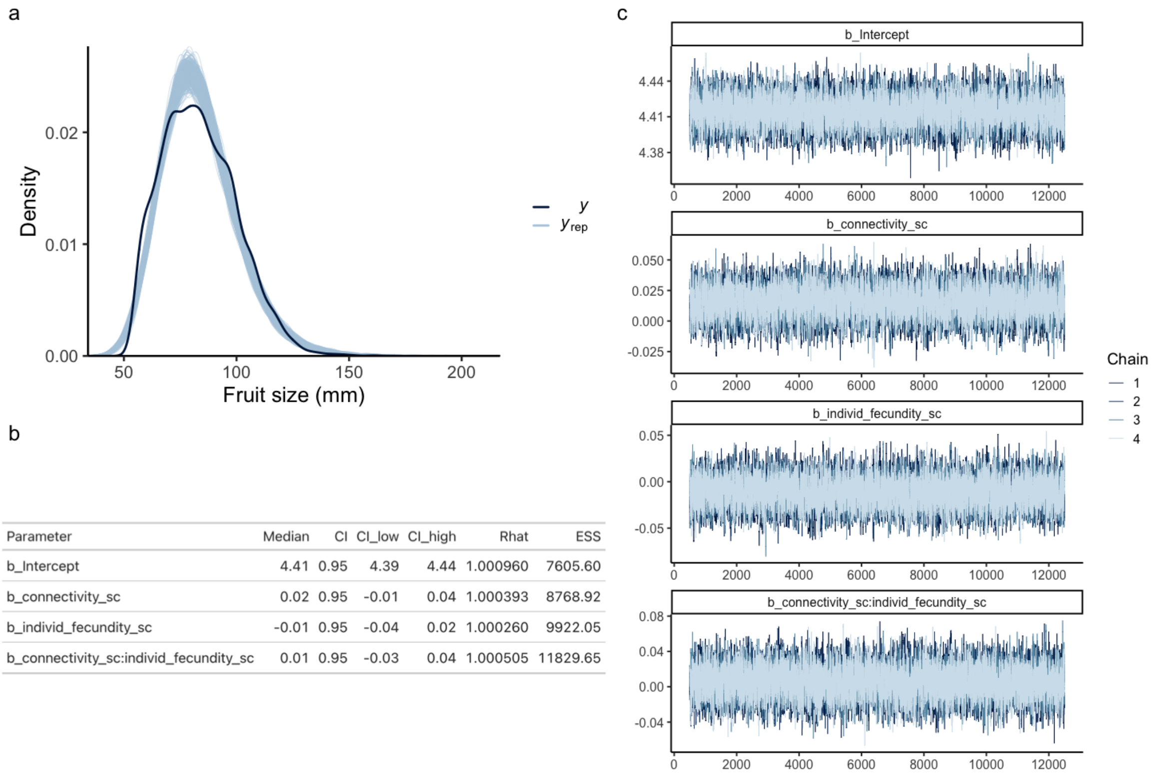
Parameter	Median	CI	CI_low	CI_high	Rhat	ESS
b_Intercept	5.14	0.95	4.93	5.35	0.9999852	49515.79
b_connectivity_sc	-0.12	0.95	-0.32	0.09	1.0000139	48044.86

Figure C.6: Output for the model predicting individual fecundity. Panel (a) is a posterior predictive check where the observed data is in dark blue (y) and simulated samples from the posterior distribution are in light blue (y_{rep}, 500 draws). Panel (b) is a table of model output which includes: posterior medians, 95% credible intervals, $\hat{R}$ and Effective Sample Size (ESS) for population-level parameters in the model. Names starting with ‘b’ indicate population-level parameters and ‘sc’ indicates variables which were centred with a mean of zero and scaled with variance equal to one standard deviation. Panel (c) shows trace plots of MCMC draws for population level parameters.



Parameter	Median	CI	CI_low	CI_high	Rhat	ESS
b_Intercept	4.55	0.95	4.34	4.79	0.9999876	42782.26
b_connectivity_sc	-0.06	0.95	-0.28	0.18	1.0000258	43541.41

Figure C.7: Output for the model predicting realised fecundity. Panel (a) is a posterior predictive check where the observed data is in dark blue (y) and simulated samples from the posterior distribution are in light blue (y_{rep}, 500 draws). Panel (b) is a table of model output which includes: posterior medians, 95% credible intervals, $\hat{R}$ and Effective Sample Size (ESS) for population-level parameters in the model. Names starting with 'b' indicate population-level parameters and 'sc' indicates variables which were centred with a mean of zero and scaled with variance equal to one standard deviation. Panel (c) shows trace plots of MCMC draws for population level parameters.



