

# INCREASING REALISM IN MODELS OF BIOTIC INTERACTIONS:

*ecological and evolutionary consequences*



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Con amor a mis padres, Rosalva Loreto y Francisco Cervantes



## ABSTRACT

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Interactions between organisms give rise to emergent properties of natural systems, which underpins their ubiquity in the study of ecological and evolutionary dynamics. The representation of biotic interactions often requires models and simplifying assumptions since it is impossible to account for all aspects of the world in a single model. Critical choices, such as the number of species that can alter the interaction between a focal pair or which abiotic variables constitute the environment, are necessary when building ecological and evolutionary models. Such simplifying assumptions inevitably lead to the omission of heterogeneities at various levels. Complexity that is unaccounted for can, in turn, make the relationships between organisms appear noisy and fundamentally change model-based predictions. Despite this, ecological and evolutionary studies often lack appropriate frameworks that allow the inclusion of different levels of complexity in representations of biotic interactions. Thus, it is unclear whether including more realistic assumptions is warranted for the vast majority of natural systems. In this thesis, I explore how incorporating complexity as abiotic and biotic modifiers, as well as different sources of uncertainty, reveals potential explanatory generalities in natural systems. I also explore how accounting for these variables changes predictions related to the maintenance of diversity at ecological and evolutionary scales. Throughout this thesis, I focus on different types of interactions and organisms and propose mathematical and statistical frameworks that can be used beyond the studied systems.

In [Chapter 2](#), I explore how the presence of multiple species and different environmental contexts change the strength of plant-pollinator interactions. I propose a framework for using pollinator functional responses to examine the role of pollinator-pollinator interactions and abiotic conditions in altering the time between floral visits of a focal pollinator. I show that both density dependent responses and abiotic conditions are necessary to explain the number of visits a pollinator makes. In [Chapter 3](#), I explore how incorporating different sources of uncertainty changes predictions of species coexistence. I do this by simultaneously exploring how different model formulations, environmental contexts, and parameter uncertainty change the probability of predicting coexistence in a pairwise competition experiment of annual plants. I provide direct evidence that predictions of species coexistence are likely to change given the models used to quantify density-dependence. I also provide a theoretical framework to explore predictions made with different models. Finally, in [Chapter 4](#), I adopt an ecological framework to examine the evolutionary dynamics of sexually antagonistic alleles. I show that environmental fluctuations can substantially increase the amount of genetic diversity in a

population under sexually antagonistic selection by contributing positively to allele's invasion growth rates. Overall, the results of my thesis show that the assumptions adopted by some ecological and evolutionary models tend to be oversimplifying. Here, I provide tools for ecologists and evolutionary biologists to explore more realistic representations of biotic interactions as well as their consequences for diversity maintenance.

# DECLARATION

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Co-authors contributed to the collection of data used in Chapters 2 and 3. Co-authors in Chapter 4 wrote part of the code used to perform simulations. All co-authors contributed to subsequent drafts of the respective manuscripts.

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Name: Daniel B. Stouffer

Signature:

A handwritten signature in red ink, appearing to be 'D.B. Stouffer'.

Date: 2021-11-22





## PREFACE

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My thesis has been prepared as a collection of three standalone scientific articles. Each chapter is a standalone piece of research and, therefore, I only provide a general Introduction and Conclusion chapters linking the three chapters together. In [Chapter 1](#), I focus on describing how my three chapters are connected. In [Chapter 5](#), I focus on summarising the results from each of my thesis chapters and their combined implications in both how we study interactions and their consequences for diversity maintenance. Finally, I further expand on new ideas beyond those presented in the different chapters to discuss about the future steps moving forward.

At the time of thesis submission, each of these three articles are at different stages of the publication process.

[Chapter 2](#): “The context dependency of pollinator interference: how environmental conditions and co-foraging species impact floral visitaion” was published in May 2021 in the journal *Ecology Letters* in volume 24, no. 7, pages 1443–1454.

[Chapter 3](#): “The interplay of environmental conditions, parameter sensitivity and structural sensitivity in predictions of species coexistence” is in preparation for submission to *Ecology Letters*.

[Chapter 4](#): “Quantifying the relative contributions of environmental fluctuations to the maintenance of a sexually antagonistic polymorphism” is in preparation for submission to *The American Naturalist*.

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## Part I

### INTRODUCTION





## GENERAL INTRODUCTION

*Things are similar: this makes science possible*  
*Things are different: this makes science necessary*

— Levins and Lewontin (1980)

Interactions between organisms underpin the persistence of almost all life forms on Earth (Lawton, 1999). Furthermore, a large body of work has shown that biotic interactions determine emergent properties of natural systems, such as stability (May, 1972; Song and Saavedra, 2018; Wootton and Stouffer, 2016), resilience (Capdevila et al., 2021), ecosystem functioning (Godoy et al., 2020; Turnbull et al., 2013), and the coexistence of multiple species (Chesson, 2000; Saavedra et al., 2017). Unsurprisingly, numerous ecological and evolutionary concepts revolve around the effects that organisms exert on each other (Chase and Leibold, 2009; Gause, 1934; HilleRisLambers et al., 2012; MacArthur and Levins, 1967; Thompson, 1999, 2014).

From their origins as natural sciences, the disciplines of ecology and evolution have shifted from a descriptive towards a more predictive and quantitative approach (Holling, 1966; Lässig, Mustonen, and Walczak, 2017; Marquet et al., 2014; Pickett, 1980; Rossberg et al., 2019; Simberloff, 2004). This shift brought with it the use of mathematical models to describe natural phenomena, such as the effects species have on each other (Holling, 1966; Levins, 1966; Maynard-Smith, 1978; Servedio et al., 2014). Mathematical descriptions of interactions are “useful fictions” (Box, Luceño, and Carmen Paniagua-Quinones, 2011) in a twofold manner. First, they create a description of how organisms that coincide in space and time affect each other. Almost all known types of interactions can be described in the form of mathematical expressions that faithfully reproduce features of the observed data (Adler et al., 2018; Holland, DeAngelis, and Bronstein, 2002; Holling, 1959; Holt, 1977; Stouffer and Novak, 2021; Vázquez, Morris, and Jordano, 2005; Volterra, 1926; Wood and Thomas, 1999). Second, models are practical tools with which to make predictions beyond the phenomena they describe and thus provide general insights into how natural systems operate (Stouffer, 2019; Sutherland, 2006).

*Model tradeoffs*

Models that capture the effect of biotic interactions are abstractions of reality, and abstractions always reflect choices (Levins, 2006). Building models that include all aspects of reality is not only impractical but also unfeasible. Therefore, ecologists and evolutionary biologists have to continuously make choices regarding which variables to include in a model and which to omit (Odenbaugh, 2005). A common assumption when building models is that to achieve general insights, we should favor simple models (Evans et al., 2013). Indeed there is a general belief in ecology and evolution that a general model should include as little as possible (Holling, 1966; May, 2019; Roughgarden et al., 2018). This belief is often rooted in an implicit philosophical stance that one can not simultaneously maximize generality (i.e., models that apply to more than one system) and realism (i.e., models that produce accurate predictions for a given system) (Levins, 1966, 1993).

Inevitably, model building in biology leads to a key question that will, in turn, modify the outcomes achieved by any model: when is a model “realistic” enough (Stouffer, 2019)? The answer to this question will depend on the purpose for which a model is built (Levins, 2006; Odenbaugh, 2005). The classification of biological models and their purposes have been and continue to be widely debated (Evans et al., 2013; Holling, 1966; Levins, 1966, 1993; Lewontin, 1963; May, 2019; Odenbaugh, 2005; Orzack and Sober, 1993; Weisberg, 2006). Overall, it is generally recognized that the purposes of different biological models fall on a continuum (Evans et al., 2013; Levins, 1993; Servedio et al., 2014). On one end of this continuum are models that aim to understand and identify general principles (called strategic models by Holling (1966) and May (2019), or a minimal model of ideas by Roughgarden et al. (2018)). On the other end are models that aim to make detailed quantitative predictions (also called tactical models by Holling (1966) or synthetic models by Roughgarden et al. (2018)). The tradeoffs between generality, realism, and precision at each end of the spectrum have sparked extensive debate among biologists (Levins, 1966, 1993; Orzack and Sober, 1993; Weisberg, 2006).

Models that capture the effect of biotic interactions tend to fall in the spectrum under the category of “demonstration models”, as first defined by Crick (1988) and later by Evans et al. (2013). These types of models are often based on phenomenological descriptions of processes and have the general aim to show that the modeled principles are sufficient to reproduce some phenomena of interest (Crick, 1988; Evans et al., 2013). Demonstration models, however, do not help decide whether the modelled principles are *necessary* (Evans et al., 2013). The task to decide the necessary principles and thus the answer to the when a model is realistic enough becomes the modeler’s responsibility. In many cases, the answer to this question can appear arbitrary or solely determined by the dominant paradigm regarding the studied system. For example, mutualistic interactions between two species can be described by a

simple model that assumes a linear functional response (Bascompte, Jordano, and Olesen, 2006a), or by a more realistic model that incorporates saturating effects (Holland, DeAngelis, and Bronstein, 2002). The choice between these two models has substantial implications for predictions related to the coexistence of species and the assembly of communities (Holland, DeAngelis, and Bronstein, 2002). However, there is no consensus on which representation to favor, as the choice is usually defined by the modeler's particular school of thought and mathematical convince (Bascompte, Jordano, and Olesen, 2006b; Holland, Okuyama, and DeAngelis, 2006).

### *The perils of simple models*

A stance that always favors simple models in ecological and evolutionary studies can be problematic from two perspectives. First, the assumption that more complex models do not lead to general insights is seldom tested. For example, most models that capture competitive interactions between plants have the implicit assumption that competitive effects between individuals are always additive and direct (Freckleton and Watkinson, 2001; Kraft, Godoy, and Levine, 2015; Schoener, 1974). However, when models were set up to capture non-additive effects of interactions between individuals of co-occurring species, the evidence overwhelmingly showed that including these levels of biotic complexity was necessary to capture plant interactions accurately (Lai et al., 2021; Martyn et al., 2021; Mayfield and Stouffer, 2017). Thus, in some cases, increasing complexity increases rather than hampers the general insights obtained from models of biotic interactions.

Second, failing to include necessary levels of complexity can hinder our ability to predict how natural communities will react to novel conditions. Predictions of how natural systems will behave in the future are inherently challenging (Sutherland, 2006). Nevertheless, ignoring heterogeneities at various levels can further complicate rather than simplify predictions (D'Andrea, Ostling, and O'Dwyer, 2018). For instance, demographic models tend to treat ecological and evolutionary dynamics separately, despite the general understanding that both processes are often intertwined (Kokko and López-Sepulcre, 2007; MacArthur, 1962). Ignoring eco-evolutionary feedbacks leads to predictions that are inconsistent with empirical data and produce counterintuitive results in novel conditions (Kokko and López-Sepulcre, 2007). Thus, the implicit assumption that good models should include as little as possible should at least be treated with caution in ecological and evolutionary contexts.

*Challenges and consequences of increasing realism*

Despite arguments in favor of increasing realism in models of biotic interactions, doing so remains a challenge in many ecological and evolutionary studies. One of those challenges arises from the lack of theoretical frameworks that allow incorporating intricate empirical observations into models (Abrams, 1983, 2001). Such is the case of competition between pollinators that forage for the same resources (Thomson and Page, 2020). An overwhelming amount of empirical evidence shows that pollinators modify their foraging behavior in the presence of other foraging species (Briggs, 2016; Brosi and Briggs, 2013; Inouye, 1978; Morse, 1977; Thompson, Nisbet, and Schmitt, 2006); however, models that incorporate these behavioral changes into population dynamics remain scarce (Thomson and Page, 2020). Furthermore, density-dependent responses could themselves depend on the abiotic conditions pollinators experience, as many studies have shown that environmental conditions can drastically change how pollinators behave and interact with plant species (Briggs et al., 2018; Classen et al., 2020; Cnaani, Thomson, and Papaj, 2006; Heinrich, 1976; Thomson, Peterson, and Harder, 1987; Westphal, Steffan-Dewenter, and Tschardt, 2006). A coherent framework with which to incorporate both abiotic and biotic drivers into plant–pollinator interactions was lacking. To this end, in [Chapter 2](#) I develop a general framework to show how pollinator functional responses can be used to incorporate biotic and abiotic drivers into models of floral visitation rates. Furthermore, I show the empirical relevance of this framework by parameterizing different models of varying complexity that incorporate pollinator–pollinator interactions and environmental conditions when predicting observed data from a highly controlled foraging chamber experiment. Results from this chapter provide important insights related to our understanding of how species loss and environmental change might affect mutualistic communities.

Another theoretical challenge emerges when alternative models to represent biotic interactions are used interchangeably. Such is the case of phenomenological models of plant competition, where more than one mathematical form can faithfully reproduce empirical data (Bimler et al., 2018; Godoy, Kraft, and Levine, 2014; Godoy and Levine, 2014; Levine and HilleRisLambers, 2009; Mayfield and Stouffer, 2017). The effect biotic and abiotic drivers have on model based predictions can be dramatically different due to uncertainty associated with phenomenological models (Aldebert and Stouffer, 2018; Flora et al., 2011; Jørgensen and Bendoricchio, 2001). To understand the interplay between uncertainty and abiotic complexity, in [Chapter 3](#) I introduce a mathematical and statistical framework to simultaneously explore how different phenomenological models of plant competition, environmental context, and parameter uncertainty impact predictions of species coexistence. Additionally, I use this framework to make predictions around a pairwise competition experiment between annual plants, where I show that the effect of abiotic conditions in pre-

dictions of coexistence outcomes is not independent of the model formulation used to describe species interactions.

Finally, even when existing studies show that increasing model realism is warranted, understanding exactly how the addition of complexity changes predictions remains a challenge. For instance, theoretical and empirical studies have shown that environmental fluctuations can substantially increase the levels of genetic diversity in populations that experience sexually antagonistic selection (Connallon and Clark, 2012; Connallon, Sharma, and Olito, 2019; Glaser-Schmitt et al., 2021). However, there are no approaches that directly quantify *how* abiotic heterogeneity promotes the maintenance of genetic diversity in populations that experience sexual conflict. Hence, in [Chapter 4](#) I adopt an ecological framework to explicitly quantify the contributions of fluctuations in population sizes and selection to alleles' growth rates when rare using simulations. I show that environmental fluctuations can help maintain genetic variance in a population by allowing disadvantageous alleles to have positive invasion growth rates, but that their effect depends on the pathway by which each allele is introduced to the population.

### *Concluding remarks*

In this thesis, I propose theoretical and statistical frameworks that allow increasing realism in models of biotic interactions with the aim of understanding when higher levels of complexity are justified. Furthermore, I also explore the consequences of increasing model realism in predictions related to diversity maintenance at ecological and evolutionary scales. The individual chapters of this thesis are thematically broad as they are focused on different types of interactions and organisms, but all address in a different way the challenges and consequences of incorporating biotic and abiotic complexity in the study of biotic interactions.



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## Part II

### FRAMEWORKS FOR INCREASE REALISM IN MODELS OF BIOTIC INTERACTIONS





## THE CONTEXT DEPENDENCY OF POLLINATOR INTERFERENCE: HOW ENVIRONMENTAL CONDITIONS AND CO-FORAGING SPECIES IMPACT FLORAL VISITATION

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### ABSTRACT

Animals often change their behavior in the presence of other species and the environmental context they experience, and these changes can substantially modify the course their populations follow. In the case of animals involved in mutualistic interactions, it is still unclear how to incorporate the effects of these behavioral changes into population dynamics. We propose a framework for using pollinator functional responses to examine the roles of pollinator–pollinator interactions and abiotic conditions in altering the times between floral visits of a focal pollinator. We then apply this framework to a unique foraging experiment with different models that allow resource availability and sub-lethal exposure to a neonicotinoid pesticide to modify how pollinators forage alone and with co-foragers. We found that all co-foragers interfere with the focal pollinator under at least one set of abiotic conditions; for most species, interference was strongest at higher levels of resource availability and with pesticide exposure. Overall our results highlight that density-dependent responses are often context-dependent themselves.

### INTRODUCTION

Interactions between pollinators have been extensively documented and described by ecologists (Mallinger, Gaines-Day, and Gratton, 2017; Thomson and

Page, 2020). For eusocial insects like some bees and bumblebees, the presence of other species has been shown to drive resource partitioning due to active avoidance (Inouye, 1978; Morse, 1977), change pollinator foraging efforts (Thomson, 2006), and to promote short-term floral specialization (Briggs, 2016; Brosi and Briggs, 2013). However, fundamental gaps remain regarding the consequences of pollinator–pollinator interactions in natural communities, mainly because of the complexity of linking the effects of the interaction to population dynamics (Thomson and Page, 2020).

One of the empirical challenges in understanding interactions between pollinators is that environmental conditions can drastically change how pollinators behave and interact with conspecifics and other species. For instance, plant–pollinator interactions tend to be contingent on the external conditions pollinators experience (Cnaani, Thomson, and Papaj, 2006; Heinrich, 1976). High resource availability—measured in flower density or nectar volume—has been shown to decrease the duration of foraging trips for bumblebees (Westphal, Steffan-Dewenter, and Tschardt, 2006) and increase floral visits (Thomson, Peterson, and Harder, 1987; Thomson, 1988). Insect pollinators also show changes in their interactions with plants due to temperature; higher temperatures have been documented to shorten the time spent on individual flowers relative to low temperatures for bumblebees (Heinrich and Raven, 1972) and to promote floral specialization within an elevation gradient (Classen et al., 2020). Hence, studying the context in which interactions occur is as important as studying the interactions themselves.

In contrast, a theoretical challenge is incorporating the behavioral changes driven by the presence of other foraging pollinators, henceforth co-foragers, into population dynamics. Pollinator functional responses, which describe how consumption rates vary with the abundance of individuals of another population (Holland and DeAngelis, 2001), are key to how pollinator and plant populations are linked to each other. When pollinators modify their behavior due to the presence of other foraging species, it echoes observations in which predators' consumption rates vary because of "interference": time spent engaging in encounters with other predators instead of feeding (Beddington, 1975; DeAngelis and Holland, 2006; Skalski and Gilliam, 2001).

Overt interference between pollinators is thought to occur only for very specific groups of pollinators that present aggressive behavior, such as stingless bees that can recruit in large numbers and inflict serious damage to their competitors (Lichtenberg et al., 2011). Nonetheless, the presence of other foragers could have the same phenomenological effect as overt interference—from a functional response perspective—as long as it decreases the visitation rates of a focal individual. Importantly, the presence of other pollinator species can also increase visitation rates (e.g. Greenleaf and Kremen, 2006). Overall, whether or not the presence of other species leads to measurable differences in the rate of floral visits has equivocal experimental evidence: some studies report an increase in visits and pollination efficiency when more than one species is

present (Fründ et al., 2013) whereas others find an overall decrease in foraging activity (Roubik, 1978; Thomson, 2006; Thomson and Page, 2020). That the effect of varying pollinator abundances is context dependent could potentially explain the equivocal evidence found across the literature.

Fully incorporating pollinator behavioral changes into population dynamics is a laborious and challenging effort since it not only requires quantifying functional responses of the populations involved but the numerical responses as well (Abrams and Ginzburg, 2000; Revilla, 2015). Nonetheless, since interactions and visitation are a necessary precursor to a quantifiable numerical response, a good starting place is to determine how biotic and abiotic factors can be incorporated into pollinator's foraging rates. In this study, we therefore show how plant–pollinator functional responses can be used to incorporate the effects of environmental conditions and pollinator–pollinator interactions into floral visitation rates. We first introduce a novel framework that examines a simple response variable: the time a pollinator takes between floral visits. We then use our functional response framework to quantify the effects of pollinator–pollinator interactions under different environmental conditions in a highly controlled foraging-chamber experiment. Our experiments simultaneously modified varying levels of resource availability, sub-lethal exposure to a neonicotinoid pesticide, and co-foraging pollinator richness and abundance. We parameterize different models that incorporate pollinator–pollinator interactions and environmental conditions when predicting observed times between floral visits. Finally, we use these model fits to show that pollinator–pollinator interactions and their effects on focal pollinators are strongly determined by abiotic conditions.

## METHODS

### *A functional response framework of times between floral visits*

To understand the effect of varying abundances of plants and pollinators, as well as different environmental conditions, we build upon a classical framework to quantify consumption rates in consumer–resource systems. First, to mathematically describe how frequently a focal individual from pollinator species  $i$  visits flowers as floral abundance changes, we assumed the per capita visitation rate takes the form of a Type II functional response (Holling, 1959) as this is the predominant form assumed in various studies employing functional responses for mutualists (Bastolla et al., 2009; Holland, DeAngelis, and Bronstein, 2002; Rohr, Saavedra, and Bascompte, 2014; Valdovinos et al., 2013). Second, to describe how floral visits change with varying abundances of pollinators, we developed an analogue to the Beddington–DeAngelis functional response (Beddington, 1975; DeAngelis, Goldstein, and O'Neill, 1975). This function assumes that the instantaneous per capita flower visitation rate of

a focal pollinator from species  $i$  on focal flowers of the species  $m$ ,  $\lambda_{i,m}$ , is a non-linear function with the form:

$$\lambda_{i,m} = \frac{a_m N_m}{1 + a_m h_m N_m + \sum_n a_n h_n N_n + c_i (P_i - 1) + \sum_j c_j P_j} , \quad (2.1)$$

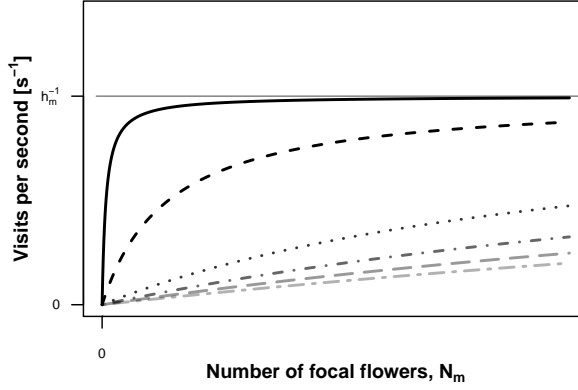
where  $N_m$  and  $N_n$  are the abundances of focal and non-focal flowers. The encounter rate of bee individuals with focal flowers is described by  $a_m$ , while  $a_n$  describes the encounter rate with non-focal flowers. Similarly,  $h_m$  and  $h_n$  denote the handling times of focal and non-focal flowers, respectively. The variables  $P_i$  and  $P_j$  represent the conspecific and heterospecific pollinator abundances, respectively, and their effects on visitation are captured by  $c_i$  and  $c_j$ . Note that for conspecific interactions between pollinators, we used  $P_i - 1$  to account for the fact that focal individuals do not interact with themselves.