Parameter	Median	CI	CI_low	CI_high	Rhat	ESS
b_Intercept	4.41	0.95	4.39	4.44	1.000960	7605.60
b_connectivity_sc	0.02	0.95	-0.01	0.04	1.000393	8768.92
b_individ_fecundity_sc	-0.01	0.95	-0.04	0.02	1.000260	9922.05
b_connectivity_sc:individ_fecundity_sc	0.01	0.95	-0.03	0.04	1.000505	11829.65

Figure C.8: Output for the model predicting fruit size. Panel (a) is a posterior predictive check where the observed data is in dark blue (y) and simulated samples from the posterior distribution are in light blue (y_{rep}, 500 draws). Panel (b) is a table of model output which includes: posterior medians, 95% credible intervals, $\hat{R}$ and Effective Sample Size (ESS) for population-level parameters in the model. Names starting with 'b' indicate population-level parameters and 'sc' indicates variables which were centred with a mean of zero and scaled with variance equal to one standard deviation. Panel (c) shows trace plots of MCMC draws for population level parameters.

Appendix D

Supporting information for Chapter 5

dGPS mapping protocol

From May 2022 to September 2022 the locations of all observed *C. monogyna* stems were recorded within a 50 m radius of each of the focal individuals using a differential global positioning system (dGPS, Emlid Reach RS2+). The RS2+ provides three levels of accuracy which vary depending on multiple factors, including the number of satellites available and the sky view around points. We only recorded location points (latitude and longitude) when the dGPS was recording in one of the two highest accuracy modes (FLOAT and FIX), proving submeter and cm level accuracy respectively. Since the dispersal distances of insects associated with *C. monogyna* are unknown and likely to be variable between species, we chose a 50 m radius based on empirical data on the average dispersal distance of a leaf mining moth associated with oak trees (Gripenberg & Roslin 2005).

For each focal tree, we measured the diameter at breast height (DBH = 1.3 m) of all established stems with a DBH greater than 10 mm within the 50 m radius, following Condit (1998). Stems with DBH <10 mm were classified as saplings and had their location recorded, but DBH was not measured. Established (non-sapling) trees were classified as either single stem or multiple stem trees. Where trees had multiple stems the DBH of each stem was recorded. Where single stems divided from a main stem into multiple, secondary stems, the height at which the division occurred on the main stem was recorded and the diameter was measured at that height. The DBH of each secondary stem was also recorded. We also noted whether stems were dead, leaning or horizontal, or if they were broken above or below breast height.

In addition to coordinates and DBH we recorded the reproductive status (whether the individual had flowers or fruits at the time of recording) of each individual.

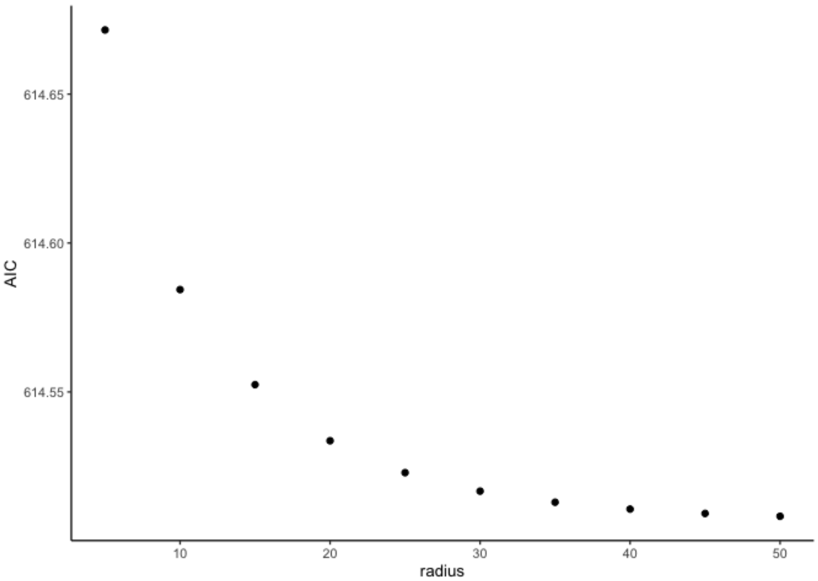


Figure D.1: AIC values for models fit with different buffer radii /m ($r = 1/\alpha$). Models were binomial general linear models fit using the R package `lme4`. The number of successes was equal to the number of dropped fruits and the number of trials was equal to the total number of fruits. The predictor was total connectivity.

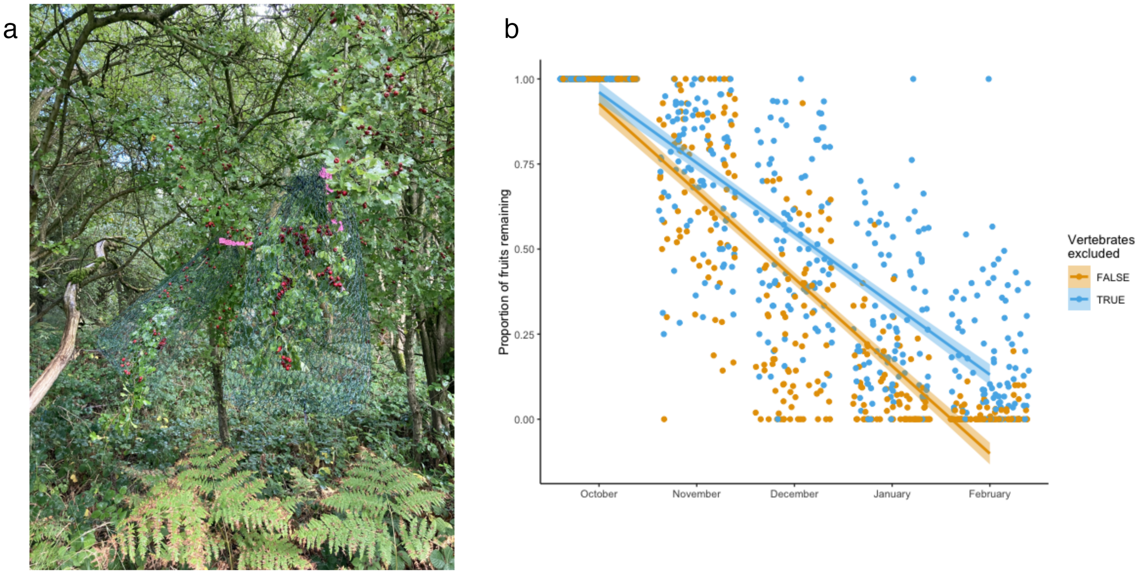


Figure D.2: Image (a) shows branches of hawthorn encased in wire mesh to protect fruits from removal by vertebrates. The figure in (b) demonstrates the relatively higher rate of fruit loss from branches which were not protected with cages. Each point corresponds to a single branch at that time point. This suggests our exclusion cages were effective in protecting fruits from removal by vertebrates and that most of the fruit removal by vertebrates happens from December onwards, in line with temporal patterns documented by Sorensen (1981).

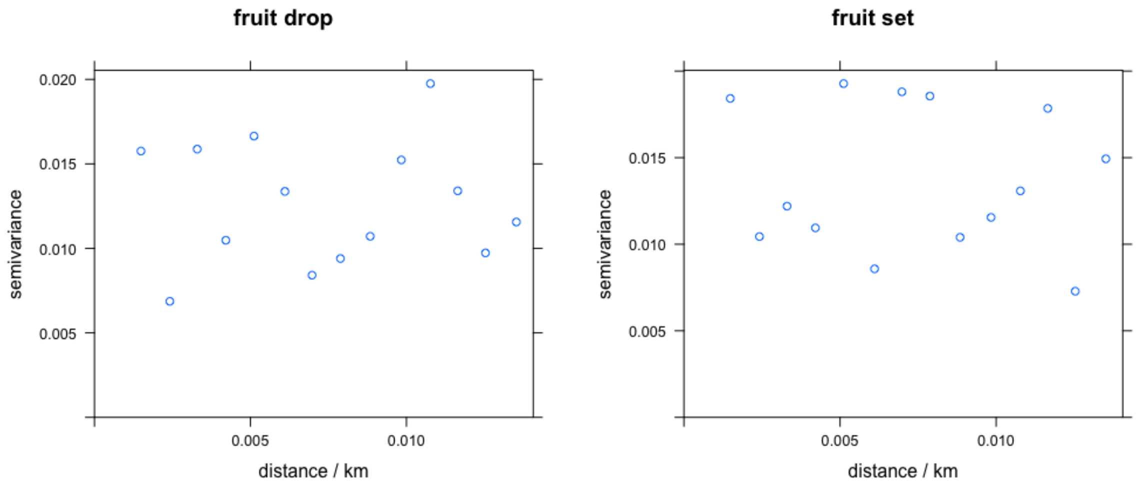


Figure D.3: Variogram for fruit drop and fruit-set. The x axis represents the distance between trees and each point represents a pair of observations.