Though they are rarely studied in this way due to the typical data available, an alternative and equivalent approach to characterize functional responses is to examine the time between feeding events instead of feeding rates themselves (Coblentz and DeLong, 2020). This approach has the advantage of allowing inference of a consumer's functional response using one or a few trials per individual (Coblentz and DeLong, 2020). Returning to the functional response given by Eq. 2.1, we can estimate time between floral visits,  $\rho_{i,m}$ , as the inverse of the per capita visitation rate:

$$\rho_{i,m} = \frac{1}{\lambda_{i,m}} = \frac{1}{a_m N_m} + h_m + \frac{1}{a_m N_m} \sum_n a_n h_n N_n + \frac{c_i}{a_m N_m} (P_i - 1) + \frac{1}{a_m N_m} \sum_j c_j P_j. \quad (2.2)$$

Written this way, the times between floral visits become the sum of the time each focal pollinator spends between visiting focal flowers, the time between visiting other flowers, and the time “added” by interactions with conspecific and heterospecific co-foragers. Importantly, the effects of pollinator–pollinator interactions can be quantified as increases or decreases to the times between floral visits. Note that conversion of times between visits to visitation rates can be done for either when the number of flowers or the number of pollinator vary (Fig. 2.1).

a)



b)

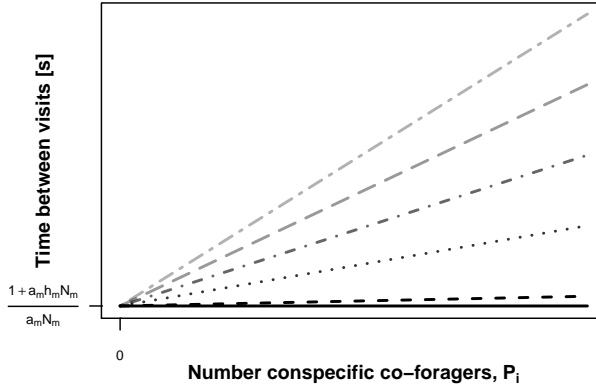


Figure 2.1: Visualizing the mathematical relationship between visitation rate and time between visits. a) Visitation rate as a function of the number of flowers  $N_m$  (Eq .2.1). For a fixed number of co-foraging conspecific pollinators  $P_i$  with no interference ( $c_i = 0$ ), no heterospecific pollinators present ( $P_j = 0$ ), and no other plants ( $N_n = 0$ ), the visitation rate saturates at  $1/h_m$  (solid black line). As  $c_i$  increases (dashed and dotted lines in lighter colours), the rate at which visitation rate reaches saturation decreases. b) Time between visits to a fixed number of focal flowers  $N_m$  as a function of conspecific co-foragers  $P_i$ , also with  $P_j = 0$  and  $N_n = 0$  (Eq .2.2). When  $c_i = 0$ , the time between floral visits does not change with increasing pollinator abundance (solid black line). As  $c_i$  increases, each co-foraging pollinator contributes more time to the time between floral visits (dashed and dotted lines in lighter colours as in a).

This general functional response framework allows us to quantify visitation rates under several experimental designs that might include scenarios (i) where floral abundances vary, (ii) where pollinator abundances vary, and (iii) under different environmental conditions. For example, when there are observations of a focal pollinator and conspecific co-foragers visiting varying abundances of two plants, Eq. 2.2 reduces to:

$$\rho_{i,m} = \frac{1}{a_m N_m} + h_m + \frac{a_n h_n N_n}{a_m N_m} + \frac{c_i}{a_m N_m} (P_i - 1). \quad (2.3)$$

Note that to parameterize Eq. 2.3, we require independent variations of the abundances of both flowers *and* of pollinators. However, it is also possible to adapt and fit a model based on our framework when only *some* abundances change. For instance, if the number of conspecific co-foragers  $P_i$  is fixed, Eq. 2.3 becomes:

$$\rho_{i,m} = h_m + \left( \frac{1}{a_m} + \frac{c_i(P_i - 1)}{a_m} \right) \frac{1}{N_m} + \left( \frac{a_n h_n}{a_m} \right) N_n \frac{1}{N_m} \quad (2.4)$$

which can be further simplified to:

$$\rho_{i,m} = h_m + \gamma_{i,m} \frac{1}{N_m} + \delta_{i,n} N_n \frac{1}{N_m}. \quad (2.5)$$

Here the composite parameter  $\gamma_{i,m}$  scales the impact of changes in focal floral abundances in the time between floral visits while  $\delta_{i,n}$  scales the relative impact of changes in non-focal floral abundances. Since  $\gamma_{i,m}$  includes encounter rates with flowers as well as the implicit impact of pollinator interference, these cannot be disentangled statistically without variation in  $P_i$ . Similarly,  $\delta_{i,n}$  is a term that includes both the encounter rates with focal and with non-focal flowers.

On the other hand, when there are observations of different abundances of co-foragers visiting a fixed number of flowers of a single species, then Eq. 2.2 becomes:

$$\rho_{i,m} = \frac{1 + a_m h_m N_m}{a_m N_m} + \frac{c_i}{a_m N_m} (P_i - 1) + \frac{c_j}{a_m N_m} P_j, \quad (2.6)$$

which can be further simplified to:

$$\rho_{i,m} = \alpha_m + \beta_{i,m} (P_i - 1) + \beta_{j,m} P_j, \quad (2.7)$$

where the composite parameter  $\alpha_m$  sets a baseline of time between visits when there are no pollinator-pollinator interactions (i.e. the pollinator density-independent foraging outcomes), and the composite parameters  $\beta_{i,m}$  and  $\beta_{j,m}$  capture the density-dependent changes to the time between visits to focal flowers. As above, both  $\beta_{i,m}$  and  $\beta_{j,m}$  incorporate both pollinator interference and encounter rates with flowers. Thus, an increase of times between floral

visits (i.e. a decrease in floral visitation rates) could be the outcome of higher pollinator interference or decreasing encounter rates with flowers.

As a final example, both the density-dependent and density-independent terms can be inferred under different environmental conditions. For example, suppose we measure an environmental variable  $E$ , and there are observations similar to those of Eq. 2.6 but under different levels of the environmental condition. Then, Eq. 2.7 can be expanded into:

$$\rho_{i,m} = \alpha_m + \alpha_{m,e}E + (\beta_{i,m} + \beta_{i,m,e}E)(P_i - 1) + (\beta_{j,m} + \beta_{j,m,e}E)P_j, \quad (2.8)$$

where  $E$  is the value of the measured environmental variable (which can take continuous or discrete values), and the parameters with the subscript  $e$  capture changes driven by abiotic conditions. For example, if  $\beta_{i,m}$  quantifies the effect of conspecific pollinators, then  $\beta_{i,m,e}$  quantifies how much the effect of conspecific pollinators changes under a certain abiotic condition. Written this way, both pollinator abundances and the environmental conditions are the factors that determine the effect of pollinator–pollinator interactions.

## Data

In the following sections, we use our framework to parameterize and compare different models of floral visits with a unique foraging experiment. To do so, we examined data from a set of experiments that allowed us to tightly monitor the time individual bumblebees spend between visits to artificial flowers, as well as the energy consumed per visit. During 2015 and 2016, we tracked the activity of commercial *Bombus impatiens* (henceforth *Bombus*) from Koppert Biological Systems (Howell, MI USA), inside a foraging chamber under (i) different richness and abundances of co-foragers and (ii) different levels of resource availability (iii) with and without pesticide exposure. These data belong the “Emory data set”, as described in Ayers, Armsworth, and Brosi (2018).

## Experimental setup

To monitor the activity of our focal species, our enclosure consisted of an array of artificial flowers that recorded the presence of a visiting bee at the same time dispensed an automatic computer-controlled reward. The system was made up of 32 artificial flowers in four rows of eight flowers each distributed uniformly inside the chamber. The artificial flowers varied by color (blue, white, yellow, pink), scent, and sucrose concentrations (2.0 M, 1.5 M, 1.0 M, 0.5 M), in a way that yielded four distinct flower types. The automatic tracking of *Bombus* individuals and co-foragers was done using mic3-TAG RFID 16 kbit

tags (Microsensys GmbH, Erfurt, Germany) attached to each bee's thorax so as to not interfere with movement of flight.

Corresponding RFID tag readers embedded in each artificial flower recorded the presence of a bee (of any species) and activated an automatic reward of 10  $\mu$ l unless the same individual had been recorded in that flower in the last 30 seconds, in which case no reward was conferred. If a different individual, of any species, visited the same flower, then the granting of a new reward depended on the floral refill time, or the time after which artificial flowers would dispense a new sucrose reward after a previous visit, a condition that we manipulated throughout the trials (see *Foraging trials*). The sucrose reward was dispensed from a pipette tip embedded in the artificial flower, which was taken up by the bee's proboscis through capillary action. Data suggests that the bees were almost always consuming the full reward offered by the artificial flowers (Fig. 6.1 in Chapter 6). This system allowed us to closely monitor the time between floral visits and energy consumption at the individual-bee level as well as resource availability using Arduino MEGA 2560 R3 hardware (Arduino LLC) and Processing software.

### *Foraging trials*

Foraging trials consisted of fasting the bees for one hour, transferring them to the foraging enclosure, and recording their behavior over 75 minutes. Before the experimental trials, we kept bees in separate training enclosures with artificial flowers identical to the ones in the experiment, except for the fact that training flowers were not computer controlled but delivered rewards *ad libitum*. We simultaneously manipulated the richness and abundance of co-foragers, floral refill time, and the sub-lethal exposure to a common dose of a neonicotinoid pesticide as follows.

We manipulated the richness and abundance of co-foragers through a series of single-species and multi-species trials. In single-species trials, we varied the abundance of *Bombus* to 4, 8 and 16 individuals foraging at the same time, with no other species present. In multi-species trials, we manipulated richness, or the number of species that were foraging at the same time as *Bombus*. We examined the combinations of one to three additional bee species foraging at the same time as *Bombus* while at all times holding total bee abundance constant at 16 individual bees. The three other species were another social bee species, *Apis mellifera* (henceforth *Apis*), and two solitary taxa, *Osmia lignaria* and *Megachile rotundata* (henceforth *Osmia* and *Megachile*). In multi-species trials, we used 8 *Bombus* individuals for 2-species trials, either 5 or 6 *Bombus* for 3-species trials, and 4 *Bombus* for 4-species trials. We present a detailed description of the abundances of the other species during the experiment in Table 6.1 in Chapter 6.



We also manipulated floral refill time to mimic different levels of resource availability since resource availability for the foraging bees decreases as refill time increases. The levels of floral refill time we examined were: instantaneous refill (0 seconds), intermediate refill (120 seconds), and delayed refill (540 seconds). We will refer to instantaneous refill (i.e. high resource availability) as the control condition.

Finally, we also manipulated bee exposure to a sub-lethal dose of neonicotinoid pesticide. While in the training enclosure, we fed individuals of all species subject to the pesticide treatment *ad libitum* on a sucrose solution with a sub-lethal concentration of 10  $\mu\text{g/L}$  of thiamethoxam ( $\text{C}_8\text{H}_{10}\text{ClN}_5\text{O}_3\text{S}$ , Sigma Aldrich); bees subject to the control condition were fed a sucrose solution without pesticide. For bees subject to pesticide treatment, the solution that contained pesticide was their only available sugar source. Thiamethoxam is applied to a wide range of crops (Maienfisch et al., 2001) and the concentration is consistent to what insects experience in the field (Blacqui re et al., 2012). We ran trials with either all exposed (of all species) or all unexposed bees to mimic exposure at the landscape level. We show a detailed description of the number of trials and replicates we performed in Tables 6.2 and 6.3 in Chapter 6, as well as an explicit account of how the data was cleaned for analysis.

## Analysis

### *Models of times between floral visits*

Given our framework and our very detailed data-set, we were able to contrast different hypotheses regarding how pollinators forage and interact, using *Bombus* as our focal species. Instead of testing *all* possible hypotheses of how co-foragers, resource availability and pesticide exposure influence the times between floral visits, we tested three relatively simple hypotheses: (i) *Bombus* individuals forage unaffected by the presence of co-foragers or by environmental conditions, (ii) only co-foragers modify how *Bombus* forages but environmental conditions do not, and (iii) environmental conditions modify how individuals forage alone and in the presence of other foragers. Our modelling aim was not to get a detailed prediction of the dynamics governing the experimental system, but rather to show that the modelled principles are sufficient to explain times between floral visits, following a demonstration modelling approach to reveal potential explanatory generalities (Evans et al., 2013).

If we map our functional response framework to our experimental setup, we can describe the functional response of the focal *Bombus* individuals with Eq. 2.7. Our hypotheses can then be tested across different foraging models that equate to further extensions or simplifications of Eq. 2.7. If the presence of co-foragers and environmental conditions have no effect on the times between

visits across experiments, then a density-independent rate will be sufficient to describe the data:

$$\rho_i = \alpha. \quad (2.9)$$

We call this our *null* model. Note that since in our experiment floral abundances remained constant, we did not explore how changes in densities of different flower types changed foraging rates. Rather, we modelled how long *Bombus* individuals would take between visits to all of the artificial flowers, regardless of the type of flower. Thus, for simplicity we dropped subscripts on terms that depended on flower types.

On the other hand, if co-foragers interact with each other but visitation is unaffected by the abiotic conditions, then an equation similar to Eq. 2.7 that only considers the effect of co-foragers would best describe the times between floral visits. We call this the *interference* model:

$$\rho_i = \alpha + \beta_i(P_i - 1) + \sum_j \beta_j P_j. \quad (2.10)$$

Finally, if the abiotic treatments modify how *Bombus* forages with and without co-foragers, similar to Eq. 2.8, we would expect the times between visits to be a function of the abundance of co-foragers, level of resource availability ( $R$ ) and pesticide exposure ( $E$ ), we call this the *treatments* model:

$$\begin{aligned} \rho_i = \alpha + \alpha_r R + \alpha_e E + \beta_i(P_i - 1) + \beta_{i,r}(P_i - 1)R + \beta_{i,e}(P_i - 1)E \\ + \sum_j \beta_j P_j + \sum_j \beta_{j,r} P_j R + \sum_j \beta_{j,e} P_j E. \end{aligned} \quad (2.11)$$

Here the subscripts  $r$  and  $e$  denote the parameters that estimate the effect of  $R$  and  $E$ , respectively. In our case,  $R$  is a continuous variable that corresponds to the floral refill time (i.e. goes from 0 to 540 seconds) and  $E$  is a dummy variable to indicate pesticide exposure (i.e.  $E = 0$  when bees are subject to the control treatment, and  $E = 1$  when bees were exposed to the pesticide treatment). The subscripts we used are consistent with the nomenclature of the density-independent and density-dependent terms described previously. Note that in our data, not all co-foraging species were tested under all experimental conditions (Table 6.3 in Chapter 6). Therefore, we did not model the three-way interaction between species identity, pesticide exposure and resource availability.

### Statistical analysis

To infer the parameters of Eqs. (2.9-2.11), we fit non-linear hierarchical models with a Bayesian framework using Hamiltonian Monte Carlo (HMC) methods. We provide the details of our statistical analysis in Chapter 6. We fit our

models using the function *brm* from the package *brms* (Bürkner, 2017) in the statistical program R (version 3.4.2) (R Core Team, 2013). We ran four chains with a warm up of 3000 iterations and 2000 sampling iterations, using weakly informative priors and a maximum treedepth of 13 and an adapt delta of 0.99. We determined convergence when trace plots were well mixed and stationary and when the Gelman-Rubin convergence diagnostic (Rhat) was less than 1.05 for all parameters (Vehtari et al., 2020).

We compared the fits of Eqs. (2.9-2.11) to each other using the the Wanatabe-Akaike information criterion (WAIC) to determine which of the hypotheses encoded within the models best predicts out of sample times between floral visits. WAIC provides a measure for model fit that is penalized for the number of model parameters, and the best fit model in terms of out of sample predictions is the one with the lowest WAIC value. Additionally, we calculated Akaike weights for each model, which can be interpreted as an estimate of the probability that the model will make the best predictions of new data based on the the set of models considered. We did model comparisons using 500 samples from the posterior distribution, and we defined best-fit models as those with the lowest WAIC and an Akaike weight greater than 0.9 (McElreath, 2018).

## RESULTS

Model comparison using Wanatabe-Akaike information criterion (WAIC) showed that the *treatments* model was the best-fit model for explaining the data by a wide margin (Table 2.1). The *treatments* model had the lowest WAIC score and received all of the Akaike weight, which means it had the highest probability to make the best predictions of new data compared to the two other models considered. Model comparison therefore showed not only that co-foraging pollinator abundances systematically modified the times between floral visits, but also that resource availability and pesticide exposure modified how bumblebees foraged alone and with other species present.

### *Density-independent effects*

The parameters of the *treatments* model allowed us to make predictions beyond the pollinator densities manipulated during the trials since it estimated density-independent effects as the intercept. Without any co-foragers present, predictions using the *treatments* model confirmed that both low resource availability and sub-lethal exposure to pesticide increased the time between floral visits (Fig. 2.2). Predictions made at low resource availability and under pesticide exposure (Fig. 2.2d) showed that a bumblebee foraging alone would spend on average 90 seconds more between floral visits when compared to predictions made at high resource availability and under no pesticide exposure

(Fig. 2.2a); this equates to a near doubling of the amount of time between floral visits. Consequently, over the course of a 75 minute experiment, an average bumblebee foraging alone would make 15 fewer floral visits if there was low resource availability and it had been exposed to pesticide.

Table 2.1: Model comparison table. WAIC (Widely Applicable Information Criteria) penalizes models for parameters, and the lowest WAIC reflects the best-fit model. pWAIC is the effective number of parameters and provides information on how flexible each model is in fitting the sample. Akaike Weight for each model is an estimate of the probability that the model will make the best predictions of new data based on the the set of models considered.

model	WAIC	pWAIC	Akaike weight
<i>treatments</i>	413322.5	2386.6	1.00
<i>interference</i>	414462.5	2135.6	< .002
<i>null</i>	416063.6	1769.6	< .002

As shown in the intercepts of Fig. 2.2a and c, we also found that the time between floral visits decreased as resource availability increased (i.e. the time between floral refill decreased). Predictions made at high resource availability (0 seconds between floral refill) showed that an average bumblebee would make 7 more floral visits over the course of an experiment than it would at low resource availability (540 seconds between floral refill).

#### *Density-dependent effects*

We found that the time between floral visits for a focal pollinator changed consistently as a function of the identity and abundance of the co-foragers (Fig. 2.2). All of the species examined could potentially interfere with a focal *Bombus* individual by increasing the time between floral visits, but the extent of the interference effect depended on the environmental context bees experienced.

Under control conditions (i.e. no pesticide exposure and high resource availability), increasing abundances of *Bombus*, *Osmia*, and *Megachile* all increased the times between visits (and therefore decreased the visitation rate) to a similar extent (Fig. 2.2a). However, *Apis* had an opposite effect under control conditions as increasing its density *decreased* the times between floral visits. Thus, when there was high resource abundance and no pesticide exposure three of the species (including conspecifics) had an interference effect. However, as environmental conditions changed, so did these interference effects. For example, increasing abundances of *Apis* changed from decreasing times between visits to increasing them when there was either pesticide exposure or low resource availability (Fig. 2.2).

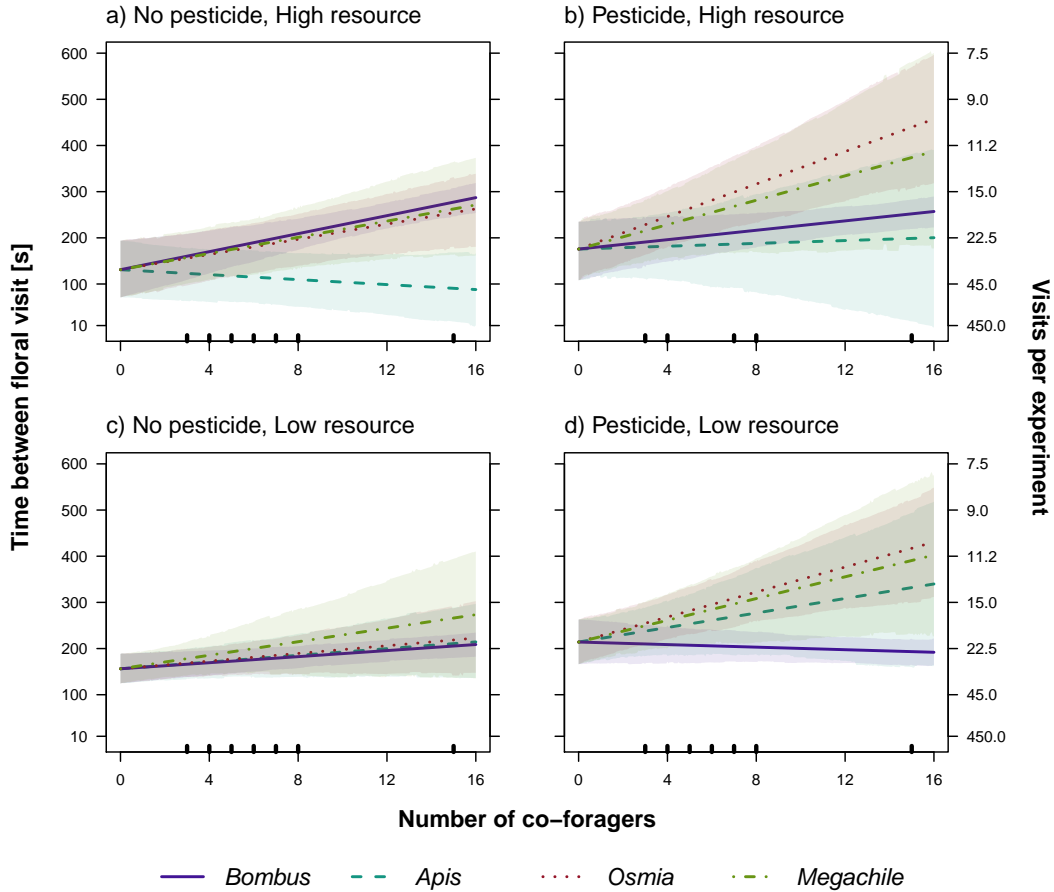


Figure 2.2: Model predictions of how the time between floral visits changed as the number of co-foragers increased and under different environmental conditions. Each color and line type correspond to a different co-forager. Lines represent predictions using the median parameter values of the *treatments* model for the average focal individual. The shaded areas correspond to the 90% highest posterior density interval (HPDI). High resource availability corresponds to 0 seconds between floral refill, and low resource availability to 540 seconds between floral refill (the maximum used during the experiments). Ticks along the x-axis indicate the actual co-forager abundances examined during the experimental trials. On the right y-axis and to help interpretation, we show how many visits per 75 minute experiment would be expected for the corresponding times between floral visits.

To better disentangle the species-specific response of interference to environmental variables, we estimated the time contributed by a single co-forager individual of each species to the total times between floral visits as resource availability increased (Fig. 2.3) and with the exposure to a neonicotinoid pesticide (Fig. 2.4). That is, given the posterior distribution of the fixed effects, we calculated how total times between floral visits changed due to the contribution of a single individual of each species under different environmental conditions. Note that due to the inverse relationship between time between floral visits and resource availability, Fig. 2.3 shows decreasing times between floral refill.

We found that, as resources became more abundant (or the time between floral refill decreased), interference by *Bombus*, *Osmia*, and *Megachile* increased (Fig. 2.3). In particular, the time contributed by a conspecific individual almost tripled when resource availability changed from low to high (Fig. 2.3a). For the majority of the species examined, interference was strongest when there was high resource availability, and its effect weakened as resources became more scarce. In contrast, as resources became more abundant, the contribution of an additional individual of *Apis* to the time between floral visits decreased. Indeed, our predictions using median parameter values showed that an individual of *Apis* went from creating net decreases in visitation rate at low resource availability to creating net increases in visitation rate at high resource availability (Fig. 2.3b). However, the predictions using the 90% highest posterior density interval (HPDI, or the narrowest interval containing the specified probability mass (McElreath, 2018)) for *Apis* included competitive and facilitative outcomes at all levels of resource availability. Thus, even though on average *Apis* individuals had a facilitative effect as resources became more abundant, we predicted some competitive effects as well when making predictions using the full posterior distribution.

In contrast to resource availability, pesticide exposure tended to increase the strength of pollinator interference for all species except *Bombus* (Fig. 2.4). That is, when all of the bees had been exposed to pesticide, increasing heterospecific abundances of pollinators generally decreased floral visitation rate because individuals contributed positively to the times between floral visits. Conspecifics, however, had the opposite effect: pesticide exposure decreased the strength of pollinator interference (Fig. 2.4).