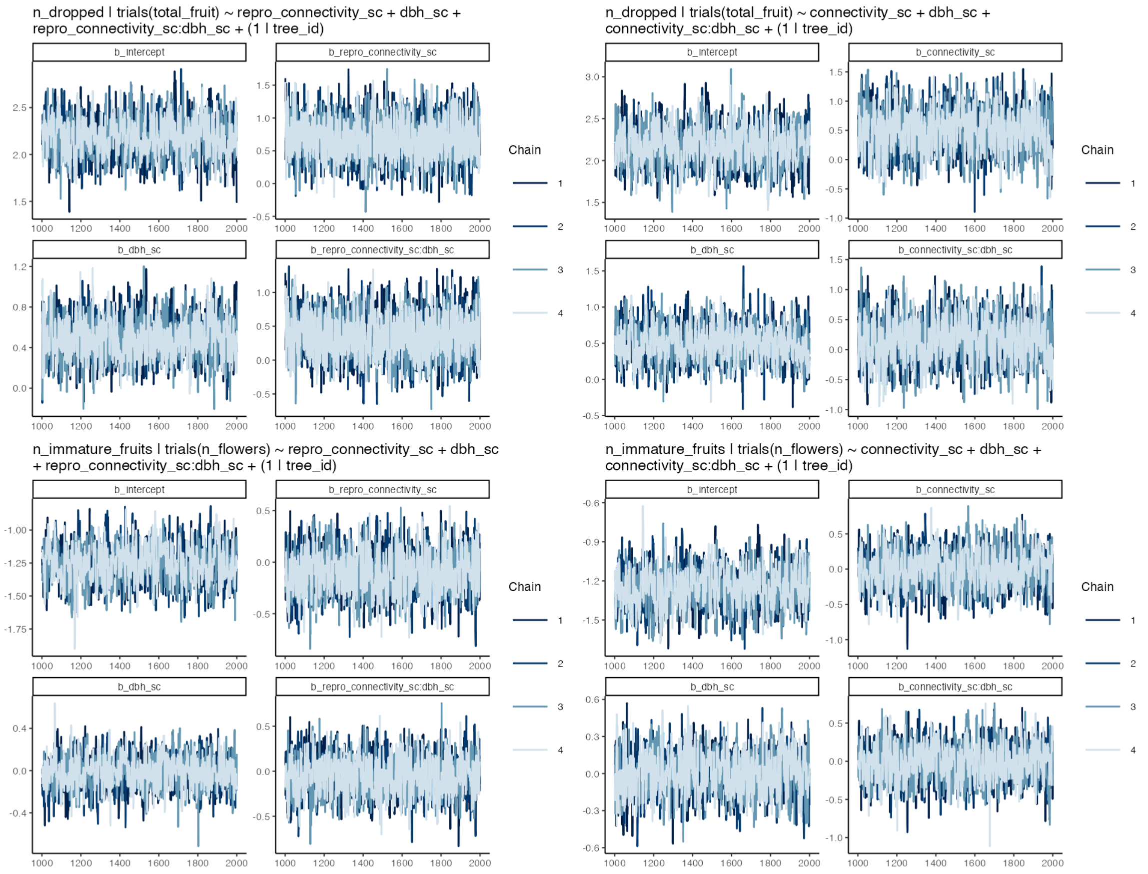
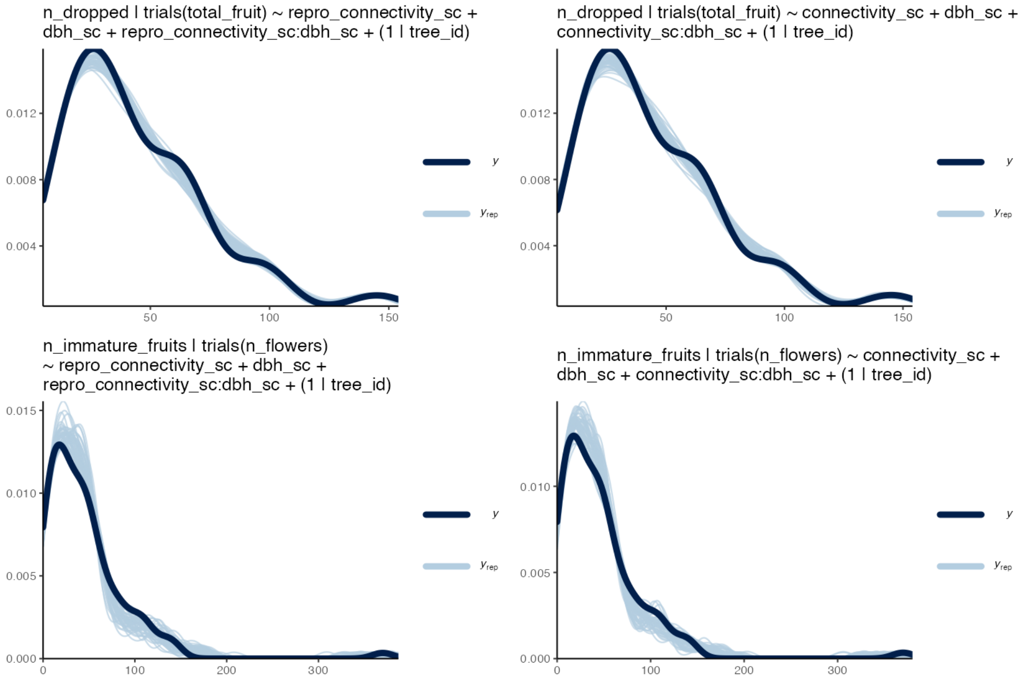


Figure D.4: Trace plots of MCMC draws for population level parameters for each fitted model.

Table D.1: Output from four models, including posterior medians, 95% credible intervals, $\hat{R}$ and Effective Sample Size (ESS) for population-level parameters in each model.

Response	**Parameter**	**median**	**95% CI**	$\hat{R}$	**ESS**
Fruit set	Intercept	-1.25	-1.52, -0.96	1.001	899.52
	Total connectivity	0.002	-0.48, 0.50	1.001	1066.44
	DBH	0.002	-0.32, 0.30	1.000	938.10
	Total connectivity * DBH	-0.02	-0.44, 0.45	1.000	1096.31
Fruit set	Intercept	-1.25	-1.53, -0.99	1.004	864.96
	Reproductive connectivity	-0.10	-0.47, 0.34	1.000	1195.04
	DBH	-0.03	-0.29, 0.29	1.004	852.46
	Reproductive connectivity * DBH	-0.05	-0.44, 0.34	1.001	1583.10
Fruit drop	Intercept	2.15	1.75, 2.61	1.003	752.99
	Total connectivity	0.49	-0.20, 1.17	1.002	1022.92
	DBH	0.50	0.05, 0.95	1.001	1035.38
	Total connectivity * DBH	0.16	-0.48, 0.86	1.002	1065.53
Fruit drop	Intercept	2.19	1.78, 2.54	1.001	828.71
	Reproductive connectivity	0.67	0.09, 1.29	1.001	1370.82
	DBH	0.49	0.13, 0.86	1.005	1035.74
	Reproductive connectivity * DBH	0.35	-0.20, 0.99	1.002	1312.19


n_dropped | trials(total_fruit) ~ repro_connectivity_sc + dbh_sc + repro_connectivity_sc:dbh_sc + (1 | tree_id)

n_dropped | trials(total_fruit) ~ connectivity_sc + dbh_sc + connectivity_sc:dbh_sc + (1 | tree_id)

n_immature_fruits | trials(n_flowers) ~ repro_connectivity_sc + dbh_sc + repro_connectivity_sc:dbh_sc + (1 | tree_id)

n_immature_fruits | trials(n_flowers) ~ connectivity_sc + dbh_sc + connectivity_sc:dbh_sc + (1 | tree_id)

Figure D.5: Posterior predictive checks for each fitted model. The observed data is in dark blue (y) and simulated samples from the posterior distribution are in light blue (y_{rep}, 50 draws).