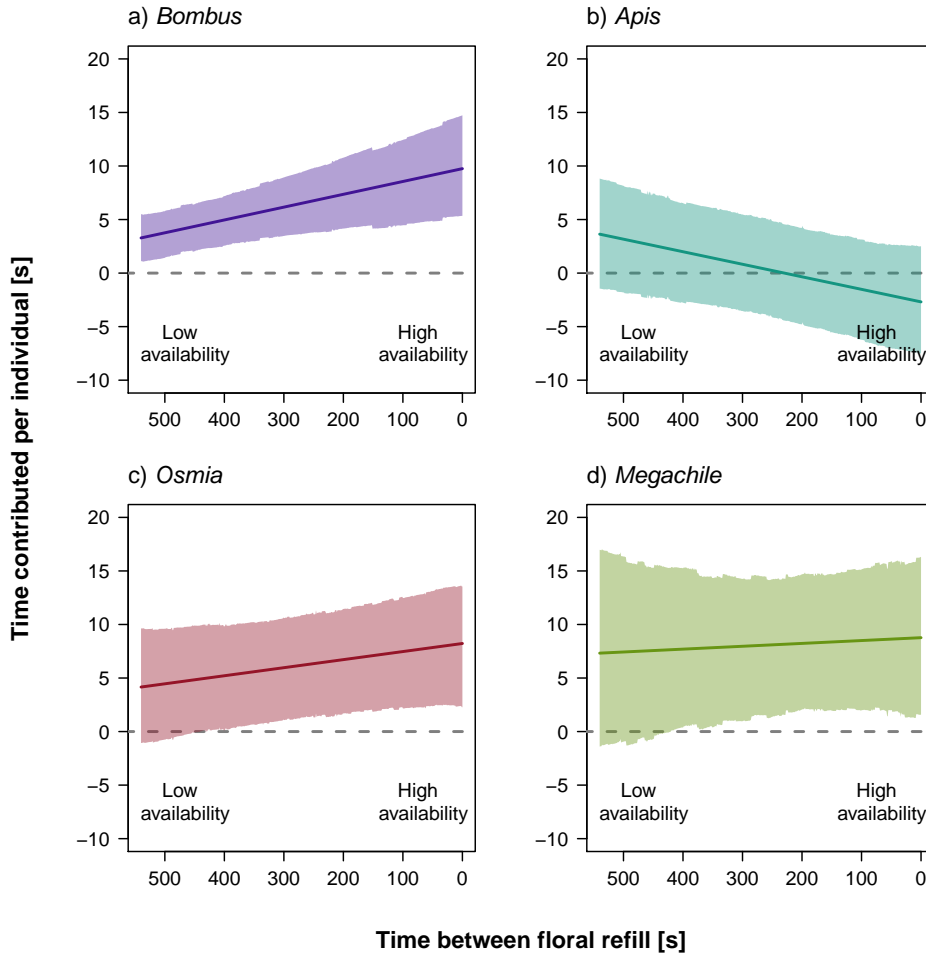


Figure 2.3: Model predictions of the effect an individual co-forager had on the time between visits of *Bombus* as resource availability increased and when there was no pesticide exposure. Each panel estimates the contribution of an individual co-forager from each of the four co-foraging species from our study. Solid lines represent the predictions made with the median parameter values of the *treatments* model for the average focal individual whereas the shaded areas correspond to the 90% highest posterior density interval (HPDI). To help interpretation, we provide the mapping between low and high resource availability and time between floral refill in each panel.

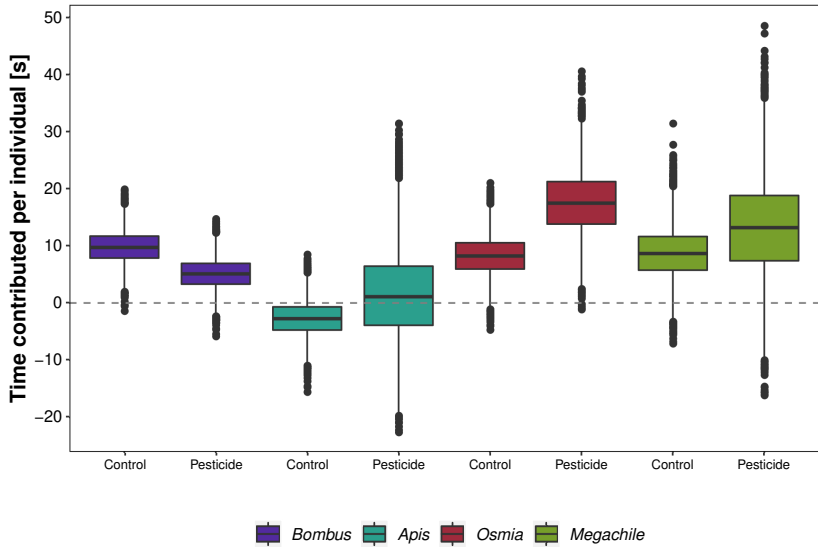


Figure 2.4: The effect an individual co-forager had on the time between floral visits when it had not been exposed to pesticide at high resource availability (Control), and when it had been exposed to a sub-lethal dose of neonicotinoid pesticide and at high resource availability (Pesticide). Each color corresponds to the different species of co-foragers. Each box plot extends from the first to third quantiles of the corresponding posterior distribution of parameter values, and the line inside the box indicates the median. The upper whisker extends to the largest value no further than 1.5 times the inter-quantile range (IQR, or the distance between the first and third quantiles); the lower whisker extends to the smallest value at most 1.5 times the IQR. Data beyond the end of the whiskers are determined to be outliers and are plotted individually with solid black points.

DISCUSSION

We applied our functional response framework to illustrate how both environmental context and pollinator–pollinator interactions can substantially change the number of visits a pollinator will make. Our model predictions showed that when a pollinator was foraging alone, conditions such as low resource availability and exposure to a sub-lethal dose of pesticide decreased the visits made to flowers. However, the same environmental conditions could have opposite effects on pollinator–pollinator interactions; for most species examined, interference was strongest when there was high resource abundance, and



pollinator interference decreased as resources became scarcer (except for *Apis*). Finally, we found a density-dependent response to pesticide exposure since, for all co-foraging species except *Bombus*, exposure to pesticide increased the sensitivity to individuals of other co-foraging species. On the whole, our results make clear that the question is not whether or not pollinators interfere with each other, but under what conditions they do so.

### *Resource abundance*

When resources are scarce, it has been previously documented that bumblebees make fewer visits to flowers than in rich-resource areas (Heinrich, 2004; Westphal, Steffan-Dewenter, and Tschardtke, 2006). Our predictions agreed on the effect of low resource availability when a pollinator is foraging *alone* (Fig. 2.2). For bumblebees, high resource availability can be associated with mass-flowering (Westphal, Steffan-Dewenter, and Tschardtke, 2003), and other studies have shown that net benefits are increased when bumblebees concentrate their efforts in areas of rich nectar resources while moving rapidly through depleted areas (Heinrich, 1979).

In contrast, the role of resources was reversed when a bumblebee foraged at the same time as other species. For most of the species examined, interference was strongest when resources were most abundant (Fig. 2.3). Recall that in our modeling framework an increase of times between floral visits can be caused by many different mechanisms. For example, we found with  $\beta_{i,r}$  that the effect of conspecifics decreased as resources became more scarce. This decrease could be due to a decrease in overt interference,  $c_i$ , or to a lower encounter rates with flowers  $a_m$ . However, observations of bees during the experiments offer some potential insights into this question. First and foremost, we never observed obvious aggressive interactions between bee individuals in the foraging arena. Instead, interference appears to have been driven by avoidance of flowers due to visual and/or olfactory cues presented by other bee individuals. The response to these cues was clearly context dependent. For example, while we did not specifically test learning within individual bees, they may have learned within the course of a trial that a visual or olfactory cue of another individual at a flower signaled that the flower was unlikely to be rewarding (in the case of delayed floral refill) or that the cues were not related to rewards (in the case of instantaneous floral refill). Indeed, overt interference has not been observed in bumblebees (Heinrich, 1976, 2004), but bumblebees have been documented to have avoidance behavior when foraging with other species (Inouye, 1978; Morse, 1977) and are able to detect and reject flowers which have been visited by other *Bombus* species using scent (Goulson, 1999).

Additionally, different bee species behaved differently in the experiments and the contribution to the times between floral visits we found (positive and negative) was also reflective of competitor species identities. For example,

*Apis* individuals generated net increases in floral visits by decreasing the time between floral visits under high resource availability. This may be because honey bees were not particularly active in foraging and may have spent more time outside of flowers, which could have led to essentially an overall decrease in competition for *Bombus*. Previous studies have found that interspecific interactions between honeybees and other species can sometimes result in an increase in pollination efficiency (Greenleaf and Kremen, 2006). In contrast, *Megachile* individuals also had low foraging rates, but based on observations may have spent more time in and near flowers, potentially leading *Bombus* individuals to avoid those flowers and increasing interference despite low foraging rates. Changes in bee foraging behavior have been shown to be species-specific before (Briggs, 2016), and it remains an exciting and open challenge to fully understand how they explicitly depend on environmental conditions.

### *Pesticide exposure*

Our results were also consistent with previous studies that saw a decrease in floral visits when pollinators are exposed to a sub-lethal dose of neonicotinoid pesticide (Gill and Raine, 2014; Henry et al., 2012; Mommaerts et al., 2009; Stanley and Raine, 2016). Neonicotinoid pesticides bind strongly to nicotinic acetylcholine receptors in the central nervous system of insects (Goulson, 2013). At sub-lethal doses, this creates difficulties for memory and learning (Henry et al., 2012), as well as compromises navigation skills (Desneux, Decourtye, and Delpuech, 2007). Unsurprisingly, exposure to thiamethoxam increased the times between floral visits when a bumblebee was foraging alone and with the addition of individuals of all of the heterospecific pollinators (Fig. 2.2 & 2.4). For conspecifics, pesticide exposure weakened the effect of conspecific interference. That is, relative to the control conditions, foraging with conspecific individuals still resulted in a net decrease of floral visits but to a lesser extent. Thus, the general effect of sub-lethal exposure to a neonicotinoid pesticide is to decrease floral visits via both by density-dependent and density-independent mechanisms.

### *Experimental limitations*

In our study, the highly controlled experimental setup allowed us to tightly monitor bee behavior and thus explicitly quantify pollinator interference and its relationship with experimental treatments. However, the artificial environment might not accurately capture how bees forage in the wild. For example, bumblebees could not leave low resource areas and concentrate their efforts in less depleted areas as they are prone to do (Heinrich, 2004). Furthermore, the non-focal species were not as active as *Bombus* during the trials, which

might further change how interference operates. Thus, the results presented here should be considered in the context of a controlled foraging experiment. This notwithstanding, we directly quantified behavioral changes driven by the presence of other pollinator species into pollinator functional responses, which has rarely been done.

#### *Consequences of pollinator–pollinator interactions*

In this study we focused on the functional responses of pollinators, and did not quantify their numerical responses (Morris, Vázquez, and Chacoff, 2010). Without knowing the numerical responses of the populations involved, we can not fully understand the dynamic consequences of pollinator–pollinator interactions (Revilla, 2015). However, our results do provide insights of how interference might affect mutualistic communities. Empirical and theoretical studies suggest that how often pollinators visit plants is a good predictor of the strength of the interaction, for both pollinators and plants involved (Vázquez et al., 2012; Vázquez, Morris, and Jordano, 2005). Indeed, in our experimental system the number of floral visits was a good predictor of the energetic gains for bees, since bees seemed to almost always consume the full reward offered by artificial flowers (Fig. 6.1, Chapter 6). Thus, from the point of view of pollinators, foraging with other species can be disadvantageous under certain conditions. For example, if high resource abundance made the other species more active, *Bombus* individuals might spend longer between flower visits because they are trying to avoid flowers that have already been visited. However, from the plant’s perspective, receiving visits from a diverse pollinator assemblage can produce more stable plant reproduction (Sahli and Conner, 2006), and greater competition tends to make bees increase floral fidelity, which also enhances plant fitness (Brosi and Briggs, 2013). Much like plant diversity (Bruninga-Socolar, Crone, and Winfree, 2016), our results show that pollinator diversity does not always have straightforward consequences on the populations involved.

#### *Conclusion*

The impact of interactions between pollinators in natural communities it is still poorly understood. In this study, we argue that in order to understand when and why those interactions change the course of plant and pollinator populations, we should also determine the environmental context in which they occur. Importantly, our study provides a theoretical framework to do so, coupled with a highly controlled foraging experiment to show how drastically abiotic conditions can change the outcomes of pollinator–pollinator interactions. By incorporating intra-guild interactions into pollinator functional responses, our study opens up an urgent avenue to study the consequences of species loss and environmental change in natural communities. It is critical to determine just how prevalent interference or facilitation between pollinator species is in

nature, in order to further understand how species loss could affect pollinator populations. We believe our study gives ecologists the theoretical and statistical tools to quantify the effects of other species both in experimental and observational studies, and contributes to closing the gap between the mutualistic and predator-prey literatures.

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# THE INTERPLAY OF ENVIRONMENTAL CONDITIONS, PARAMETER SENSITIVITY AND STRUCTURAL SENSITIVITY IN PREDICTIONS OF SPECIES COEXISTENCE

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## ABSTRACT

Predicting the outcome of competitive interactions among species that share resources is central to our current understanding of diversity maintenance. However, we have little information about how robust are predictions of species coexistence. This limitation is partly because several sources of uncertainty are often ignored when making predictions. Here, we introduce a mathematical and statistical framework to simultaneously explore how different models, environmental contexts and parameter uncertainty change the probability of predicting species coexistence. Using a set of pairwise competition experiments of annual plants, we provide direct evidence that seemingly subtle differences between models led to predictions of both coexistence and competitive exclusion based around the exact same experimental data. We also show that the effects of environmental context-dependency and parameter uncertainty on predictions of species coexistence are not independent of the model formulation used to describe species dynamics. Our work suggests that predictions of species coexistence and extrapolations made from them are particularly vulnerable to change due to the three sources of uncertainty we studied.

## INTRODUCTION

The effects species have on one another are the result of multiple processes that often act simultaneously. In the case of competition between plants, examples include the depletion of local resources in the soil (Craine and Dybzinski, 2013; Dybzinski and Tilman, 2007), visits from shared pollinators (Lanuza, Bartomeus, and Godoy, 2018), or the frequency and intensity of disturbance events (Pickett, 1980; Villarreal-Barajas and Martorell, 2009). Notwithstanding their importance, fully including all such phenomena in the study of plant dynamics is often impractical. Hence, it is more straightforward to treat these processes implicitly and model the relationship between interacting species phenomenologically, for example by fitting models that describe how the densities of intraspecific and interspecific neighbors change plant fitness and growth (Adler et al., 2018; Case, 1999).

Despite their “necessary incompleteness”, phenomenological models can accurately reproduce the observed data in various natural systems and contexts (Bolker, 2008). Perhaps more importantly, they are useful tools with which to make predictions that extend beyond the phenomena they describe. Such predictions are possible because of the implicit assumption that models that reproduce the observed data faithfully also capture how the studied system operates (Marquet et al., 2015). For example, models that describe the effects neighboring plants have on each other can be used to make quantitative predictions about changes of biomass in the system (Godoy et al., 2020; Lai et al., 2020) or qualitative predictions such as whether or not co-occurring plant species can coexist (Levine and HilleRisLambers, 2009; Zepeda and Martorell, 2019).

The practicality of phenomenological models of plant competition, however, is a double-edged sword. Indeed, predictions made with them are subject to uncertainty arising from many distinct sources. One of these is environmental context dependency, or the extent to which the outcomes of species interactions change as a function of the abiotic conditions species experience (Chamberlain, Bronstein, and Rudgers, 2014). Many studies have documented how the sign and magnitude of species interactions change with environmental conditions, such as interspecific interactions between plants switching from competitive to facilitative in harsh environments (Brooker et al., 2008; Callaway et al., 2002; Maestre et al., 2009; Maestre, Valladares, and Reynolds, 2005), changes to the identity of the competitive superior plant species as abiotic conditions change (Dybzinski and Tilman, 2007; Poorter and Lambers, 1986), or variations in interaction strength between plants along environmental gradients (Bimler et al., 2018; Lanuza, Bartomeus, and Godoy, 2018; Villarreal-Barajas and Martorell, 2009). Extrapolations from phenomenological models of plant competition can therefore be highly specific to the set of conditions under which models were parameterized (Bimler et al., 2018).

Model-based predictions are also subject to two forms of uncertainty that arise from the use of models themselves: parameter sensitivity and structural sensitivity. Parameter sensitivity refers to the sensitivity of model outputs to variation in parameter values (Flora et al., 2011), and exploring it constitutes a routine analysis in the domain of the biological sciences (Jørgensen and Bendoricchio, 2001). On the other hand, structural sensitivity characterizes how mathematical expressions that have similar phenomenological behavior can produce qualitatively different outcomes (Aldebert and Stouffer, 2018; Flora et al., 2011; Myerscough, Darwen, and Hogarth, 1996). Parameter and structural sensitivity are often intertwined (Wood and Thomas, 1999), and both have been shown to drastically change model predictions in a vast array of biological systems (Aldebert and Stouffer, 2018; Flora et al., 2011; Fussmann and Blasius, 2005; Poggiale et al., 2010; Wood and Thomas, 1999).

The interplay between environmental context dependency, parameter sensitivity, and structural sensitivity is rarely explored simultaneously, and to the best of our knowledge has never been explicitly explored in the case of models of density dependence in plant performance. In this study, we therefore aim to understand how these three sources of uncertainty change predictions of a widely studied and vastly important ecological process: species coexistence. We focused our analysis on annual plants, which is a common natural system used to study species coexistence (Godoy and Levine, 2014; Levine and HilleRisLambers, 2009; Mayfield and Stouffer, 2017; Zepeda and Martorell, 2019). We assessed the empirical relevance of the three different sources of uncertainty by making coexistence predictions based around data from a competition experiment between two annual plants conducted in two contrasting abiotic conditions. Our analyses provide evidence that uncertainty can radically change predictions made from a simple competition experiment, and highlights the importance of incorporating uncertainty from different sources in predictions made with phenomenological models.

## METHODS

We will first provide a mathematical description of how to make and interpret coexistence predictions made with a single phenomenological model of two species of annual plants growing in proximity to each other. We then expand our framework to introduce an alternative phenomenological model of plant density dependence, and show how our framework can be used to make predictions using a different model per species. Second, we describe how to use a Bayesian framework to parameterize the aforementioned phenomenological models to data from a set of competition experiments between two annual plants growing in two contrasting abiotic conditions. Finally, we describe how we simultaneously explored structural sensitivity, parameter sensitivity, and environmental context dependency to make predictions of species coexistence.

### *Model-based predictions of species coexistence*

We used the Cohen model (Cohen, 1966; Watkinson, 1980) to describe annual-plant population dynamics and as the starting point for our model-based predictions of species coexistence. This model predicts the number of seeds  $N_{i,t+1}$  from species  $i$  in year  $t + 1$  with:

$$N_{i,t+1} = (1 - g_i)s_iN_{i,t} + g_iN_{i,t}F_{i,t}, \quad (3.1)$$

which is a function of prior number of seeds in the soil ( $N_{i,t}$ ) that survive that year in the seed bank (as weighted by  $s_i$ , the fraction of non-germinating seeds that survive in the soil), and the seeds that germinate (described by  $g_i$ ) multiplied by the number of viable seeds produced per seed germinated, often called their realized fecundity ( $F_{i,t}$ ). The realized fecundity of species  $i$  can be accurately described by many different phenomenological forms (Godwin, Chang, and Cardinale, 2020; Law and Watkinson, 1987). Note that the phenomenological descriptions of  $F_{i,t}$  generally try to capture the density dependence of plant performance on the number of conspecific and heterospecific neighbors, but do not necessarily imply a hypothesis about the mechanisms underpinning this density dependence.

As an example,  $F_{i,t}$  can be given by the Beverton–Holt model (Beverton, 1954), which in a two-species context equals:

$$F_{i,t} = \frac{\lambda_i}{1 + \alpha_{ii}g_iN_{i,t} + \alpha_{ij}g_jN_{j,t}}. \quad (3.2)$$

In this model, the per germinant fecundity of species  $i$  in the absence of competition is described by the parameter  $\lambda_i$ , while the numbers of germinants of species  $i$  and  $j$  in year  $t$  are given by  $g_iN_{i,t}$  and  $g_jN_{j,t}$ , respectively. The density-dependent effects are captured by the interaction coefficients  $\alpha_{ii}$  and  $\alpha_{ij}$ , which describe the interaction strength of conspecifics and heterospecifics, respectively. The Beverton–Holt model is a commonly used phenomenological model to make coexistence predictions and can be easily parameterized with empirical observations of annual plants growing in proximity to each other (Godoy, Kraft, and Levine, 2014; Godoy and Levine, 2014; Levine and HilleRisLambers, 2009).

### *Coexistence predictions*

From the population dynamics that result from using Eqn. 3.1 and estimates of the relevant parameters of Eqns. 3.1 and 3.2, it is possible to predict if a pair of species can coexist. Multiple approaches exist to predict species coexistence (Barabás, D’Andrea, and Stump, 2018; Chesson, 2000, 2018; Letten, Ke, and Fukami, 2017; Saavedra et al., 2017). One of them is to directly evaluate,

given the competitive constraints each species experiences, if the set of species intrinsic growth rates is feasible (i.e., if there exists an equilibrium point under which both species have positive abundances; Rohr, Saavedra, and Bascompte, 2014; Saavedra et al., 2017). To do so, it is necessary to derive the equations determining the equilibrium density for each species, which for species  $i$  is found at:

$$\frac{N_{i,t+1}}{N_{i,t}} = (1 - g_i)s_i + \frac{g_i\lambda_i}{1 + \alpha_{ii}g_jN_i^* + \alpha_{ij}g_jN_j^*} = 1. \quad (3.3)$$

This equilibrium condition can be arranged to provide a linear equation in terms of seed densities:

$$-1 + \left( \frac{g_i\lambda_i}{1 - (1 - g_i)s_i} \right) = \alpha_{ii}g_iN_i^* + \alpha_{ij}g_jN_j^*. \quad (3.4)$$

For reasons that will hopefully become clear later, Eqn. 3.4 can be rewritten as:

$$r_i = \alpha_{ii}g_iN_i^* + \alpha_{ij}g_jN_j^*, \quad (3.5)$$

where  $r_i$  is the intrinsic growth rate of species  $i$ . Note that  $r_i$  is a composite parameter that depends on the values of  $s_i$ ,  $g_i$ , and  $\lambda_i$ . Equivalent expressions for species  $j$  can be derived from its equilibrium condition. The combined two-species equilibrium condition is:

$$\begin{bmatrix} r_i \\ r_j \end{bmatrix} = \begin{bmatrix} \alpha_{ii} & \alpha_{ij} \\ \alpha_{ji} & \alpha_{jj} \end{bmatrix} \begin{bmatrix} g_iN_i^* \\ g_jN_j^* \end{bmatrix}. \quad (3.6)$$

Given estimates of  $r_i$ ,  $r_j$ , and the matrix of competition coefficients,  $A$ , predicted species densities at equilibrium can be solved for by rearranging Eqn. 3.6 to:

$$\begin{bmatrix} g_iN_i^* \\ g_jN_j^* \end{bmatrix} = A^{-1} \begin{bmatrix} r_i \\ r_j \end{bmatrix}. \quad (3.7)$$

When predicted equilibrium abundances for both species are positive, then the model-based prediction is that they can coexist (Rohr, Saavedra, and Bascompte, 2014; Saavedra et al., 2017). In contrast, if one of the predicted equilibrium abundances is less or equal to zero, then model-based predictions is that one of the species is competitively excluding the other. Finally, if both predicted equilibrium abundances are less or equal to zero, then none of the species can persist in the system according to the model used to make predictions.

### *Biologically-constrained feasibility domain*

In practice, it is useful not only to determine if fixed values of  $r_i$  and  $r_j$  allow species to coexist, but to explore the full set of values of species growth rates that are compatible with species coexistence. This approach is often referred to as *the structural approach*, and is easily applicable to annual-plant dynamics (Saavedra et al., 2017). The parameter space where both species can have positive abundances at equilibrium, given the constraints imposed through the competition matrix, is called the feasibility domain (Rohr, Saavedra, and Bascompte, 2014; Saavedra et al., 2017; Song, Rohr, and Saavedra, 2018; Song et al., 2020). Biologically, a large feasibility domain means that competition is lax, and species can grow at different rates without excluding each other. In contrast, a small feasibility domain means that competitive constraints are harsh, and only a handful of growth rates allow their coexistence.

Importantly, locations in the growth-rate parameter space carry direct biological interpretations with them. Consider, for example, a growth-rate vector  $r$  that allows for positive equilibrium abundances  $N$ . Any proportional vector  $xr$  will also produce  $xN$  as a solution to Eqn. 3.7. However, it is reasonable to assume that there exists an upper limit to species' abundances in nature (i.e., we do not expect species to achieve infinite abundances). If a growth-rate vector leads to predicted abundances beyond a particular species' observable limit, we argue it should not be considered biologically feasible. The imposition of an abundance constraint such as this one will tend to create an upper bound on the growth rates that define the feasibility domain.

In addition, the Beverton–Holt model implicitly imposes further biological constraints on the values species growth rates can take. Recall that a species' composite growth rate,  $r_i$ , is a product of three biologically-meaningful parameters. Those parameters have bounds themselves and when combined together they can further impact the values species' composite growth rates can take. Specifically,  $s_i$  and  $g_i$  are proportions and can only have values between zero and one, while the per germinant fecundity in the absence of competition  $\lambda_i$  can only have positive values. By assuming density dependence for a given species follows the Beverton–Holt model, these parameter constraints together imply that growth rates  $r_i < -1$  are not biologically feasible. Any value of  $r_i < -1$  corresponds to  $\left(\frac{g_i \lambda_i}{1 - (1 - g_i)s_i}\right) < 0$ . But for this second condition to be met, we require either  $1 - (1 - g_i)s_i < 0$  or  $g_i \lambda_i < 0$ . Since  $s_i$  and  $g_i$  are proportions,  $1 - (1 - g_i)s_i$  can never be lower than zero. Thus, the only way to obtain  $r_i < -1$  is for species  $i$  to have a negative intrinsic fecundity ( $\lambda_i < 0$ ), which is not biologically plausible. Note, however, that the Beverton–Holt model itself imposes no upper bound to species' composite growth rates. These lower and upper bounds are specific to the Beverton–Holt model. As we will note later, different models of density-dependent fecundity will have different bounds.



Building upon previous approaches, we called the parameter space where both species can have positive abundances given a) intra and interspecific competition, b) constraints on species abundances, and c) the constraints imposed by each phenomenological model of competition, the biologically-constrained feasibility domain. In the two species case, the biologically-constrained feasibility domain can also be expressed as an area, that we called  $\beta$ . We estimated the size of  $\beta$  using Monte Carlo integration methods as described in [Chapter 7](#), and show an example in [Fig. 3.1](#).

### *Distance from the edge*

If two species' set of growth rates  $r_i$  and  $r_j$  are inside  $\beta$ , the two species are predicted to coexist. But there is more information contained in this comparison than a yes or no outcome. For example, the further those growth rates are from the edge of  $\beta$ , the less likely it is that perturbations to them will change the coexistence prediction. The minimum distance from the set of growth rates to the edge of  $\beta$  is a measure of the susceptibility of qualitative coexistence predictions to perturbations of species' growth rates and interactions. We called this minimum distance  $\delta$ . To indicate when species growth rates are outside  $\beta$ , we multiplied  $\delta$  by negative one. Large, positive values of  $\delta$  thus imply species are confidently coexisting, large negative values imply species are confidently excluding each other, and values closer to zero imply small perturbations might change the predicted outcomes. We describe how exactly we quantify  $\delta$  in [Chapter 7](#).

### *Relative coexistence ratio*

As a basis of comparison, it is also convenient to quantify the parameter space that allows both species to grow in monoculture. Importantly, this parameter space can also be expressed as an area, and this area is also subject to abundance and model constraints. We called this area  $\gamma$ , and mathematical details of how to calculate the size of it can be found in [Chapter 7](#). By comparing the size of the parameter space where both species can coexist ( $\beta$ ) to the size of the space where species can grow in monoculture ( $\gamma$ ), we can quantify the importance of interspecific interactions relative to intraspecific interactions. This comparison can be expressed as a ratio  $\rho$  that we call the relative coexistence ratio. If this ratio is equal to one, then species coexistence is as likely as species growing in monoculture; if this ratio is lower than one, then the parameter space where the two species can coexist is smaller than the parameter space where each species can grow in monoculture, and it is less likely they can coexist when interacting; finally, ratios bigger than one imply that species facilitate each other, and it is more likely for them to coexist when interacting than to grow in monoculture. We show an example of how different values of  $\beta$  and  $\gamma$  determine the values of  $\rho$ , as well as their relationship to the distance from the edge  $\delta$  in [Fig. 3.2](#).

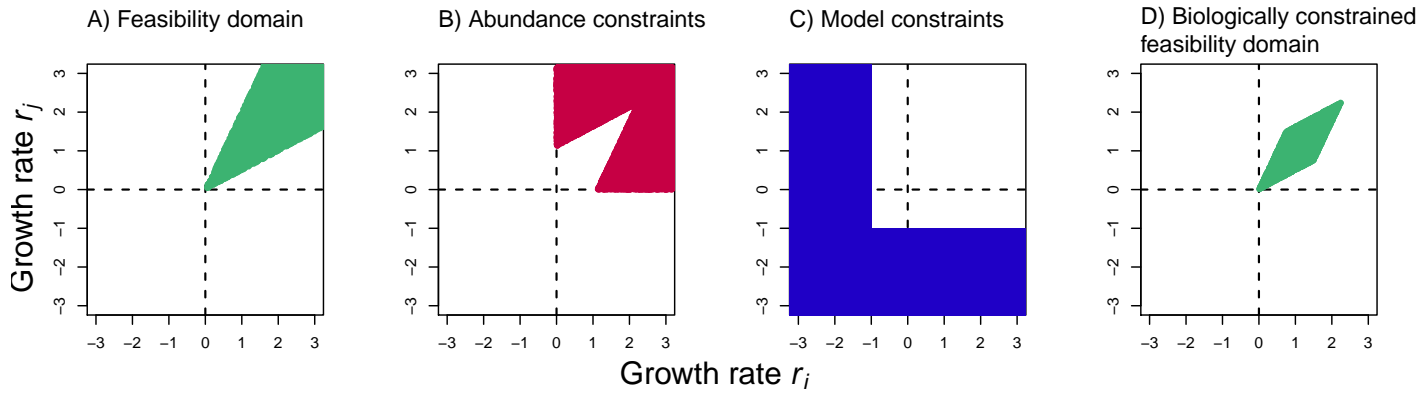


Figure 3.1: Estimation of the biologically-constrained feasibility domain ( $\beta$ ). A) We show the feasibility domain (green) given a hypothetical competition matrix with intraspecific competition coefficients equal to 1 and interspecific competition coefficients equal to 0.5. B) Part of the parameter space corresponds to species equilibrium abundances that are greater than specified abundance constraints (red). For simplicity, we used the same hypothetical abundance constraints for both species of  $N^* \leq 1.5$ . C) Part of the parameter space also falls outside model-based constraints (blue), assuming both species' density dependence is described by the Beverton–Holt model. D) The space of the feasibility domain that does not overlap with abundance or model-based constraints gives the biologically-constrained feasibility domain ( $\beta$ , green).

### *An alternative model of density dependence*

The Beverton–Holt model is only one of many phenomenological models used to describe density-dependent performance of annual plants. There is no general rule on how to choose the appropriate phenomenological model to describe the effect of species interactions, and it is often a choice governed by mathematical convenience (Mayfield and Stouffer, 2017), the type of study system (Godwin, Chang, and Cardinale, 2020), and the governing paradigm around species interactions (Martyn et al., 2021). Indeed, there exists a plethora of related mathematical expressions that can quantify interactions between plants. One of them is the Ricker model:

$$F_{i,t} = \lambda_i e^{(-\alpha_{ii}g_i N_{i,t} - \alpha_{ij}g_j N_{j,t})}, \quad (3.8)$$

where the interpretation of the parameters remains the same as previously described (Ricker, 1954). The Ricker model is known to be a biologically plausible and versatile model to quantify density dependence in annual plant communities, plus it has the virtue of being better able to capture both competitive and facilitative interactions (Bimler et al., 2018; Mayfield and Stouffer, 2017).

Similar to the process we followed from Eqns. 3.4 to 3.7, the Ricker model has its own expression of growth rate at equilibrium. For species  $i$ , it is given by:

$$r_i = \ln \left( \frac{g_i \lambda_i}{1 - (1 - g_i) s_i} \right). \quad (3.9)$$

This expression necessarily implies that the model constraints on growth rates are different when using the Ricker model than when using the Beverton–Holt model: it has no model-based constraints on the lower and upper bounds of species growth rates. We summarize each of the models presented so far, their expressions of growth rates at equilibrium, and their lower and upper bounds in Table 3.1

### *Multi-model predictions of species coexistence*

By parameterizing a phenomenological model of plant competition, like the Beverton–Holt (Eqn. 3.2), we get a description of how seed set decreases with neighbor density. Perhaps more importantly, by linking this model to Eqn. 3.1 we can make a prediction about whether or not two species are able to coexist. So far, we have been working with the implicit assumption that the same model describes the density dependence of the two species. However, there is no *a priori* reason to assume this is the case, especially in an empirical case where different models can provide comparable fits (Hart, Freckleton, and Levine, 2018).

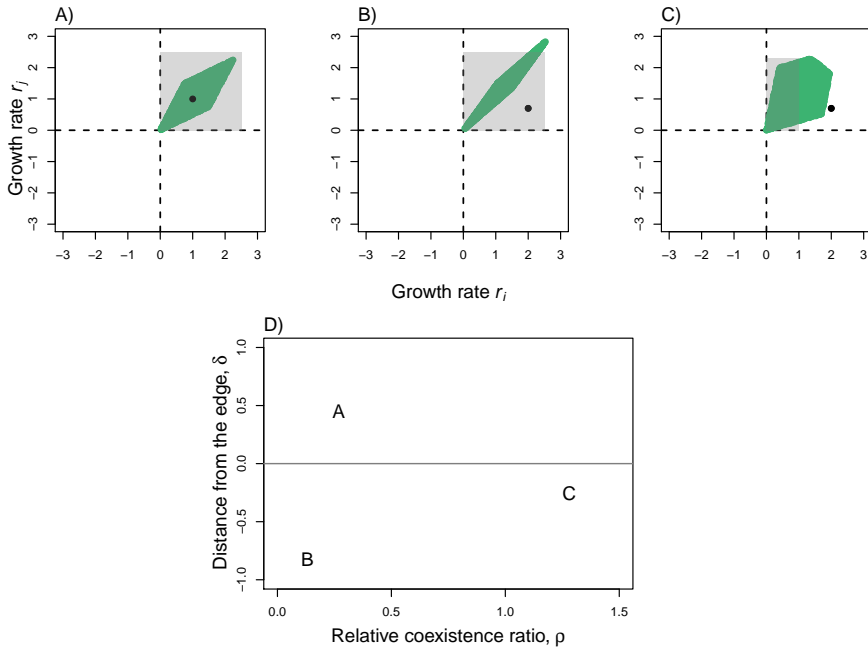


Figure 3.2: Examples of how different values of the biologically-constrained feasibility domain ( $\beta$ ), the area in monoculture ( $\gamma$ ), and species growth rates ( $r_i$  and  $r_j$ ) determine the values of the relative coexistence ratio ( $\rho$ ) and the minimum distance from the edge ( $\delta$ ). In A), B), and C) we show three hypothetical combinations of the biologically-constrained feasibility domain ( $\beta$  in green), the parameter space where species can grow in monoculture ( $\gamma$  in light grey), and a set of species growth rates (black circles). D) We show how the examples shown in A, B, and C correspond to different values of the relative coexistence ratio ( $\rho$ ) and the distance from the edge ( $\delta$ ).

To predict coexistence using a different density-dependence model per species, we still must solve for species equilibrium abundances as a function of growth rates and competition (Eqn. 3.7). Unlike the single-model approach, each species' growth rate has its own formulation based on the model describing each species realized fecundity (Table 3.1). As in the previous approach, if Eqn. 3.7 predicts positive abundances for both species within the bounds of each species' model and abundance constraints, species are predicted to coexist. Importantly, both  $\beta$  and  $\gamma$  become a function of four potential constraints: the set of lower and upper bounds per species. Having imposed those constraints,

Table 3.1: Equilibrium growth rates and model constraints for the two models we used to make coexistence predictions. Growth rates are given by solving each model's equilibrium conditions in terms of seed densities. Upper and lower bounds are the result of how parameter bounds impact the values growth rate can take given the phenomenological model used to quantify density dependence.

Model	Growth rate	Lower bound	Upper bound
Beverton–Holt	$-1 + \left( \frac{g_i \lambda_i}{1 - (1 - g_i) s_i} \right)$	-1	Inf
Ricker	$\ln \left( \frac{g_i \lambda_i}{1 - (1 - g_i) s_i} \right)$	-Inf	Inf

the relative coexistence ratio  $\rho$  and the distance from the edge  $\delta$  can again be calculated as described previously.

### *The interplay of different forms of uncertainty*

#### *Data*

To assess the empirical relevance of different sources of uncertainty, we made coexistence predictions using parameter estimates inferred directly from a set of competition experiments. During 2017, we conducted pairwise competition experiments between two annual plants, *Vellia rosea* and *Trachymene cyanopetala*. Our experiments took place in the West Perenjori Nature Reserve in Western Australia (−29.479°S, 116.199°E). The reserve is dominated by York gum-jam woodlands, which support an understory of mixed native and exotic annual grasses and forbs (Dwyer et al., 2015).

Using locally-collected seeds, we set up pairwise response–surface experiments. Response–surface experiments vary the densities of both species independently by using treatments with factorial combinations of the two species at two or more densities, and have the advantage of being able to accurately distinguish intra and interspecific competition (Hart, Freckleton, and Levine, 2018; Inouye, 2001). To study how abiotic conditions change coexistence predictions, we conducted the experiments in two contrasting environments: a *woody* environment, where plants interacted within 30 cm of woody debris, and a *open* environment, where plants interacted at least 1 m outside the woody debris.

To implement our response–surface experiments, in October 2017 we first weeded out aboveground biomass of plants inside of circular plots with a 7.5 cm radius. This neighborhood radius is sufficiently large to capture local plant–plant interactions within the study system (Martyn et al., 2021). Each plot was then sown at different densities of each species as a focal: an invasion

density where only one individual was sown, low density (15 seeds in total), medium density (30 seeds in total), and high density (60 seeds in total). In each plot, we also varied the densities with which the non-focal species was sown: either absent, medium or high. Treatments therefore consisted of combinations of the density of each species sown as a focal, the density of each species sown as a competitor, and the environment where interactions took place. We had four replicates per treatment, which yielded 256 plots in total. Plants germinated, and we thinned plots in composition in July 2018 (i.e., we weeded out neighbors that were not originally sowed). We collected the seeds produced after the growing season in October 2018 and also counted the number of conspecifics plant individuals ( $n_i$ ), heterospecifics ( $n_j$ ), and other neighbors ( $n_k$  i.e., plants that germinated after the plots were thinned in composition) in the plot at the time of seed collection.

Finally, we relied on a different set of data to obtain estimates of the survival and germination rates of each of our focal species in the field (Towers et al., 2021), as well as the maximum abundance each species could achieve in the neighborhood radius where interactions took place. We show these values of seed survival rate, germination rate, and maximum abundance per species in [Chapter 7](#).

### *Statistical inference*

We fit Eqns. 3.2 and 3.8 separately for both of our focal species in order to get the relevant parameter estimates necessary to make coexistence predictions. For both species, we fit these non-linear models with a Bayesian framework using Hamiltonian Monte Carlo (HMC) methods. We used Bayesian inference to explicitly incorporate the uncertainty surrounding model parameters in probability distributions (McElreath, 2018). Across all models, we explicitly accounted for the environment where seeds were sown in our parameter estimates. For all of the parameters across all models, we did this by allowing the *woody* environment to act as a dummy variable,  $W$ , that indicates the change in the environmental condition. For example, the fecundity in the absence of competition for species  $i$  while in the *woody* environment would be given by  $\lambda_i + \lambda_{i,w}W$ , where parameters with the subscript  $w$  quantify the change due to the *woody* environment.

For all models and all environmental conditions, we constrained the fecundity in the absence of competition to be positive in order to keep our predictions biologically plausible. However, we did not constrain interaction parameters to be positive, allowing them to capture both competitive and facilitative interactions. Across all model fits, we included an extra term ( $\alpha_{ik}$ ) to account for the effect of unidentified species in the experiment ( $n_k$ ). We fit this extra interaction term to improve the parameter estimates related to our focal species,

but because we do not know their other parameters we could not model coexistence outcomes with these other neighbors.

We assumed the response variable, seeds produced per focal individual, followed a Poisson distribution for both species. Consequently we fit our non-linear models using the Poisson family and the identity link. We used the same weakly informative priors for the parameters in the Beverton–Holt model (Eqn. 3.2) and the Ricker model (Eqn. 3.8). As an example, the full description of the Beverton–Holt model for species  $i$  is:

$$F_i \sim \text{Poisson}(\rho_i) \quad (3.10)$$

$$\rho_i = \frac{e^{\lambda_i + \lambda_{i,w}W}}{1 + (\alpha_{ii} + \alpha_{ii,w}W)n_i + (\alpha_{ij} + \alpha_{ij,w}W)n_j + (\alpha_{ik} + \alpha_{ik,w}W)n_k} \quad (3.11)$$

$$\{\lambda_i, \lambda_{i,w}\} \sim \text{Normal}(0, 1) \quad (3.12)$$

$$\{\alpha_{ii}, \alpha_{ii,w}\} \sim \text{Normal}(0, 1) \quad (3.13)$$

$$\{\alpha_{ij}, \alpha_{ij,w}\} \sim \text{Normal}(0, 1) \quad (3.14)$$

$$\{\alpha_{ik}, \alpha_{ik,w}\} \sim \text{Normal}(0, 1) \quad (3.15)$$

We fit all models using the function *brm* from the package *brms* (Bürkner, 2017) in the statistical program R version 4.0.2 (R Core Team, 2013). For each model, we ran four chains with a warmup of 2000 iterations and 2000 sampling iterations. We determined convergence when trace plots were well mixed and stationary and when the Gelman–Rubin convergence diagnostic (Rhat) was less than 1.05 for all parameters (Vehtari et al., 2020).

We compared the fits of each model for each species using the Leave-One-Out cross-validation Information Criteria (LOOIC). This goodness of fit measure is used for estimating the out-of-sample prediction accuracy of Bayesian models and provides a measure of model fit that is penalized for the number of model parameters. As with other information criteria, lower values of LOOIC correspond to better supported models. Additionally, LOOIC is more robust for models with weak priors or influential observations compared to other information criteria (Vehtari, Gelman, and Gabry, 2017). We calculated out-of-sample deviance separately for models in *open* and *woody* environments because LOOIC is calculated additively over observations. We also calculated Akaike weights for each model in each environmental condition, which can be interpreted as an estimate of the probability that the model will make the best predictions of new data, based on the set of models considered (McElreath, 2018).

### *Predictions incorporating uncertainty*

To study how model formulation changes predictions of species coexistence, we used our framework to make predictions using median parameter estimates and a different model per species (Eqn. 3.2 or 3.8). We examined all the possible combinations of each species being defined by a different model, which yielded a total of 4 different predictions. Furthermore, we also explored how abiotic conditions change predicted coexistence outcomes by making predictions using median parameter estimates in the *open* and *woody* condition. We therefore had a total of 8 coexistence predictions (4 for each environmental condition), as well as the corresponding values of  $\beta$ ,  $\gamma$ ,  $\rho$ , and  $\delta$ .

To incorporate parameter uncertainty, we made predictions using 500 draws from the parameters' posterior distributions. For each of the 8 predictions made using median parameter values, this gives us 500 additional coexistence predictions. Posterior distributions of parameters contain the relative plausibility of different parameter values, conditional on the data and the model we used (McElreath, 2018). This approach yielded a posterior distribution of coexistence outcomes, as well as distributions of  $\beta$ ,  $\gamma$ ,  $\rho$ , and  $\delta$  values.

For each model combination and each environmental condition, we determined the proportion of posterior predictions that predicted coexistence and competitive exclusion driven by *Vellia rosea* or *Trachymene cyanopetala*. We also calculated the combined LOOIC and weight for each model combination as the sum and product of both model's LOOIC and weights, respectively. Finally, we defined the weighted average of our coexistence predictions as the combined model weight in a given environmental condition, and the proportion of coexistence outcomes. Our approach thus allowed us to not only make predictions incorporating one source of uncertainty at a time but to integrate multiple sources of uncertainty together into a probabilistic interpretation of species coexistence.

## RESULTS

Model comparison using LOOIC showed that the Beverton–Holt model was the preferred model for both species in both environments since it consistently had the lowest LOOIC score (Table 3.2). However, Akaike weights showed that the Ricker model shared some of probability to make the best prediction of new data for the species *Vellia rosea* in both environments (Table 3.2). Indeed, some parameter values and their distributions overlap between the two models for both species (Figs. 7.1 and 7.2 in Chapter 7).



Table 3.2: Model comparison in the *open* and *woody* environments. LOOIC (leave-one-out cross-validation information criteria) penalizes models for the number of parameters, and the lowest value reflects the best-performing model. The weight for each model is an estimate of the probability that the model will make the best predictions of new data based on the the set of models considered.

Species	Model	Open		Woody	
		LOOIC	Weight	LOOIC	Weight
<i>Vellia rosea</i>	Beverton–Holt	1001.16	0.99	1006.80	0.95
<i>Vellia rosea</i>	Ricker	1017.99	0.01	1018.44	0.05
<i>Trachymene cyanopetala</i>	Beverton–Holt	2025.51	1.00	2049.27	1.00
<i>Trachymene cyanopetala</i>	Ricker	2048.80	0.00	2082.25	0.00

### *Structural sensitivity in the open environment*

In the *open* environment, median predictions of species coexistence were contingent on the model formulation used for both species (triangles on Fig. 3.3). We predicted *Vellia rosea* and *Trachymene cyanopetala* would coexist in three of the model combinations we explored, while we predicted competitive exclusion of *Vellia rosea* when the predictions used the Ricker model for *Vellia rosea* and the Beverton–Holt model for *Trachymene cyanopetala* (Fig. 3.3) .

We predicted the median relative coexistence ratio ( $\rho$ ) would be around 0.5 for all of the model combinations examined, implying that interspecific interactions were competitive and approximately half the magnitude of intraspecific interactions (Fig. 3.3). On the other hand, the distance from the edge ( $\delta$ ) was close to zero for three of the model combinations we explored (Fig. 3.3). That is, in the *open* environment, median predictions of species coexistence—whether they predicted coexistence or competitive exclusion—were likely susceptible to change given small perturbations to either species growth rates or interaction coefficients.

### *Structural sensitivity & environmental context dependency*

The consequences of structural sensitivity were different when interactions took place in the *woody* environment. We predicted species coexistence in only one of the four model combinations we explored: when median predictions used the Beverton–Holt model for *Vellia rosea* and the Ricker model for *Trachymene cyanopetala* (Fig. 3.4). That is, when we made predictions in the *woody* environment, median parameter values mostly predicted competitive exclusion. However, unlike median predictions made for the *open* environment, *Trachymene cyanopetala* was predicted to be competitively excluded instead of *Vellia rosea* (Fig. 3.4). Additionally, our median estimates of  $\rho$  were higher in

the woody environment for 2 out of 4 model combinations examined (Fig. 3.4). Note that  $\rho$  values above one indicate that it is more likely for species to coexist when growing together than when growing in monoculture.

In the *woody* environment, estimates of  $\delta$  were mostly negative (Fig. 3.4). That is, for most of the model combinations we examined, species growth rates were far away from the biologically-constrained feasibility domain, and the coexistence outcome unlikely to change given small perturbations. These values of  $\delta$  seem to be driving the changes in coexistence outcomes regardless of the values of  $\rho$ . Similar to the *open* environment, the value of  $\delta$  was positive and close to zero in the one instance where we predicted species coexistence.

### *Structural sensitivity, environmental context dependency & parameter sensitivity*

Predictions made with the posterior distribution of parameter values could be quantitatively and qualitatively very different to predictions made with median parameter values (Figs. 3.3 and 3.4). Importantly, the extent of parameter sensitivity depended on the models used and the environment where interactions took place. When species were interacting in the *open* environment, we predicted both competitive exclusion and coexistence regardless of the outcome of the median prediction (Fig. 3.3). For posterior predictions of competitive exclusion, the species predicted to competitively exclude the other varied between model combinations and posterior draws (Fig. 3.3). The proportion of posterior draws that predicted coexistence ranged from 96% to 33%, depending on the model combination used to make predictions (Table 3.3).

In contrast, when interactions took place in the *woody* environment most of the posterior predictions resulted in competitive exclusion (Fig. 3.4). For 3 out of 4 model combinations examined, the proportion of posterior draws that predicted coexistence was less than 10% (Table 3.4). However, the outcome of competitive exclusion varied between posterior predictions. That is, even if species were predicted to be confidently experiencing competitive exclusion, the outcome of competition was uncertain (Fig. 3.4).

The probability of predicting species coexistence given each phenomenological model used and the proportion of posterior predictions of coexistence was 67% in the *open* environment when we used the Beverton–Holt model to describe the dynamics of both species (Table 3.3). Other model combinations had little statistical support (Table 3.3). Similarly, in the *woody* environment, the model combination where the Beverton–Holt model described the dynamics of both species had most of the statistical support (Table 3.4). However, that model combination also confidently predicted competitive exclusion (Table 3.4). Other model combinations in the *woody* environment varied in their extent

of posterior draws that predicted coexistence, however, they also had little statistical support (Table 3.4).

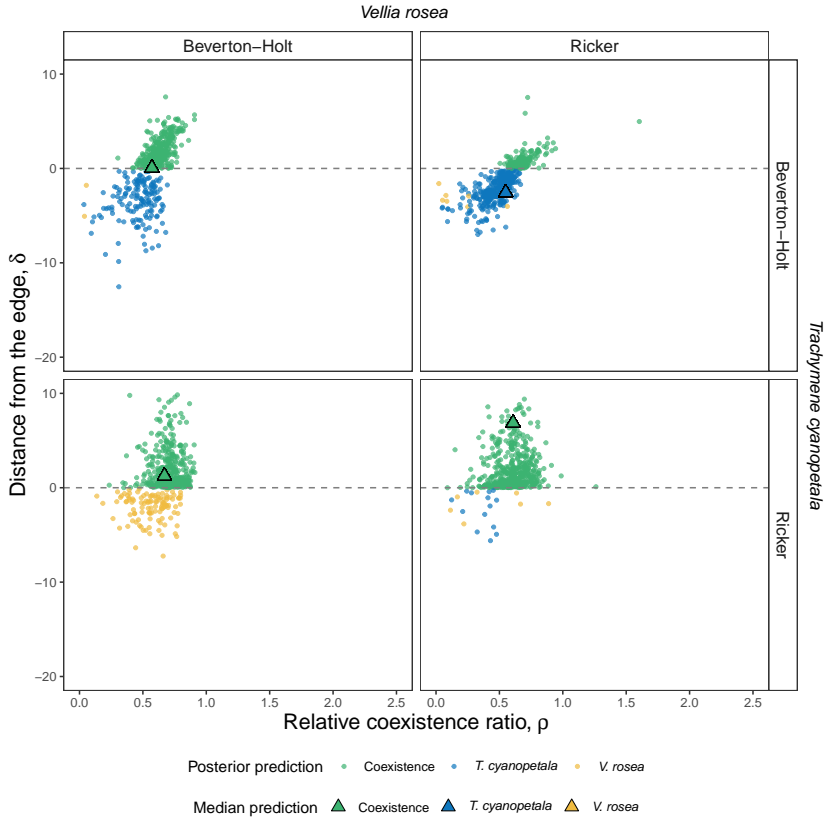


Figure 3.3: Predictions made with different model combinations in the *open* environment. Each panel corresponds to a different model combination, labels on the top indicate the model used for the species *Vellia rosea*, and labels on the right show the model used for *Trachymene cyanopetala*. In each panel, we show median estimates of  $\rho$  and  $\delta$  (triangles), and the color of these estimates indicates coexistence (green), competitive exclusion by *Vellia rosea* (yellow), and competitive exclusion by *Trachymene cyanopetala* (blue). Finally, we show the 500 predictions made using posterior draws of parameter values (circles) with the same color scheme.

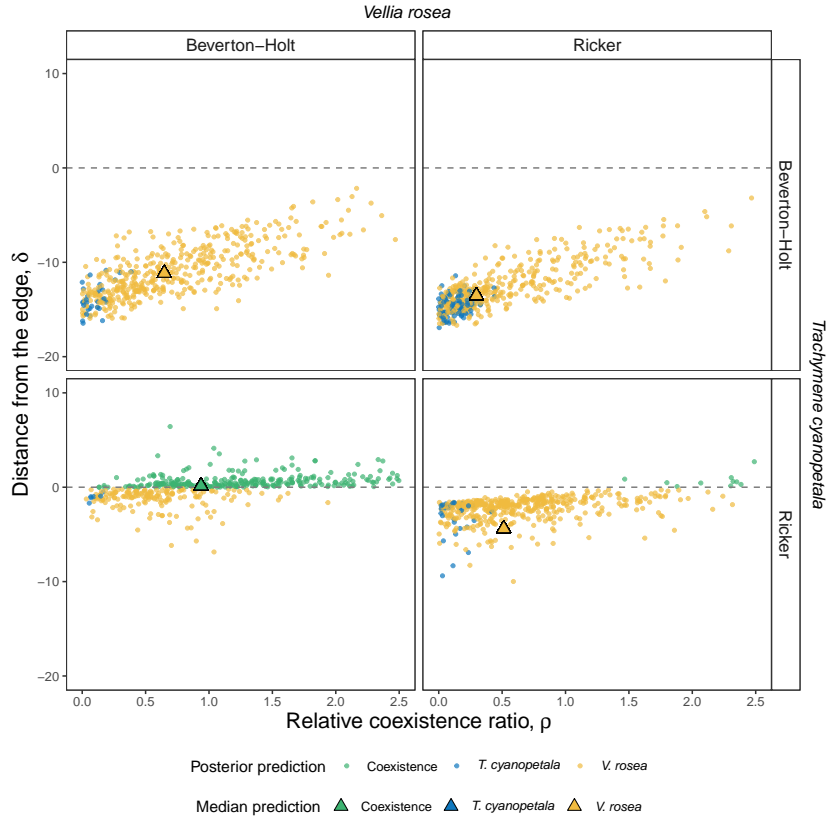


Figure 3.4: Predictions made with different model combinations in the *woody* environment. Each panel corresponds to a different model combination, labels on the top indicate the model used for the species *Vellia rosea*, and labels on the right show the model used for *Trachymene cyanopetala*. In each panel, we show median estimates of  $\rho$  and  $\delta$  (triangles), and the color of these estimates indicates coexistence (green), competitive exclusion by *Vellia rosea* (yellow), and competitive exclusion by *Trachymene cyanopetala* (blue). Finally, we show the 500 predictions made using posterior draws of parameter values (circles) with the same color scheme.

Table 3.3: Combined LOOIC, weights and proportion of coexistence for different model combinations in the *open* environment. Combined LOOIC and weights were calculated as the sum and product of both model's LOOIC and weights, respectively. Proportion of coexistence quantifies the proportion of coexistence predictions relative to competitive exclusion predictions for each model combination.

<i>V. rosea</i> model	<i>T. cyanopetala</i> model	Combined LOOIC	Combined weight	Proportion <i>V. rosea</i> wins	Proportion <i>T. cyanopetala</i> wins	Proportion of coexistence
Beverton–Holt	Beverton–Holt	3026.66	0.99	0.01	0.31	0.68
Ricker	Beverton–Holt	3043.50	0.01	0.02	0.66	0.33
Beverton–Holt	Ricker	3049.96	0.00	0.22	0.00	0.78
Ricker	Ricker	3066.79	0.00	0.01	0.03	0.96

Table 3.4: Combined LOOIC, weights and proportion of coexistence for different model combinations in the *woody* environment. Combined LOOIC and weights were calculated as the sum and product of both model's LOOIC and weights, respectively. Proportion of coexistence quantifies the proportion of coexistence predictions relative to competitive exclusion predictions for each model combination.

<i>V. rosea</i> model	<i>T. cyanopetala</i> model	Combined LOOIC	Combined weight	Proportion <i>V. rosea</i> wins	Proportion <i>T. cyanopetala</i> wins	Proportion of coexistence
Beverton–Holt	Beverton–Holt	3056.07	0.95	0.93	0.06	0.01
Ricker	Beverton–Holt	367.71	0.05	0.78	0.22	0.00
Beverton–Holt	Ricker	3089.05	0.00	0.34	0.01	0.65
Ricker	Ricker	3100.69	0.00	0.88	0.07	0.05

### *The drivers of parameter sensitivity*

To better understand parameter sensitivity, we made predictions of  $\beta$ ,  $\gamma$ ,  $\rho$ , and  $\delta$  holding all parameters but one at their median estimate and for the other we used draws from its posterior distribution (Fig. 3.5). Since it was consistently the best fit model, we used the Beverton–Holt model for both species. We found that parameter sensitivity was driven mostly by a few key parameters. In both environments, predictions that substantially deviated from the median prediction were mainly driven by uncertainty surrounding the competitive effects of *Trachymene cyanopetala* (Fig. 3.5).

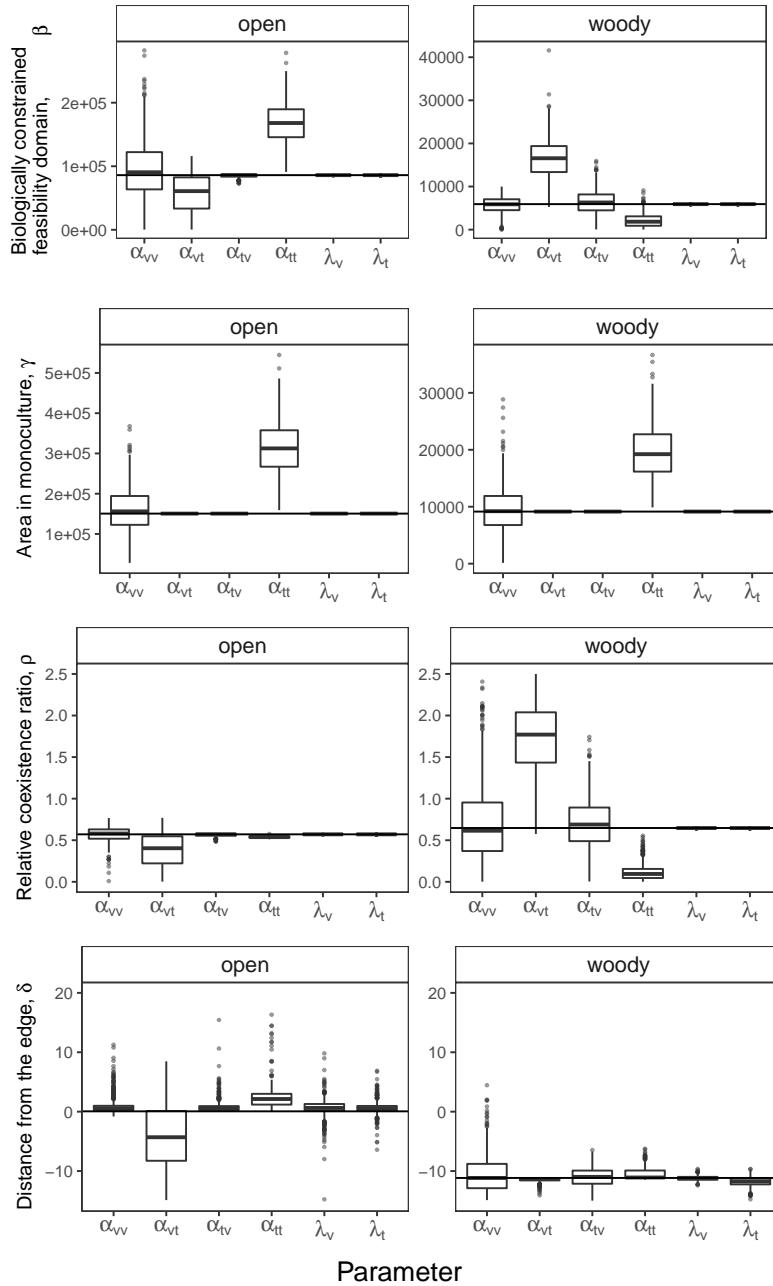


Figure 3.5: Predictions of  $\beta$ ,  $\gamma$ ,  $\rho$ , and  $\delta$  made while including the posterior distribution of each parameter separately and using the Beverton–Holt model for both species in both environments. The parameter names on the x-axis denote the parameter whose distribution was sampled from. The subscript  $v$  in parameter names denotes the species *Vellia rosea*, while the subscript  $t$  denotes the species *Trachymene cyanopetala*. The solid black line in each panel denotes predictions when all parameters are set to their median estimates. Each boxplot extends from the first to third quantiles of the corresponding posterior predictions and the line inside the box indicates the median posterior prediction.

## DISCUSSION

Our results show that using phenomenological models to predict whether or not a pair of species can coexist is far from a trivial matter. Indeed, even seemingly subtle differences led to predictions of both coexistence and competitive exclusion based around the exact same experimental data. Even in the cases where we predicted competitive exclusion, the predicted dominant species varied between predictions. Nonetheless, our analyses also showed that the uncertainty surrounding our predictions can be dismantled and understood by understanding differences between models, the environment where models were parameterized, and the uncertainty associated to certain parameter values.

In our experimental system, the Beverton–Holt model was the best phenomenological description of how seed set changed with neighbor density, for both species in both environments (Table 3.2). The Beverton–Holt model frequently provides a good phenomenological fit for annual plant data (Godoy, Kraft, and Levine, 2014; Godoy and Levine, 2014; Levine and HilleRisLambers, 2009). However, the Ricker model shared some of the model weight with the Beverton–Holt model for *Vellia rosea* in our experimental system, in both environmental conditions (Table 3.2). It is often the case in annual-plant studies that more than one phenomenological model has statistical support for different species or sites (Bimler et al., 2018; Levine and HilleRisLambers, 2009; Martyn et al., 2021; Mayfield and Stouffer, 2017). Nonetheless, exploring predictions made by more than one model is not common practice in the study of species coexistence, unlike the study of other ecological processes like predator–prey dynamics (Aldebert and Stouffer, 2018; Fussmann and Blasius, 2005; Myerscough, Darwen, and Hogarth, 1996). By limiting our predictions to a single type of phenomenological model, we not only have to ignore other models that share statistical support, but we also limit our understanding of how model formulation itself changes our predictions.

### *Small differences, amplified*

We showed that predictions of species coexistence using the annual-plant model are structurally sensitive. Focusing on the *open* environment, median estimates of  $\rho$  and  $\delta$  were similar in all of the model combinations we explored; coexistence outcomes were not (Fig. 3.3). Our study thus provides another clear example where predictions made with different models can be quantitatively similar and still have different qualitative properties, one of the hallmarks of structural sensitivity (Flora et al., 2011). Structural sensitivity can arise because slight perturbations in model formulation become largely amplified (Flora et al., 2011; Wood and Thomas, 1999), and predictions can be structurally sensitive in different ways depending on the qualitative behavior examined (Aldebert

and Stouffer, 2018; Flora et al., 2011). In the case of coexistence outcomes, predictions require the choice of a model to use for each species, which can further amplify small differences between models.

In the *open* environment, we predicted coexistence in 3 out of 4 model combinations we explored (Fig. 3.3). Overall, the Beverton–Holt and the Ricker model predicted intraspecific interactions to be larger than interspecific interactions for both species (Figs. S1 and S2), which tends to promote coexistence since species limit themselves more than what they limit others (Chesson, 2000). We only predicted competitive exclusion when we used the Ricker model for *Vellia rosea* and the Beverton–Holt model for *Trachymene cyanopetala* (Fig. 3.3). The differences between intraspecific and interspecific interactions for *Vellia rosea* predicted by the Ricker model were slightly smaller than the ones predicted by the Beverton–Holt model (Fig. 7.1 in Chapter 7). Furthermore, the fecundity in the absence of competition of *Trachymene cyanopetala* was predicted to be higher by Beverton–Holt model than by the Ricker model (Fig. 7.2 in Chapter 7). These two small differences between models together resulted in a more restricted feasibility domain, and a shift in the position of species growth rates in the parameter space, compared to other model combinations. These changes caused the growth rates to fall outside  $\beta$ ,  $\delta$  to have a negative sign, and to predict the competitive exclusion of *Vellia rosea* (Fig. 3.3).

### *The importance of environmental context*

The extent of structural sensitivity observed in our focal system changed in the *woody* environment. When we made predictions using median parameter estimates in the *woody* environment, 3 out of 4 model combinations predicted competitive exclusion (Fig. 3.4). The increased likelihood of predicting competitive exclusion compared to the *open* environment seemed to be driven by several factors. One of them is that predicted interspecific interactions were larger than intraspecific interactions for *Vellia rosea* using both models (Fig. 7.1 in Chapter 7), which resulted in a smaller  $\beta$  in the *woody* environment. However, since all intraspecific interactions were predicted to be weaker in the *woody* environment compared to the *open* environment for all models (Figs. 7.1 and 7.2 in Chapter 7), the predicted values of  $\gamma$  also decreased. Thus, values of  $\rho$  in the *woody* environment were larger in two out of four cases (Fig. 3.4).

Furthermore, both species were predicted to have lower fecundities in the absence of competition compared to the *open* environment, which supports previous empirical studies that have recorded that plant abundances in this system decline while growing inside litter (Wainwright, Dwyer, and Mayfield, 2017) (Figs. 7.1 and 7.2 in Chapter 7). Of the two species, *Trachymene cyanopetala* was predicted to experience a sharper reduction in seed set by both models (Fig. 7.2, Chapter 7). Thus, in the *woody* environment, reductions in  $\beta$  and changes in the predicted fecundity in the absence of competition



for *Trachymene cyanopetala* resulted in predictions of competitive exclusion of *Trachymene cyanopetala* in three out of four model combinations (Fig. 3.4). Even though the presence of woody debris in semiarid systems can reduce solar radiation and ameliorate drought stress (Wainwright, Dwyer, and Mayfield, 2017), our results suggest that species are less likely to coexist in this environment due to an increase in strength of interspecific interactions for *Vellia rosea*, and a sharp reduction in the seed set of *Trachymene cyanopetala*.

Our results provide another example where interaction strengths, and thus coexistence predictions change with environmental conditions, a result that has been empirically demonstrated before in this system (Bimler et al., 2018; Mayfield and Stouffer, 2017; Wainwright et al., 2017). Other studies have documented that both species indeed change their fecundities while growing inside coarse woody debris, but spatial mechanisms of coexistence between these two species have not been found (Towers et al., 2020). Importantly, the extent of environmental context dependency in our experimental system is determined by the models used to quantify density dependence for both species. That is, the effect of abiotic conditions can be enhanced or diminished in predictions of species coexistence due to use of phenomenological models.

#### *Parameter uncertainty and the probability of predicting species coexistence*

Using a Bayesian Approach to fit models to data also allowed us to have a better understanding of the parameter uncertainty associated with our predictions. Our results showed that estimating pairwise coexistence only using median estimates of parameter values might bypass instances where the uncertainty encompasses outcomes different to the median prediction (Fig. 3.3 and 3.4). Other approaches have incorporated parameter uncertainty in coexistence predictions by propagating standard errors (Matías et al., 2018) or bootstrapping observations (García-Callejas, Godoy, Bartomeus, et al., 2020). However, these approaches were only incorporated to show the robustness of predictions rather than to examine the causes and effects of parameter uncertainty in predictions of species coexistence.

Our results also show that even when we predicted competitive exclusion, the species we predicted to be competitively excluded varied across posterior draws (Fig. 3.3 and 3.4). Other studies that have incorporated posterior distribution of parameter values in coexistence predictions have also encountered this uncertainty regarding the outcome of competition (Terry, Chen, and Lewis, 2021). However, they also found that posterior predictions mostly agree with predictions using median parameter values (i.e., species were confidently coexisting or not) (Terry, Chen, and Lewis, 2021). Our results did not show as clear differences, particularly in the *open* environment where species were very close to the coexistence boundary (Fig. 3.3).

Importantly, the effect parameter sensitivity on predictions of species coexistence has been mostly interpreted as statements of uncertainty in the underlying data, rather than implying a probabilistic outcome (Matías et al., 2018; Terry, Chen, and Lewis, 2021). Our study goes beyond that interpretation by combining model weights and posterior predictions to calculate the probability of predicting coexistence given the phenomenological models used to quantify density dependence. Our results suggest that given the uncertainty associated with our predictions, coexistence between *Vellia rosea* and *Trachymene cyanopetala* is likely in the *open* environment (Table 3.3) and virtually impossible in the *woody* environment (Table 3.4).

Finally, our results also suggest that parameter sensitivity is mostly driven by the uncertainty of the competitive effect of *Trachymene cyanopetala* (Fig. 3.5). Indeed, the posterior distribution of parameter values in the Beverton–Holt model that best captured the effect of *Trachymene cyanopetala*, encompass a larger range of values compared to other competition coefficients (Fig. 7.2 in Chapter 7). More accurate predictions of coexistence can be achieved by improving the estimates of parameters associated to the competitive effect of this species, for example with a separate experiment designed exclusively to capture the effects of *Trachymene cyanopetala* on itself and on *Vellia rosea*.

## Conclusion

Predictions of species coexistence constitute the building blocks for many ecological studies, such as community assembly (Grainger et al., 2019; HilleRisLambers et al., 2012; Kraft et al., 2015), the evolution of competitive communities (Letten, Hall, and Levine, 2021; Pastore et al., 2021), or the role of species richness in ecosystem functioning (Godoy et al., 2020). Many of these studies rely on phenomenological models of plant competition as the basis of their predictions. Species coexistence is determined by multi-level processes acting simultaneously, and studying it often involves a process of abstraction from the reality to mathematical objects such as phenomenological models (Levins, 2006). Structural sensitivity is likely to arise when multi-level processes are summarized into equations after adopting assumptions regarding the complexity of the biological system (Aldebert and Stouffer, 2018), making predictions of species coexistence made with phenomenological models particularly vulnerable. Furthermore our study has shown that different phenomenological models can enhance or diminish the effect of environmental context-dependency and parameter sensitivity, and thus our predictions of species coexistence. Overall, our study demonstrates that the interplay between different sources of uncertainty should not be ignored when we make predictions based on phenomenological models of plant competition.

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## QUANTIFYING THE RELATIVE CONTRIBUTIONS OF ENVIRONMENTAL FLUCTUATIONS TO THE MAINTENANCE OF A SEXUALLY ANTAGONISTIC POLYMORPHISM

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### ABSTRACT

Sexually antagonistic selection occurs when the direction of selection on traits or loci differs between the sexes. Sexually antagonistic selection can maintain disadvantageous alleles in a population, which underpins its importance in maintaining polymorphism in populations with separate sexes. Importantly, theoretical studies have shown that the balancing effect of sexually antagonistic selection can increase with environmental fluctuations. Nonetheless, the quantification of the contributions of environmental fluctuations to the maintenance of polymorphism remains unknown. Thus, here we explicitly quantify the contributions of temporal fluctuations in population sizes and selection to the polymorphism of sexually antagonistic alleles. We do so by adopting an ecological framework that quantifies the relative contributions of environmental fluctuations to species growth rates when rare by using simulations. We perform simulations of alleles invading a population while allowing selection and populations sizes to fluctuate over time. Then, we used a *functional decomposition* approach to quantify the relative importance of fluctuations across the selection parameter space. Our results showed that fluctuations in selection against one allele contributed positively to the growth rate of the other allele as an invader. In contrast, fluctuations in population sizes contributed positively to alleles growth rates when rare only when alleles invaded via the fluctuating population. Finally, our results showed the importance of the correlation between fluctuations, as positively correlated fluctuations in selection but negatively correlated fluctuations in population sizes promoted the maintenance of polymorphism. Our study highlights the importance of identifying exactly how environmental drivers contribute to maintaining levels of diversity.

## INTRODUCTION

The question of how genetic variation is maintained despite the effects of selection and drift is central within evolutionary biology (Walsh and Lynch, 2018). Classical explanations include overdominance (heterozygote advantage) or frequency-dependent selection (Hedrick, 2007), but in the modern era of genomic data, all patterns of variation that exceed the expected variation under neutrality tend to be categorized broadly as balancing selection, regardless of the evolutionary mechanism (Mitchell-Olds, Willis, and Goldstein, 2007). In species with separate sexes, balancing selection can arise due to sexually antagonistic selection (Connallon and Clark, 2014), which occurs when the direction of natural selection on traits or loci differs between the sexes (Arnqvist and Rowe, 2013; Lande, 1980).

Sexually antagonistic selection can maintain genetic variation in a population (Chippindale, Gibson, and Rice, 2001; Gavrillets, 2014), which in turn can result in phenotypically distinct sexes that express different morphological, physiological, and behavioral traits (Connallon and Hall, 2018; Mori, Mazza, and Lovari, 2017). Nonetheless, the extent to which sexually antagonistic selection can maintain polymorphism in a population is thought to be limited (Connallon and Clark, 2012; Connallon and Hall, 2018). This is because theoretical studies have found that the necessary parameter conditions that give rise to balancing selection are often highly restrictive (Curtsinger, Service, and Prout, 1994; Hedrick, 1999; Kidwell et al., 1977; Pamilo, 1979). Importantly, the effect of sexually antagonistic selection generally has been studied under strong simplifying assumptions such as constant population sizes and homogeneous environments (Immler, Arnqvist, and Otto, 2012; Kidwell et al., 1977; Pamilo, 1979). Studies that have explored the effect of sexually antagonistic selection with more realistic assumptions, such as temporal fluctuations in selection (Connallon and Hall, 2018) or demographic fluctuations (Connallon and Clark, 2012) have found that polymorphism can be maintained in a much wider set of conditions than classical studies predict. These results suggest that environmental fluctuations are essential to fully understand the effects of sexually antagonistic selection.

The contribution of environmental fluctuations to genetic diversity remains a debated issue in evolutionary biology. Classic theoretical models predict that temporal fluctuations in environmental conditions are unlikely to maintain a genetic polymorphism in haploid populations (Dempster, 1955; Hedrick, 1974, 1986). However, other studies have found that fluctuating selection can maintain genetic variance when populations experience density dependence (Dean, 2005), overlapping generations (Ellner and Hairston Jr, 1994; Ellner and Sasaki, 1996), or when selection occurs on sex-linked traits (Reinhold, 2000). Similarly, temporal changes in population sizes have been shown to aid in the maintenance of genetic variance (Whitlock, 1992) and to mitigate the effect of genetic drift (Nunney, 2002; Pemberton et al., 1996). Importantly, progress

requires more than just identifying *if* environmental fluctuations can maintain genetic diversity in a population, but to quantify *how* exactly they contribute to its maintenance (Ellner, Snyder, and Adler, 2016).

The mechanisms by which environmental fluctuations promote diversity maintenance have been thoroughly studied in ecological contexts (Armstrong and McGehee, 1980; Barabás, D’Andrea, and Stump, 2018; Chesson, 2000; Levins, 1979). From an ecological perspective, polymorphism of sexually antagonistic alleles is equivalent to the coexistence of species, and the fixation of one allele in a population is equivalent to competitive exclusion. Allelic polymorphism can thus be examined through the same lens as the coexistence of competing species (Dean, 2005; Ellner and Hairston Jr, 1994; Ellner and Sasaki, 1996; Schreiber, 2010). A benefit of analyzing evolutionary dynamics through this lens is that the main theoretical framework used to examine how competing species coexist, Modern Coexistence Theory (Barabás, D’Andrea, and Stump, 2018; Chesson, 2000), allows the explicit quantification of how environmental fluctuations contribute to coexistence.

Modern Coexistence Theory posits that coexistence is promoted by processes that give any species, when rare, an advantage over the existing species in a community (Chesson, 1994; Chesson, 2000). Environmental fluctuations can give species advantages when rare if competitors respond differently to limiting competitive factors, a mechanism known as *relative non-linearity* (Chesson, 2000; Ellner, Snyder, and Adler, 2016; Zepeda and Martorell, 2019). Differential responses to environmental fluctuations can further give species advantages when rare if fluctuations in environmental factors covary with competitive factors and species are less sensitive to competition in good environmental conditions, a mechanism known as the *storage effect* (Barabás, D’Andrea, and Stump, 2018; Chesson, 2000; Ellner, Snyder, and Adler, 2016; Schreiber, 2021). This list is not exclusive, as there are a plethora of ways in which environmental heterogeneity can give species advantages when rare (Ellner et al., 2019). Nonetheless, there is no study to our knowledge that directly quantifies how environmental fluctuations contribute to the maintenance of a sexually antagonistic polymorphism under the lens of Modern Coexistence Theory.

The use of Modern Coexistence Theory historically required complex mathematical analysis of the models describing the systems dynamics and restrictive assumptions (Barabás, D’Andrea, and Stump, 2018); however, recent computational approaches allow the quantification of the relative importance of environmental fluctuations to coexistence using simulations (Ellner, Snyder, and Adler, 2016; Ellner et al., 2019; Shoemaker et al., 2020). Here, we seek to explicitly quantify how temporal environmental fluctuations contribute to the maintenance of polymorphism under sexually antagonistic selection by applying recent advances in Modern Coexistence Theory. We examined how fluctuations in selection, fluctuations in population sizes, and its interaction can further or hinder the maintenance of polymorphism. In particular, we

examined i) Can fluctuations in population sizes and selection allow sexually antagonistic alleles to coexist when differences in their fitness would typically not allow them to? and ii) What are the relative contributions of different types of fluctuations that allow or impede two sexually antagonistic alleles to be maintained in a population? Our study provides the tools to analyze sexual antagonism from a novel perspective and contributes to answering long-lasting questions regarding the effect of non-constant environments on genetic diversity.

## METHODS

We first present a model that describes the evolutionary dynamics of sexually antagonistic alleles. We then show how we simulated different scenarios of alleles invading a population, where we allowed selection, population sizes, both, or neither to vary. Finally, we detail how we examined the relative contribution of each type of fluctuation to the maintenance or loss of polymorphism.

### *Population dynamics of sexually antagonistic alleles*

Our model examines evolution at a single, biallelic locus. We further assume the relative fitness of each allele was frequency and density independent. We examine the dynamics of two sexually antagonistic alleles,  $j$  and  $k$ , that affect fitness in the haploid state. The frequencies of each allele in each sex at the beginning of a life-cycle at generation  $t$  are given by:

$$p_{jm,t} = \frac{n_{jm,t}}{N_{m,t}} \quad (4.1)$$

$$p_{jf,t} = \frac{n_{jf,t}}{N_{f,t}} \quad (4.2)$$

$$p_{km,t} = \frac{N_{m,t} - n_{jm,t}}{N_{m,t}} \quad (4.3)$$

$$p_{kf,t} = \frac{N_{f,t} - n_{jf,t}}{N_{f,t}} \quad (4.4)$$

where  $N_{m,t}$  and  $N_{f,t}$  are the total numbers of males and females in the population at generation  $t$ , respectively, while  $n_{jf,t}$  is the number of females  $f$  with allele  $j$ , and  $n_{jm,t}$  is the number of males  $m$  with allele  $j$  at time  $t$ . Since the locus is biallelic, the number of males with allele  $k$  at generation  $t$  is

given by  $n_{km,t} = N_{m,t} - n_{jm,t}$  and the number of females with allele  $k$  by  $n_{kf,t} = N_{f,t} - n_{jf,t}$ .

The individuals in the population mate at random before selection occurs, and therefore the frequency of offspring with allele  $j$  after mating,  $p'_{j,t}$  can be expressed as:

$$p'_{j,t} = \frac{n_{jf,t}}{N_{f,t}} \frac{n_{jm,t}}{N_{m,t}} + \frac{1}{2} \frac{n_{jf,t}}{N_{f,t}} \frac{(N_{m,t} - n_{jm,t})}{N_{m,t}} + \frac{1}{2} \frac{(N_{f,t} - n_{jf,t})}{N_{f,t}} \frac{n_{jm,t}}{N_{m,t}} \quad (4.5)$$

which upon rearranging and simplifying gives:

$$p'_{j,t} = \frac{N_{m,t}n_{jf,t} + N_{f,t}n_{jm,t}}{2N_{f,t}N_{m,t}} \quad (4.6)$$

To illustrate how allele frequencies change through time, we use allele  $j$  as an example. However, an equivalent expression for allele  $k$  can be obtained by interchanging  $k$  subscripts for  $j$  in Eqn. 4.6. Selection acts upon these offspring in order to determine the allelic frequencies in females and males in the generation  $t + 1$ . As an example, the frequency of females with allele  $j$  after selection is given by:

$$p_{jf,t+1} = \frac{n_{jf,t+1}}{N_{f,t+1}} = \frac{p'_{j,t}w_{jf}}{p'_{t,j}w_{jf} + (1 - p'_{t,j})w_{kf}} \quad (4.7)$$

Changes in alleles frequencies can also be expressed in terms of growth rates, which is useful to consider when doing analysis under Modern Coexistence Theory. The logarithmic per capita growth rate of allele  $j$  in females is given by the number of females carrying allele  $j$  after selection divided by the original number of females carrying allele  $j$ :

$$r_{jf,t} = \ln \left( \frac{n_{jf,t+1}}{n_{jf,t}} \right) \quad (4.8)$$

An equivalent expression for the logarithmic per capita growth rate of allele  $j$  in males  $m$  can be obtained by exchanging  $f$  for  $m$  across the various subscripts in Eqn. 4.8. Polymorphism in a sexual population, however, is ultimately influenced by growth and establishment of an allele across both sexes. Therefore, the growth rate of allele  $j$  across the entire population of females *and* males is given by:

$$r_{j,t} = \ln \left( \frac{n_{jf,t+1} + n_{jm,t+1}}{n_{jf,t} + n_{jm,t}} \right) \quad (4.9)$$

An equivalent expression describes  $r_{k,t}$ , the growth rate of allele  $k$ .

Our model further assumed allele  $j$  always has a high fitness in females ( $w_{jf} = 1$ ) with lower fitness in males ( $w_{jm} < 1$ ); and allele  $k$  has a high fitness in males ( $w_{km} = 1$ ) with lower fitness in females ( $w_{kf} < 1$ ). The strength of selection against allele  $j$  in males is therefore  $S_m = 1 - w_{jm}$ , and the strength of selection against allele  $k$  in females is  $S_f = 1 - w_{kf}$ . When population sizes and selection are constant, selection maintains both alleles in the population under the condition that:

$$\frac{S_m}{1 + S_m} < S_f < \frac{S_m}{1 - S_m} \quad (4.10)$$

(Connallon and Hall, 2018; Kidwell et al., 1977; Pamilo, 1979; Patten, Haig, and Ubeda, 2010). Thus, the maintenance of polymorphism of sexually antagonistic alleles is solely determined by the values of  $S_m$  and  $S_f$ . Note that in our model, the values  $S_m$  and  $S_f$  are bounded from 0 to 1. Therefore the parameter space of sexually antagonistic selection is within the range  $0 < S_m, S_f < 1$ . Classic theoretical models predict that, in constant environments, polymorphism is maintained in  $\approx 38\%$  of the parameter space (Connallon, Sharma, and Olito, 2019; Kidwell et al., 1977; Pamilo, 1979). Nonetheless, it is unrealistic to assume population sizes and selection are constant through time. Temporal changes in population densities are ubiquitous in nature (Connallon and Clark, 2012; Reinhold, 2000; Whitlock, 1992). Similarly, the effect of sexual selection has been shown to vary through space and time (Kasumovic et al., 2008). If fluctuations in population sizes or selection values affect the coexistence of sexually antagonistic alleles, it should be reflected in increases or decreases of the proportion of the parameter space across which polymorphism is maintained.

### *Simulations*

We examined the effect of fluctuating population sizes and selection in the maintenance of a genetic polymorphism across the selection parameter space ( $0 < S_m, S_f < 1$ ). To do so, we partitioned the parameter space into a  $50 \times 50$  element grid, which yielded 2500 different pairwise combinations of  $w_{jm}$  and  $w_{kf}$  values. Henceforth, we will refer to the set of combinations of  $w_{jm}$  and  $w_{kf}$  values that make up the parameter space of sexually antagonistic selection as a grid. For each pairwise combination of  $w_{jm}$  and  $w_{kf}$ , as we detail in the next sections, our simulation approach consisted of three main parts. First, we incorporated fluctuations in population sizes and selection into our population dynamics model. Second, we performed simulations to evaluate if both alleles could be maintained in a population when the environment fluctuated. Finally, we determined the relative contribution of each type of fluctuation to the maintenance of each allele.

For each grid, which was our unit of replication, we controlled the effect size of fluctuations in selection ( $\sigma_w$ ) and their correlation ( $\rho_w$ ), as well as the effect size of fluctuations in population sizes ( $\sigma_g$ ) and their correlation ( $\rho_g$ ). We explored all of the combinations of low, intermediate, and high fluctuations in selection and population sizes, with different extents of correlations between fluctuations (Table 4.1). As a control simulation, we set  $\sigma_w = 1e^{-4}$  and  $\sigma_g = 1e^{-4}$ , with no correlation between fluctuations. In total, we explored 378 parameter combinations. We ran ten replicates per parameter combination, which resulted in 3780 grids.

Table 4.1: Parameters used in our simulations to control the effect sizes of fluctuations in population sizes ( $\sigma_g$ ) and selection values ( $\sigma_w$ ) and their respective correlations ( $\rho_g$  and  $\rho_w$ ). We ran ten replicates for each of the factorial combinations of the following parameters, which yielded a total of grids.

Parameter	Values	Description
$\sigma_w$	0.0001, 0.1, 0.3, 0.5, 0.7, 0.9	Effect size of fluctuations in fitness values
$\sigma_g$	0.0001, 10, 20, 30, 50, 70	Effect size of fluctuations in population sizes
$\rho_w$	-0.75, 0, 0.75	Correlation between fluctuations in fitness values
$\rho_g$	-0.75, 0, 0.75	Correlation between fluctuation in population sizes

### *Environmental timeseries*

To incorporate the effects of fluctuations into our population dynamics model, we generated independent timeseries of fluctuations in selection and population sizes. In the case of fluctuations in selection values, for a given value of  $w_{jm}$  and  $w_{kf}$  (i.e., a fixed point in the parameter space), we generated a timeseries of 500 generations made up of correlated fluctuations of  $w_{jm}$  and  $w_{kf}$ . We controlled the size of fluctuations in selection ( $\sigma_w$ ) and correlation between sexes ( $\rho_w$ ) by using the variance-covariance matrix:

$$C_w = \begin{bmatrix} \sigma_w^2 & \rho_w \sigma_w^2 \\ \rho_w \sigma_w^2 & \sigma_w^2 \end{bmatrix} \quad (4.11)$$

We then performed a Cholesky decomposition of  $C_w$  and multiplied it by a  $2 \times 500$  matrix of random uncorrelated numbers from a unit normal distribution, which yielded  $\gamma_{j,t}$  and  $\gamma_{k,t}$ . Since fitness values are bounded from zero to one, we transformed fitness values as  $w'_{jm} = \ln \frac{w_{jm}}{1-w_{jm}}$  and  $w'_{kf} = \ln \frac{w_{kf}}{1-w_{kf}}$ . Finally, we calculated the fitness values at generation  $t$  as:

$$w_{jm,t} = \frac{e^{(w'_{jm} + \gamma_{j,t})}}{1 + e^{(w'_{jm} + \gamma_{j,t})}} \quad (4.12)$$

$$w_{kf,t} = \frac{e^{(w'_{kf} + \gamma_{k,t})}}{1 + e^{(w'_{kf} + \gamma_{k,t})}} \quad (4.13)$$

This approach guaranteed that fluctuations in  $w_{jm}$  and  $w_{kf}$  were always bounded from zero to one.

Similarly, we generated an independent timeseries of 499 generations made up of correlated fluctuations in population sizes. Note, that in contrast to fluctuations in selection, we controlled the initial values of the timeseries by setting the male and female populations at 200 individuals each ( $N_{m,0} = 200$  and  $N_{f,0} = 200$ ). Then, we used the Cholesky factorization of the variance-covariance matrix to control the size of fluctuations in population sizes with  $\sigma_g$  and their correlation with  $\rho_g$ . Similar to our previous approach, we multiplied this factorization by a  $2 \times 499$  matrix of random uncorrelated numbers from a unit normal distribution, which yielded  $\gamma_{m,t}$  and  $\gamma_{f,t}$ . We calculated the number of males and females in the population at generation  $t$  as  $N_{m,t} = N_{m,0} + \gamma_{m,t}$  and  $N_{f,t} = N_{f,0} + \gamma_{f,t}$ . Therefore, the population sizes in each generation differed from the initial value of 200 individuals on the order of  $\sigma_g$ . To avoid extinction due to fluctuations in population sizes, we imposed a lower bound of one individual on the population sizes of both sexes. Note that the scales of  $\sigma_g$  and  $\sigma_w$  are different from each other. While  $\sigma_w$  controls the change in fitness values in logistic space,  $\sigma_g$  controls the number of individuals added or removed from the initial population.

Finally, we performed simulations where our population dynamics model (Eqns. 4.1 to 4.9) was iterated over 500 generations while selection and population sizes fluctuated in each generation. We started each simulation with initial values of 200 individuals of males and females and equal frequencies of allele  $j$  and allele  $k$  in each sex. For each generation  $t$  in our simulations, the values of  $w_{jm,t}$ ,  $w_{kf,t}$ ,  $N_{m,t}$  and  $N_{f,t}$  used to calculate allele frequencies in generation  $t$  (e.g., Eqn. 4.7), corresponded to the values at generation  $t$  calculated in the corresponding timeseries, as described previously. This approach yielded a final timeseries that captured the dynamics of sexually antagonistic alleles with fluctuating values of selection and population sizes.

### *Invasion simulations*

To evaluate if both alleles could be maintained in a population when the environment fluctuated, we turned towards Modern Coexistence Theory. Modern Coexistence Theory has shown that coexistence is promoted by mechanisms that give a species when rare, a population growth rate advantage over other



species (Barabás, D’Andrea, and Stump, 2018; Chesson, 1994; Chesson, 2000). To test this idea, one species is held at its *resident* state, as given by its steady-state abundance, while the rare species is called the *invader*. In the context of alleles in a population, an allele is an *invader* when a mutation occurs that introduces that allele into a population in which it is absent (e.g., in a population with only  $k$  alleles, if a random mutation leads to one individual carrying the  $j$  allele). Within a sexual population, each allele has two pathways of invasion, depending on whether the mutation arises in a female or in a male. If an allele’s *invasion growth rate* (or the average per capita logarithmic growth rate when rare) is positive, it buffers it against extinction, maintaining its persistence in the population. Coexistence, and hence polymorphism, occurs when both alleles have positive invasion growth rates.

We used the timeseries that captured the dynamics of our population model with environmental fluctuations as a template to perform invasion simulations of both alleles. Following the approach of Ellner, Snyder, and Adler (2016), we treated each invasion simulation independently, and hence we performed 500 invasion simulations, one for each generation in our timeseries. We explored all four potential combinations of each allele “invading” through each sex (e.g., allele  $j$  invading through males, allele  $k$  invading through females, and so on). To simulate invasion, we set the numbers of individuals carrying the invading allele to one individual. Since we treated each invasion simulation as an independent event, we denoted the initial timestep in an invasion simulation with the subscript  $i$ . For example, if allele  $j$  was invading via males, then we would set  $n_{jm,i} = 1$  and  $n_{jf,i} = 0$ . We also set the resident allele, in this case  $k$ , to the corresponding population size of the timeseries minus the one invading individual,  $n_{km,i} = N_{m,t} - 1$  and  $n_{kf,i} = N_{f,t}$ . We then simulated invasion by simulating one generation of our population dynamics model (i.e., to generate  $i + 1$ ) and calculated the logarithmic growth rate of the invading allele according to Eqn. 4.9, which in this example would be given by:

$$r_{j,i} = \ln \left( \frac{n_{jm,i+1} + n_{jf,i+1}}{1} \right) \quad (4.14)$$

Similarly, the logarithmic growth rate of the resident allele would be given by:

$$r_{k,i} = \ln \left( \frac{n_{km,i+1} + n_{kf,i+1}}{n_{km,i} + n_{kf,i}} \right) \quad (4.15)$$

We then calculated the mean logarithmic growth rate of each allele as an invader as the average of the 500 invasion growth rates. We also calculated the mean logarithmic growth rate of each allele as a resident as the average of the 500 resident growth rates. We determined alleles could coexist and therefore polymorphism could be maintained when both alleles had positive

mean invasion growth rates, which is often referred to as the mutual invasibility criterion (Barabás, D’Andrea, and Stump, 2018).

### *Functional decomposition*

Our invasion simulations allows us to evaluate whether or not polymorphism can be maintained at a given point of the parameter space with and without environmental fluctuations. However, we also quantify the relative contributions of fluctuations in selection and population sizes to the predicted coexistence outcome using a *functional decomposition* approach (Ellner, Snyder, and Adler, 2016; Ellner et al., 2019; Shoemaker et al., 2020). This approach allows the quantification of processes affecting growth rates in an analogous way, but not limited to, the mechanisms proposed by Modern Coexistence Theory (Ellner, Snyder, and Adler, 2016; Ellner et al., 2019)

The functional decomposition approach separates the average growth rate of each allele into a null growth rate in the absences of fluctuations in all selected variables, a set of main effect terms that represent the effect of only one variable fluctuating, a set of two-way interaction terms representing the effect of variables fluctuating simultaneously, and so on (Ellner et al., 2019). In our simulations, this is a function of four variables: the number of males in the population ( $N_m$ ), the number of females in the population ( $N_f$ ), the fitness of allele  $j$  in males ( $w_{jm}$ ), and the fitness of allele  $k$  in females ( $w_{kf}$ ). As a simplified example, if only  $N_m$  and  $N_f$  were fluctuating, the growth rate of allele  $j$  as an invader (Eqn. 4.14) at generation  $i$  could be decomposed into:

$$r_{j,i}(N_m, N_f) = \mathcal{E}_j^0 + \mathcal{E}_j^{N_m} + \mathcal{E}_j^{N_f} + \mathcal{E}_j^{N_m N_f} \quad (4.16)$$

where  $\mathcal{E}^0$  is the null growth rate when  $N_m$  and  $N_f$  are set to their averages from the timeseries. Terms with superscripts represent the marginal effects of letting all superscripted variables vary while fixing all the other variables to their average values. For example, the term  $\mathcal{E}_j^{N_m}$  expresses the contribution of fluctuations in  $N_m$  when  $N_f$  is set to its average, without the contribution when both variables are set to their averages:

$$\mathcal{E}_j^{N_m} = r_{j,i}(N_m, \overline{N_f}) - \mathcal{E}_j^0 \quad (4.17)$$

If we average Eqn. 4.16 across the 500 invasion simulations, we get a partition of the average population growth rate into the variation free growth rate, the

main effect of variability in  $N_m$ , the main effect of variability in  $N_f$ , and the interaction between variability in  $N_m$  and  $N_f$ :

$$\bar{r}_j = \mathcal{E}_j^0 + \bar{\mathcal{E}}_j^{N_m} + \bar{\mathcal{E}}_j^{N_f} + \bar{\mathcal{E}}_j^{N_m N_f} \quad (4.18)$$

In our simulations,  $w_{jm}$  and  $w_{kf}$  also fluctuate, therefore the full functional decomposition of the growth rate of allele  $j$  as an invader is found in Table 4.2, as well as a brief description of the meaning of each term. For simplicity, we only show terms related to allele  $j$  as an invader; however, the functional decomposition approach can be applied analogously when allele  $k$  invades. Note that Table 4.2 does not include three-way or four-way interactions (e.g.,  $\bar{\mathcal{E}}_j^{N_m N_f w_{jm} w_{kf}}$ ). This is because we did not allow fluctuations in selection and population sizes to be correlated in our simulations. Therefore their effects are fully captured by the terms in Table 4.2. We calculated the value of each of the terms in Table 4.2 by performing additional sets of invasion simulations controlling which variables were allowed to fluctuate. For example, to calculate the value of  $\mathcal{E}_j^0$ , we performed another 500 simulations of allele  $j$  invading but, instead of using the values of  $w_{jm,i}$ ,  $w_{kf,i}$ ,  $N_{m,i}$  and  $N_{f,i}$  used to simulate the frequency of allele  $j$  in generation  $i + 1$ , we set all of them to their mean value. To calculate the value of  $\mathcal{E}_j^{N_m}$ , we set all variables except  $N_m$  to their mean value and subtracted the value of  $\mathcal{E}_j^0$ , and so on with subsequent terms.

Table 4.2: Functional decomposition of the growth rate of allele  $j$ . As defined in Eqn. (4.18), the partition of the average population growth rate is made up of the variation free growth rate ( $\mathcal{E}_j^0$ ), main effects of each variable fluctuating, and the interaction between fluctuations in correlated variables.

Term	Formula	Meaning
$\mathcal{E}_j^0$	$\bar{r}_j(\bar{N}_m, \bar{N}_f, \bar{w}_{jm}, \bar{w}_{kf})$	Growth rate at mean population size and selection values
$\bar{\mathcal{E}}_j^{N_m}$	$\bar{r}_j(N_m, \bar{N}_f, \bar{w}_{jm}, \bar{w}_{kf}) - \mathcal{E}_j^0$	Main effect of fluctuations in $N_m$
$\bar{\mathcal{E}}_j^{N_f}$	$\bar{r}_j(\bar{N}_m, N_f, \bar{w}_{jm}, \bar{w}_{kf}) - \mathcal{E}_j^0$	Main effect of fluctuations in $N_f$
$\bar{\mathcal{E}}_j^{w_{jm}}$	$\bar{r}_j(\bar{N}_m, \bar{N}_f, w_{jm}, \bar{w}_{kf}) - \mathcal{E}_j^0$	Main effect of fluctuations in $w_{jm}$
$\bar{\mathcal{E}}_j^{w_{kf}}$	$\bar{r}_j(\bar{N}_m, \bar{N}_f, \bar{w}_{jm}, w_{kf}) - \mathcal{E}_j^0$	Main effect of fluctuations in $w_{kf}$
$\bar{\mathcal{E}}_j^{N_m N_f}$	$\bar{r}_j(N_m, N_f, \bar{w}_{jm}, \bar{w}_{kf}) - [\mathcal{E}_j^0 + \bar{\mathcal{E}}_j^{N_m} + \bar{\mathcal{E}}_j^{N_f}]$	Interaction effect of fluctuations in $N_m$ and $N_f$
$\bar{\mathcal{E}}_j^{w_{jm} w_{kf}}$	$\bar{r}_j(N_m, \bar{N}_f, w_{jm}, w_{kf}) - [\mathcal{E}_j^0 + \bar{\mathcal{E}}_j^{w_{jm}} + \bar{\mathcal{E}}_j^{w_{kf}}]$	Interaction effect of fluctuations in $w_{jm}$ and $w_{kf}$

The functional decomposition approach further allows the *comparison* of each term to understand how it affects invaders and residents (i.e., the relative contribution). This is because fluctuations can promote the maintenance of polymorphism by helping whichever allele is rare or by hurting whichever allele is common. Therefore, to understand the role of each type of fluctuation,

it is necessary to compare how it affects both invader *and* resident growth rates. In the example presented in Eqn. 4.18, if allele  $j$  is invading, then allele  $k$  is at its resident state and there exists an analogous decomposition of  $\bar{r}_k$ . Therefore we can express the difference between contributions of fluctuations in  $N_m$  as:

$$\Delta_j^{N_m} = \bar{\mathcal{E}}_j^{N_m} - \bar{\mathcal{E}}_k^{N_m} \quad (4.19)$$

If  $\Delta_j^{N_m}$  is positive, then fluctuations in  $N_m$  overall contribute *more* positively to the growth rate of allele  $j$  when it is rare than to allele  $k$  as a resident. If  $\Delta_j^{N_m}$  is negative, then fluctuations contribute more positively to the resident growth rate of allele  $k$  than to the growth rate of  $j$  as an invader. Therefore, for each allele invading via a different pathway, we calculated seven separate  $\Delta$  values, one for each one of the  $\mathcal{E}$  terms in Table 4.2.

In the course of our analysis, we noticed that the magnitude of the  $\Delta$  values could vary considerably across the parameter space. To make them more comparable and ease interpretation, we normalized each  $\Delta$  value by dividing it by the square root of the sum of the squares of the seven  $\Delta$  values. For example, the normalized value of Eqn. 4.19 would be given by:

$$\delta_j^{N_m} = \frac{\Delta_j^{N_m}}{\sqrt{\sum_x (\Delta_j^x)^2}} \quad (4.20)$$

This normalization bounds  $\delta$  values between  $-1$  and  $1$ . Similar to the interpretation of  $\Delta$  terms, positive  $\delta$  values mean that fluctuations overall contribute more positively to the invasion growth rate of an allele and negative  $\delta$  values imply that fluctuations overall contribute more positively to the growth rate of an allele as a resident more than the other allele as an invader.

## RESULTS

Our results showed that both fluctuations in selection and population sizes can substantially increase the genetic variability expected under sexually antagonistic selection. The proportion of the parameter space where polymorphism was maintained increased with the effect size of both types of fluctuations (Fig. 4.1). Increases in the proportion of polymorphism were more likely when fluctuations in selection and population sizes were large, fluctuations in population sizes were negatively correlated, and fluctuations in selection were positively correlated. Importantly, our results show that when both selection

and population sizes have large fluctuations, the proportion of polymorphism in the parameter space can reach up to 60% (Fig. 4.1).

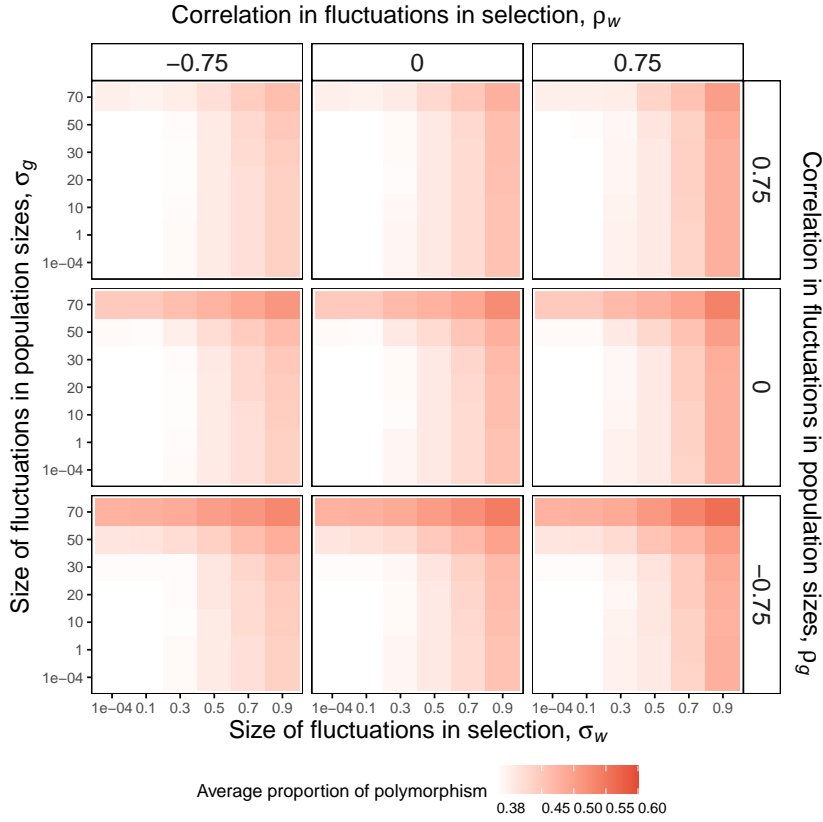


Figure 4.1: The average proportion of the selection parameter space corresponding to polymorphism. For all parameter combinations in our simulations, we show the average proportion of polymorphism in our grids, for all ten replicates and invasion scenarios (each allele invading a different sex). Each panel corresponds to a different combination of correlations between fluctuations and rows and columns within a panel show the size of fluctuations in population sizes and in selection, respectively. Labels on top indicate the correlation between fluctuations in selection  $\rho_w$ , while labels on the right show the correlation in fluctuations between fluctuations in population sizes  $\rho_g$ . As a basis of comparison, we show the expected proportion of polymorphism in constant environments (0.38) as white in our color scheme.

Our results matched previous findings that in constant environments, polymorphism can be maintained in  $\approx 38\%$  of the parameter space, which corresponds to the parameter space where balancing selection maintains a domain bounded by Eqn. 4.10 (Fig. 4.2A). Increases in polymorphism when population sizes fluctuated occurred near the limit of the domain of balancing selection and were particularly pronounced when selection against both alleles was weak (Fig. 4.2B). When selection against either of the alleles was strong ( $S_m, S_f > 0.75$ ), fluctuations in population sizes did not increase polymorphism compared to the control (Fig. 4.2B). Similarly, increases in polymorphism when selection fluctuated also occurred near the limit of the domain of balancing selection; however, fluctuations in selection did not affect polymorphism when selection against both alleles was weak ( $S_m, S_f < 0.25$ ) (Fig. 4.2C). When both population sizes and selection fluctuated, increases in polymorphism occurred regardless of the strength of selection (Fig. 4.2D).

The effect of fluctuations in population sizes and selection was not homogeneous across the parameter space. The values of  $\delta^0$ , which captured the difference between invader and resident growth rates when selection and population sizes were set to their mean, were close to zero near the limit of the domain of balancing selection (Fig. 4.3). In contrast, the rest of the  $\delta$  values were generally stronger in magnitude near the limit of the domain of selection (Fig. 4.3). Despite their similar patterns in the parameter space, the relative contribution of each type of fluctuation to the growth rate of alleles when rare depended on the allele and sex where the invasion took place (Fig. 4.3).

Fluctuations in population sizes of males and females facilitated polymorphism when alleles invaded via the fluctuating population (Fig. 4.4). In contrast, fluctuations in the population size of one sex made it more difficult for either allele to invade via the other sex (Fig. 4.4). For example, the relative contribution of fluctuations in the male population,  $\delta^{N_m}$ , was positive for both alleles when they invaded via males and negative when they invaded via females, regardless of the correlation between fluctuations (Fig. 4.4). The relative contribution of both populations fluctuating,  $\delta^{N_m N_f}$ , was positive when fluctuations were negatively correlated, had a negligible effect when fluctuations were not correlated, and had a negative effect when fluctuations were positively correlated (Fig. 4.4).

In contrast, the relative contribution of fluctuations in selection depended on the allele that was the invader, regardless of the sex where invasion occurred (Fig. 4.5). For example,  $\delta^{w_{jm}}$  which captured the relative contribution of fluctuations in selection against  $j$  in males, was always positive when allele  $k$  invaded but had negligible effects when allele  $j$  invaded (Fig. 4.5). The relative contribution of fluctuations of both types of selection was negative when fluctuations were negatively correlated, had a negligible effect when fluctuations were not correlated, and had a positive effect when fluctuations were positively correlated (Fig. 4.5).

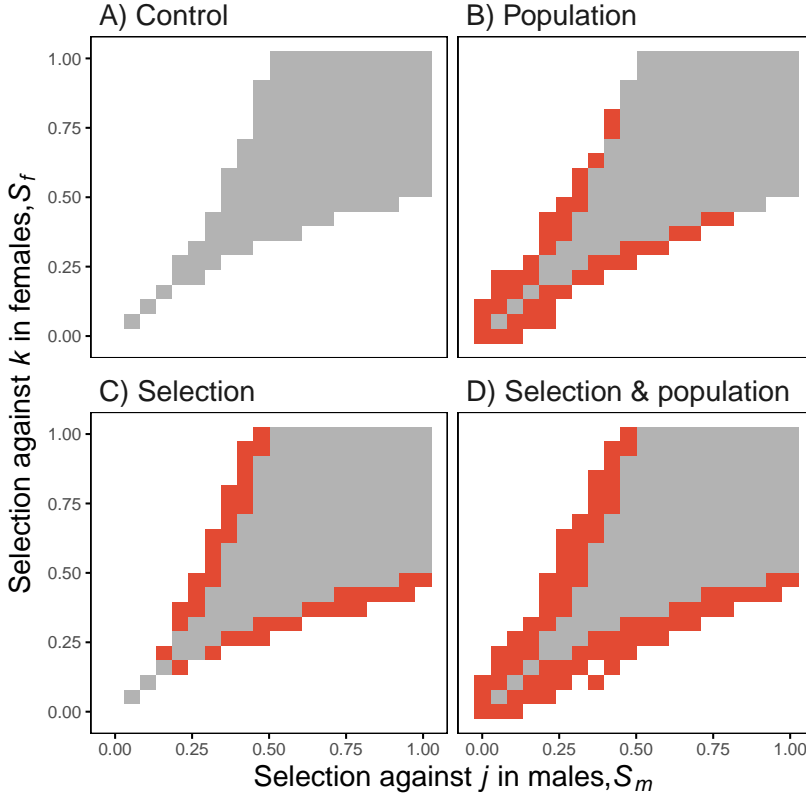


Figure 4.2: Polymorphism in the parameter space. We show the outcomes of our invasion simulations when  $j$  invaded via males and  $k$  invaded via females. As a reference,  $j$  is favored in females and  $k$  is favored in males. Each panel corresponds to a different replicate of our simulation grids. Grey areas indicate parts of the selection parameter space where polymorphism can be maintained without fluctuations while white areas indicate parts of the parameter space that correspond to the fixation of one of the alleles (following Eqn.4.10). Red areas indicate parts of the parameter space where polymorphism can be maintained when fluctuations were incorporated. In A) we show the outcomes of our control grid ( $\sigma_g = 0.0001$ ,  $\rho_g = 0$ ,  $\sigma_w = 0.0001$ ,  $\rho_w = 0$ ). In B) we show the outcomes when we incorporated high fluctuations in population sizes that were negatively correlated ( $\sigma_g = 70$ ,  $\rho_g = -0.75$ ,  $\sigma_w = 0.001$ ,  $\rho_w = 0$ ). In C) we show the outcomes when we incorporated fluctuations in selection that were positively correlated ( $\sigma_g = 0.0001$ ,  $\rho_g = 0$ ,  $\sigma_w = 0.9$ ,  $\rho_w = 0.75$ ). In D) we show the outcomes when both population sizes and selection fluctuated ( $\sigma_g = 70$ ,  $\rho_g = -0.75$ ,  $\sigma_w = 0.9$ ,  $\rho_w = 0.75$ ).

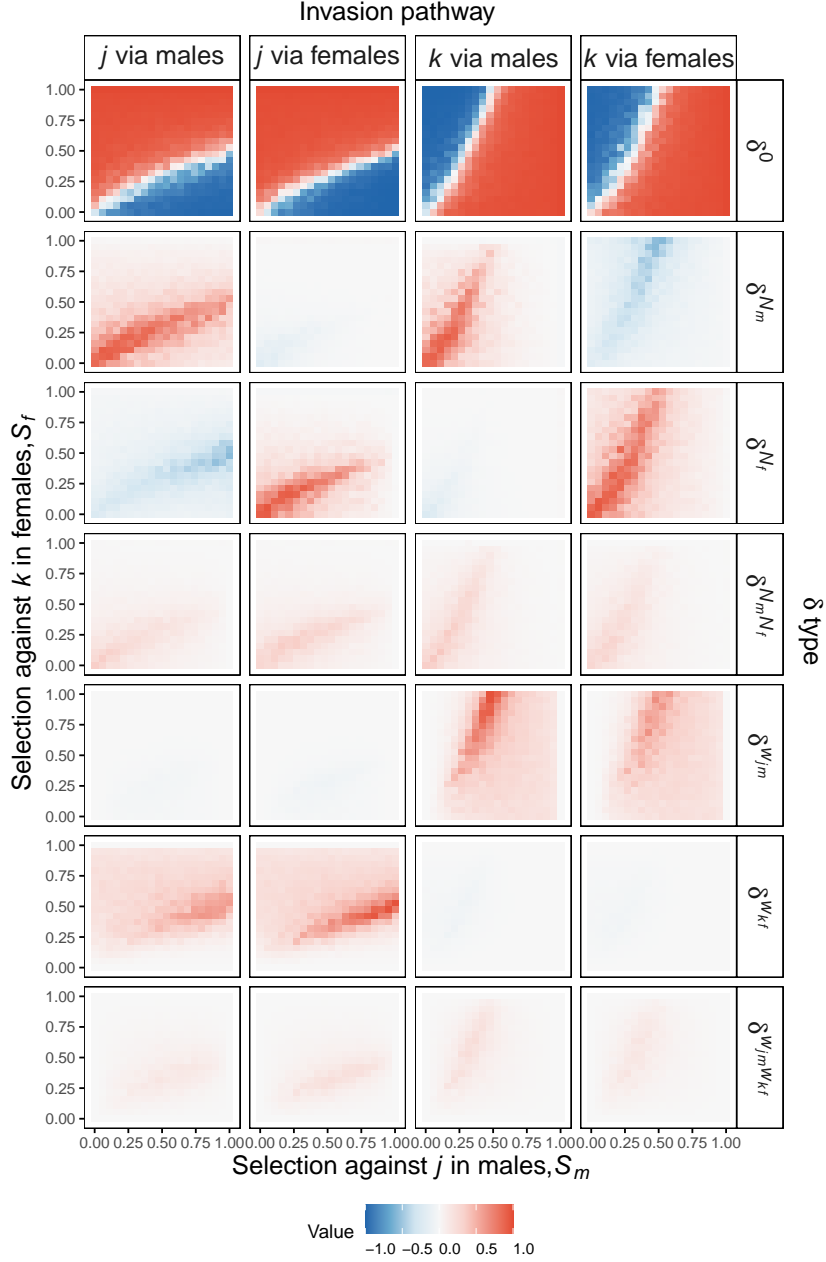


Figure 4.3: Distribution of  $\delta$  values across the parameter space. We show the results of the functional decomposition approach for one replicate of our simulation grids where both population sizes and selection fluctuated with correlated effects ( $\sigma_g = 70$ ,  $\rho_g = -0.75$ ,  $\sigma_w = 0.9$ ,  $\rho_w = 0.75$ ). Each row corresponds to a different type of  $\delta$  value, as indicated with labels on the right. Each column corresponds to an allele invading a different pathway, as indicated with labels on top. Areas in red correspond to  $\delta$  values that contributed positively to each allele's invasion growth rate, while blue areas denote points in the parameter space where fluctuations had a negative contribution to invasion growth rates.



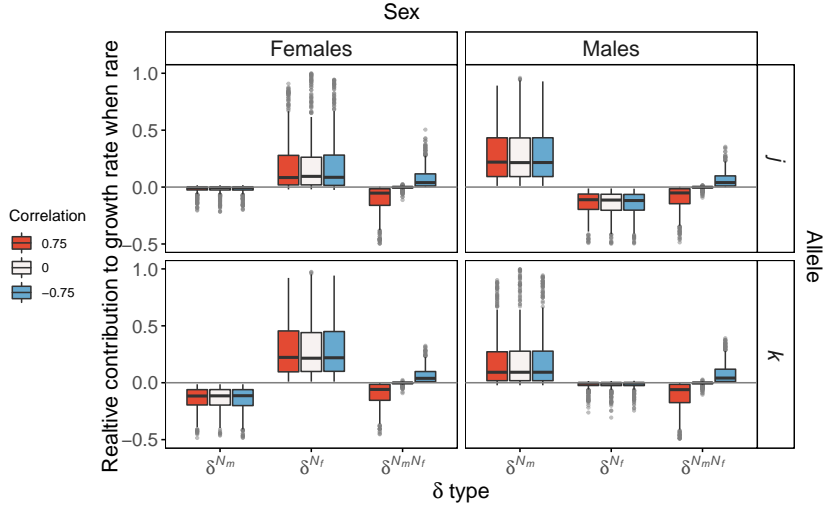


Figure 4.4: The relative contributions of fluctuations in population sizes to alleles' growth rates when rare. Positive  $\delta$  values imply that the corresponding fluctuation benefits that allele as an invader more than the other allele as a resident while negative  $\delta$  values indicate fluctuations benefit the residents more than the invader. Each panel corresponds to the result of simulations where each allele invaded via a different pathway, as indicated by top and right labels. We show the boxplots of the three distinct  $\delta$  values that captured the effects of fluctuations in population sizes, for all of the replicates in our simulation in which  $\sigma_g = 70$ . Each color corresponds to a different correlation between fluctuations in population sizes ( $\rho_g$ ), as the legend indicates. Box plots extend from the first to third quantiles of the corresponding  $\delta$  values, and the line inside the the box indicates the median. The upper whisker extends to the largest value no further than 1.5 times the inter-quantile range (IQR, or the distance between the first and third quartiles); the lower whisker extends to the smallest value at most 1.5 times the IQR. Data beyond the end of the whiskers are determined to be outliers and are plotted individually with solid grey points.

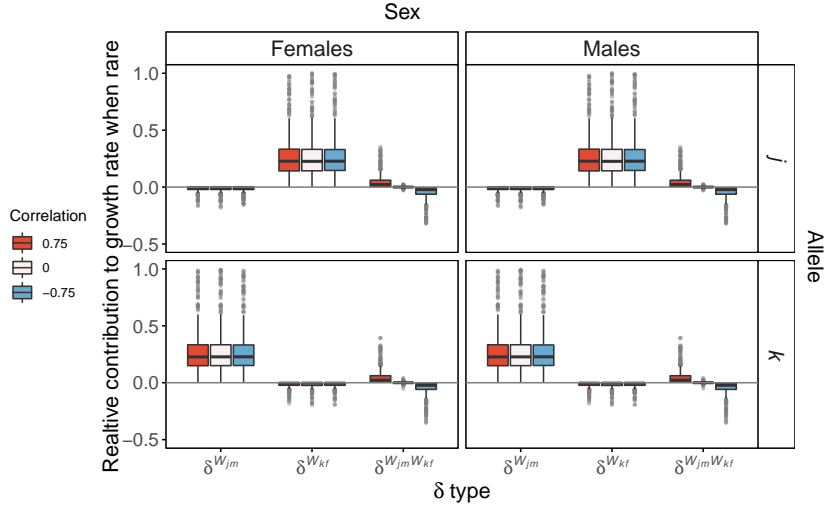


Figure 4.5: The relative contributions of fluctuations in selection to alleles' growth rates when rare. Positive  $\delta$  values imply that the corresponding fluctuation benefits that allele as an invader more than the other allele as a resident while negative  $\delta$  values indicate fluctuations benefit the residents more than the invader. Each panel corresponds to the result of simulations where each allele invaded via a different pathway, as indicated by top and right labels. We show the boxplots of the three distinct  $\delta$  values that captured the effects of fluctuations in selection, for all of the replicates in our simulation in which  $\sigma_w = 0.9$ . Each color corresponds to a different correlation between fluctuations in population sizes ( $\rho_w$ ), as the legend indicates. Box plots extend from the first to third quantiles of the corresponding  $\delta$  values, and the line inside the box indicates the median. The upper whisker extends to the largest value no further than 1.5 times the inter-quantile range (IQR, or the distance between the first and third quantiles); the lower whisker extends to the smallest value at most 1.5 times the IQR. Data beyond the end of the whiskers are determined to be outliers and are plotted individually with solid grey points.

## DISCUSSION

The results of our study provide supporting evidence that environmental fluctuations can substantially increase the expected genetic variance maintained under sexually antagonistic selection (Fig. 4.1). Perhaps more importantly, our study shows *how* environmental fluctuations help maintain polymorphism by quantifying the relative contribution of fluctuations to alleles growth rates when

rare. Antagonistically selected alleles are an important component of genetic variation for many species (Bonduriansky and Chenoweth, 2009; Foerster et al., 2007; Innocenti and Morrow, 2010; Van Doorn, 2009). Indeed, as much as 20% of traits for which data are available are thought to be under sexually antagonistic selection (Morrissey, 2016). Yet, a large body of work suggests that the criteria for maintaining antagonistic genetic variation are very restrictive (i.e., we would expect polymorphism to be maintained in a population in few scenarios) (Curtsinger, Service, and Prout, 1994; Hedrick, 1999; Kidwell et al., 1977; Pamilo, 1979; Patten, Haig, and Ubeda, 2010). In contrast, our study shows that when we incorporated more realistic assumptions, a sexually antagonistic polymorphism can be maintained in up to 60% of the parameter space (Fig. 4.1).

### *The relative contribution of fluctuations in selection*

Our simulations indicate that large fluctuations in the strength of selection can substantially increase the proportion of polymorphism compared to when selection is constant (Fig. 4.1). The effect of fluctuations in selection was generally greater in magnitude near the limit of the domain of selection and where selection against alleles was strong (Fig. 4.3). In contrast, fluctuations in selection had a minor effect when both alleles had similar fitness, suggesting that fluctuations in selection become advantageous when there exist greater fitness differences between sexually antagonistic alleles (Fig. 4.3). The effect of fluctuations in selection depended on the identity of the invading allele, regardless of the sex where invasion occurred (Fig. 4.5). Our results suggest that in parts of the parameter space where one would expect selection to fix the allele with higher fitness, the allele with lower fitness can be maintained in a population if the fitter allele experiences high fluctuations in selection (Fig. 4.2). This could be the case, for example, if traits associated with sexual dimorphism like ornaments or bright colors are also associated with higher predator rates (Bildstein, McDowell, and Brisbin, 1989; Götmark et al., 1997) or sex-biased mortality (Promislow, Montgomerie, and Martin, 1992). However, if the allele with lower fitness is the one associated with higher fluctuations in selection, then fluctuations are not likely to promote the maintenance of both alleles in a population (Fig. 4.5).

An exact correspondence with Modern Coexistence Theory is unlikely to be achieved when using the functional decomposition approach (Ellner, Snyder, and Adler, 2016; Shoemaker et al., 2020). Similarly, when comparing evolutionary dynamics to competitive dynamics, the interpretation of coexistence mechanisms is not straightforward. Nonetheless, our quantification of the relative contributions of fluctuations to alleles' invasion growth rates show similarities to fluctuation dependent coexistence mechanisms. For example, the relative contributions of fluctuations in selection (captured by  $\delta^{w_{jm}}$  and  $\delta^{w_{kf}}$ ) is similar to the expected contributions to growth rates made by *relative*

*non-linearity*. This fluctuation dependent mechanism requires that competitors differ in the degree of non-linear responses to limiting competitive factors (Chesson, 2000, 2003; Zepeda and Martorell, 2019). If differences in response to limiting factors exist, and the limiting factors fluctuate, non-linear averaging can benefit some species and hurt others (Ellner et al., 2019). In our model, fluctuations in selection against one allele affect both alleles differently (e.g., fluctuations in the fitness of allele  $j$  in males affect both allele  $j$  and  $k$  to different extents). Thus, when selection against one allele fluctuated, it contributed positively to the growth rate of the other allele as an invader (Fig. 4.5).

The interactive effect of fluctuations in selection,  $\delta^{w_{jm}, w_{kf}}$ , promoted allelic coexistence when fluctuations were positively correlated, and it contributed negatively to each allele's invasion growth rate if fluctuations were negatively correlated (Fig. 4.5). Environmental fluctuations are often correlated (Steele, 1985). Previous studies have shown that positively correlated environmental fluctuations can increase the invasion growth rate of a species when there are species-specific environmental responses, and there is buffered population growth where species are shielded from competition (Chesson, 2000; Schreiber, 2021). This coexistence mechanism is known as the *storage effect*, and it is often quantified as the contribution to an invasion growth rate of covariance between the environment and competitive factors (Ellner, Snyder, and Adler, 2016; Zepeda and Martorell, 2019). In our model, fluctuations in  $w_{jm}$  and  $w_{kf}$  are not easily separated into environmental and competitive factors, therefore referring to this type of contribution as a storage effect would be misleading. Nonetheless, our results show that there exists a benefit when both  $w_{jm}$  and  $w_{kf}$  vary, beyond the contribution of each effect varying on its own when fluctuations are positively correlated. This could arise, for example, in environments where sexual selection on both sexes is stronger when climatic conditions are favorable and becomes negligible in stressful conditions (Cockburn, Osmond, and Double, 2008).

#### *The relative contribution of fluctuations in population sizes*

Fluctuations in population sizes caused overall increases in the proportion of coexistence compared to the control simulation (Fig. 4.1). The effect of fluctuations in population sizes was generally greater in magnitude near the limit of the domain of selection where both alleles had similar fitness values and had a weaker effect as differences in fitness were larger (Fig. 4.3). This suggests that fluctuations in population sizes will likely play a minor role in maintaining polymorphism in populations where sexual antagonism is strong. Similar to fluctuations in selection, fluctuations in population sizes had positive contributions to the invasion growth rate of alleles due to a mechanism similar to *relative non-linearity*. Fluctuations in the population sizes of males and females had different effects on each allele. They thus, contributed positively to invasion growth rates if alleles invaded via the fluctuating population (Fig. 4.4). If an

allele invaded via the non-fluctuating sex, however, fluctuations contributed negatively to its invasion growth rate and thus hampered the maintenance of polymorphism (Fig. 4.4).

Our results suggest that in parts of the parameter space where we would expect selection to fix the allele with higher fitness the allele with lower fitness could achieve a positive invasion growth rate if it invaded via a population experiencing temporal changes in its size. Temporal changes in population sizes of males and females can arise due to sex differences in movement (e.g., if males immigrate to higher quality areas; Matter and Roland, 2002), development (e.g., females requiring more time to mature than males; Kasumovic et al., 2008), and behavior (e.g., cannibalistic mating; Elgar et al., 2003). When males and females experience different population dynamics, sexual antagonism allows alleles to respond differently to fluctuations and thus promotes the maintenance of polymorphism. The interactive effect of fluctuations in males and females,  $\delta^{N_m, N_f}$ , shows that, when both populations fluctuate, negatively correlated fluctuations promote the maintenance of genetic diversity while positively correlated fluctuations likely impair it (Fig. 4.4). These insights offer an exciting avenue of research to understand if sexually selected traits are more often found in populations that experience negatively correlated temporal changes in population sizes, and could help explain the high heritabilities of those traits (Reinhold, 2000).

### *Polymorphism and sexual conflict*

Our study exclusively focused on the conditions for maintaining polymorphism in a population with and without environmental fluctuations. However, maintaining non-advantageous alleles in a population is costly and can result in a decrease in the overall fitness of a population (Connallon and Hall, 2018; Gavrillets, 2014). Sexually antagonistic selection necessarily creates a mismatch between the traits a population expresses and the optimal expression of those traits (Lande, 1980). It is often resolved once members of both sexes express traits that match the sex-specific optima (e.g., when alleles with lower fitness are eliminated from a population, the evolution of sex chromosomes or sex-specific expression of traits)(Arnqvist and Rowe, 2013; Lande, 1980). Our results show that large fluctuations in selection and population sizes can impede the resolution of sexual conflict by maintaining multiple alleles in a population, even when selection against some of those alleles is strong (Fig. 4.2D). Thus, the maintenance of genetic diversity promoted by fluctuations might involve strong trade-offs in the fitness and evolution of a population. These trade-offs can, in turn, result in an erosion of genetic diversity even when fluctuations are present.

## *Conclusion*

Our study contributes to the growing body of work that shows that the usual criteria for maintaining genetic variation under sexually antagonistic selection are overly conservative (Connallon and Clark, 2012; Connallon, Sharma, and Olito, 2019). Processes like recurrent mutations (Radwan, 2008), genetic drift (Connallon and Clark, 2012), local adaptations (Connallon, Sharma, and Olito, 2019), and alleles that experience seasonal changes in dominance (Wittmann et al., 2017) have all been shown to dramatically change the levels of sexually antagonistic variance in natural populations. Our results show that non-constant environments might promote the maintenance of genetic diversity of sexually antagonistic alleles without the need for local adaptations or life-history stages that involve overlapping generations. The environmental drivers that maintain sexually antagonistic traits are still poorly understood (Connallon and Hall, 2018). Our study provides a necessary precursor to fully characterize the effect of environmental drivers on genetic diversity by explicitly quantifying the contribution of environmental fluctuations to the maintenance of polymorphism across the selection parameter space.

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## Part III

### FINAL WORDS



## CONCLUSION

*Where is the rest of the world?  
That is the question we must always ask about any model:  
where is the rest of the world?*

— Levins (2006)

In this thesis, I show how to incorporate biotic and abiotic complexity in models of biotic interactions to increase realism. Furthermore, I provide direct evidence that many models used to describe biotic interactions are oversimplistic, as they fail to capture dynamics accurately by *a priori* ignoring abiotic and biotic factors. Throughout this thesis, I also show that increasing realism in models of biotic interactions has important repercussions on our understanding and predictions about the maintenance of diversity at ecological and evolutionary scales.

## SUMMARY OF RESULTS

In [Chapter 2](#), I found that the abundance of co-foragers can fundamentally change the number of visits pollinators make. These results imply that it is necessary to account for the density of species other than the focal pair to characterize plant-pollinator interactions accurately. However, results from this chapter also show that the environmental context pollinators experience mediates density-dependent responses to co-foraging species. Thus, abiotic drivers can modify the number of visits made by pollinators through both density-independent and density-dependent responses. These two types of responses can cause the same environmental context to have opposite effects on floral visits. Such is the case of high resource abundance in our foraging experiment. Additionally, in this chapter, I show that pollinators do not respond equally to all co-foraging species. Therefore, the effects of biotic and abiotic drivers depend on the identity of the interacting species. Results from this chapter clearly show that including these levels of complexity in a model of floral visits is justified, despite the increasing number of parameters necessary to fit such a model. Since floral visitation is a good predictor of the strength of plant-pollinator interactions (Vázquez, Morris, and Jordano, 2005; Vázquez et al., 2012) my results demonstrate that failing to account for biotic and abiotic

## CONCLUSION

complexity can result in misleading estimations of the level of interdependence of animal and plant populations.

In [Chapter 3](#), I found that accounting for the abiotic context where interactions occur can fundamentally change predictions of species coexistence. While other studies have previously shown that predictions of coexistence between plant species can be context-dependent (Bimler et al., 2018; Lanuza, Bartomeus, and Godoy, 2018), my results are the first to show that the estimated effect of the abiotic context depends on the model used to describe species interactions. Thus, my results show that incorporating abiotic complexity in models of biotic interactions is far from straightforward, as different phenomenological models can enhance or diminish its effect. Additionally, parameter uncertainty can further hinder the interpretation of the effect abiotic drivers have on predictions. For instance, predictions showed that in the *woody* environment our focal species were unlikely to coexist, however, the species predicted to be competitively excluded varied across posterior draws. Therefore, my results show that robust predictions of species coexistence need to consider the abiotic context where interactions occur *and* different sources of uncertainty associated with phenomenological models.

Finally, in [Chapter 4](#) I found that environmental fluctuations can substantially increase the level of polymorphism in populations that experience sexually antagonistic selection. Perhaps most importantly, the results of this chapter show that environmental fluctuations can maintain disadvantageous alleles in a population by contributing positively to their growth rates when rare. However, the positive contributions of fluctuations depended on the pathway by which each allele was introduced into the population. Thus, I show that abiotic heterogeneity must be coupled with aspects of the evolutionary dynamics of the populations involved to maintain genetic diversity. This chapter highlights that not all types of abiotic drivers have the same effects on the populations involved. For instance, fluctuations in selection contributed positively to allele's invasion growth rates when fluctuations were positively correlated. In contrast, fluctuations in population sizes needed to be negatively correlated to have positive contributions. Therefore, my results show the importance of not only investigating *if* environmental drivers change predictions but also *how* they do it.

## GENERAL IMPLICATIONS

Increasing model realism can be achieved in multiple ways. One of them is to add independent variables to a model that represent previously ignored aspects of the real world (Evans et al., 2013; Orzack and Sober, 1993). For example, in [Chapter 2](#) I increased realism by adding variables that accounted for the densities of co-foragers to a model of floral visits. Other methods include adding a new link to variables already present or imposing bounds to some



aspects of the model (Levins, 1993). For example, in [Chapter 3](#) I assumed unlimited growth was unrealistic and imposed abundance constraints when predicting species coexistence. Importantly, whether any of these methods increase the correspondence between model and phenomena of interest can not be evaluated *a priori*. For instance, in [Chapter 2](#) it may have been the case that abiotic conditions had no effect on how a pollinator forages the presence of other species. Then, a model that included density-dependent responses to environmental conditions would have been over-parameterized. However, this assessment can only be done *after* the fit a more complex model.

In this thesis, I show that models of biotic interactions aimed to make predictions regarding diversity maintenance tend to be oversimplistic. The implicit assumption that general insights can only be achieved with simple models (Holling, 1966; May, 2019; Roughgarden et al., 2018) has led to the automatic omission of biotic and abiotic heterogeneities in many models of biotic interactions. However, scientific generality is not the same as mathematical generality (Levins, 1993). For instance, to build a simple model in mathematical terms, we should include as little as possible (Orzack, 2012). In contrast, building a simple model in biological terms might entail accounting for abiotic and biotic dependency.

A key simplifying assumption in many models of biotic interactions is that species pairs is the relevant unit of study (Levine et al., 2017). However, many theoretical and empirical studies have shown that this assumption is likely a major oversimplification (Abrams, 1983; Billick and Case, 1994; Letten and Stouffer, 2019; Mayfield and Stouffer, 2017). Various biological mechanisms can cause individuals of the same or different species to modify the interaction between a focal pair, a phenomenon broadly referred to as higher order interactions (Kleinhesselink, Kraft, and Levine, 2019). One of these mechanisms, interaction modification, arises when an intermediary species induces behavioral changes in one or both of the species in the focal pair, thereby modifying their interaction (Adler and Morris, 1994; Billick and Case, 1994). In [Chapter 2](#), I show that interaction modifications are likely to occur in mutualistic communities by behavioral responses of pollinators to other foraging species. Evidence that shows higher order interactions have non-negligible effect in natural communities continues to accumulate (Lai et al., 2020; Levine et al., 2017; Martyn et al., 2021; Mayfield and Stouffer, 2017). Therefore, ignoring biotic complexity in favor of mathematical simplicity can be detrimental to understanding how multispecies communities are assembled and maintained.

The environmental dependence of biotic interactions has broad empirical and theoretical support (Bimler et al., 2018; Callaway et al., 2002; Chamberlain, Bronstein, and Rudgers, 2014; Chesson, 2000; Lanuza, Bartomeus, and Godoy, 2018; Tylianakis et al., 2008). Furthermore, the importance of heterogeneous environments in the maintenance of diversity has been shown at ecological (Amarasekare, 2003; Kneitel and Chase, 2004) and evolutionary scales (Connallon, Sharma, and Olito, 2019; Dean, 2005; Ellner and Hairston Jr, 1994). Yet, most

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models used to make predictions regarding diversity maintenance tend to keep changes in biotic interactions due to environmental effects implicit or treat them as constant (but see Bimler et al. (2018), or Connallon, Sharma, and Olito (2019)). In Chapter 3 and Chapter 4 I address two different challenges when accounting for environmental dependency in models of biotic interactions: the interplay between model uncertainty and environmental heterogeneity, and the interpretation of environmental effects in model predictions. While in natural systems, as opposed to experimental systems or simulations, it is challenging to determine exactly what variables constitute “the environment”, an inability to account for abiotic dependence prevents ecologists and evolutionary biologists to correctly identify the drivers of diversity maintenance (Connallon, Sharma, and Olito, 2019; Freckleton, Watkinson, and Rees, 2009).

## FUTURE DIRECTIONS

While it might be tempting to argue that increasing model realism is a Sisyphean endeavor, there are limits to the level of complexity that can be added to a model without losing its usefulness. Where those limits are and whether a model is realistic enough will depend on the state of science at the time (Levins, 1993). In this thesis, I argue that automatically excluding biotic and abiotic factors from models of biotic interactions in favor of mathematical simplicity obstacles our understanding of how natural systems operate. The level of realism needed to describe biotic interactions accurately will undoubtedly depend on the system studied, as not all types of interactions are equally likely to be affected by the biotic and abiotic context they are embedded in (Chamberlain, Bronstein, and Rudgers, 2014). Nonetheless, scientific progress requires that we acknowledge and explore this complexity. This has been and continues to be done by studies that compare models of varying levels of complexity to understand when its inclusion is warranted (Bimler et al., 2018; Lai et al., 2020; Martyn et al., 2021; Weiss-Lehman et al., 2021), studies that investigate the biological rationale for why certain levels of complexity should be included in models (Abrams, 1983; Abrams and Ginzburg, 2000; AlAdwani and Saavedra, 2019; Letten and Stouffer, 2019; Stouffer and Novak, 2021), and studies that show how to account for unmeasured biotic and abiotic drivers (D’Andrea, Ostling, and O’Dwyer, 2018; Song et al., 2020).

Finally, a key aspect missing from most ecological and evolutionary research focused on diversity maintenance is the bidirectional link between organisms and the environment. Extensive research, including this thesis, has been done to disentangle the effects of abiotic and biotic factors on the performance of organisms. The reciprocal phenomenon, the reaction and evolution of the environment in response to the organisms embedded in it, is generally ignored in many ecological and evolutionary studies (Laland, Odling-Smee, and Feldman, 1999; Levins and Lewontin, 1980). However, including the feedback loop

between organism and environment is essential to fully understand the interplay between biotic and abiotic variables in natural communities (Callaway, 2007; Hastings et al., 2007). Additionally, theoretical studies suggest that this feedback process can fundamentally change predictions related to diversity maintenance in natural communities (Kylafis and Loreau, 2008, 2011). Thus, subsequent efforts should examine how biotic and abiotic complexity jointly modifies the responses of organisms and the environment. This thesis offers some theoretical tools for ecologists and evolutionary biologists to explore the first part of this puzzle.



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## Part IV

## APPENDICES



## APPENDIX A

## ENERGY GAINS DURING THE EXPERIMENT

To evaluate the energy gains of *Bombus* individuals during the experiments, we first determined the maximum energy gains per floral visits (Table 6.1). Then, we fit a model to predict the energy gains per visit for species  $i$ , using flower types as predictors:

$$\kappa_i = \epsilon_p F_{pink} + \epsilon_b F_{blue} + \epsilon_w F_{white} + \epsilon_y F_{yellow}, \quad (6.1)$$

where  $\kappa_i$  is energy consumed per visit for species  $i$ ,  $\epsilon_j$ , are parameters that describe the energy gains, and  $F_j$  are dummy variables that represent the type of flower visited. The subscripts denote the type of flowers by colors. We fit the model from Eq. 6.1 to the data of energy per visit described in the main text. We fit this model using a Bayesian framework with Hamiltonian Monte Carlo (HMC) methods:

$$e_i \sim \text{Normal}(\mu_i, \sigma) \quad (6.2)$$

$$\mu_i = \epsilon_p F_{pink} + \epsilon_b F_{blue} + \epsilon_w F_{white} + \epsilon_y F_{yellow} \quad (6.3)$$

$$\epsilon_p, \epsilon_b, \epsilon_w, \epsilon_y \sim \text{Normal}(0, 10) \quad (6.4)$$

$$\sigma \sim \text{Student-t}(3, 0, 10) \quad (6.5)$$

We ran four chains with a warmup of 1000 iterations and 1000 sampling iterations and using weakly informative priors. We fit our model and determined convergence using the same approach as described in Chapter 2. Finally we used Bayes  $R^2$  to estimate the proportion of variance explained by our model for new data.

The model of energy consumption with flower types as predictors had a value of Bayes  $R^2$  of 0.847. That is, if we were to fit the energy model to new data, we would expect it to estimate around 85% of the variance. Furthermore, the parameter distribution of the energy mode yields estimates very similar to the maximum energy gains per visit Fig. 6.1. That is, each time a bee visited a flower, we would expect it to gain as much energy as the maximum a flower has to offer. Thus, the more visits an individual makes, the more energy gains it obtains.

Table 6.1: Maximum energy gains per visit, for each of the different flower types. Each visit triggered the automatic reward of  $10 \mu\text{l}$ , and each gram of sugar has 17 kilojoules of energy.

Flower type	Sucrose concentration	Max. kilojoules per visit
Blue	2.0 M	0.1165
White	1.5 M	0.0877
Yellow	1.0 M	0.0581
Pink	0.5 M	0.0290

Indeed, plots of total number of floral visits per bee per trial and total energy gains per trial (Fig. 6.2), show that energy gains are strongly correlated with the number of floral visits an individual makes. Thus, we can be confident that *Bombus* individuals were consuming close to the full reward each time they visited an artificial flower.

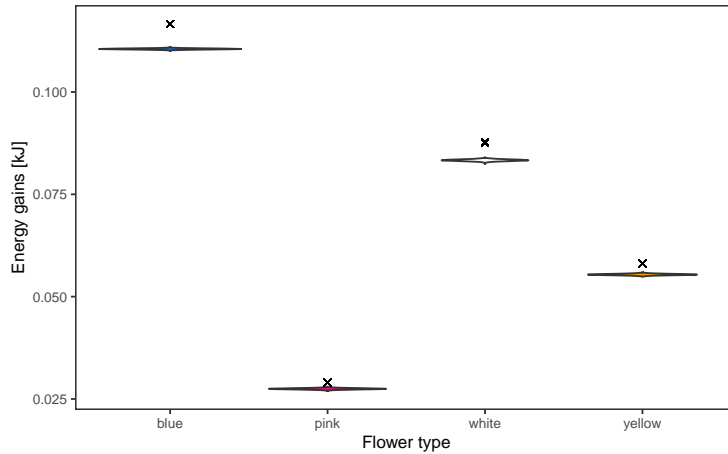


Figure 6.1: Posterior distribution of  $\epsilon$  parameters from Eq. 6.1. Each parameter estimates the mean energetic gain per visit (in kilojoules), per flower type. We have also indicated the maximum gains per visit of the different flower types with an x.

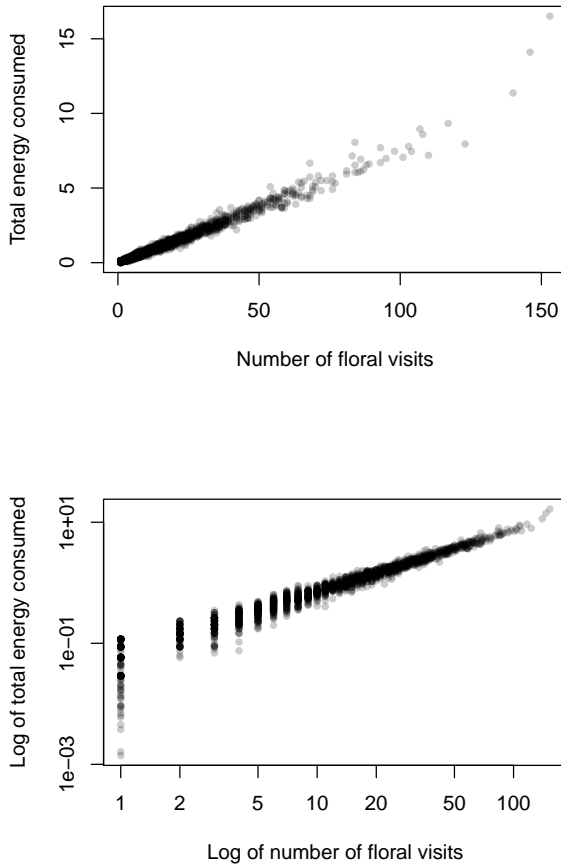


Figure 6.2: Relationship between the total number of visits made by an individual bee and its total energy gains during an experiment trial. In the top panel, the total energy consumed per trial is clearly an increasing function of the number of floral visits an individual makes during the trial. Each point corresponds to observations at the individual level. In the bottom panel, we show the same relationship with log-log axes.

## FORAGING TRIALS AND DATA STRUCTURE

In single-species trials, all but one of the factorial combinations of conspecific co-foragers, pesticide exposure, and two levels of resource availability (instantaneous and delayed refill) had at least two replicates. The only exceptions were the combinations of four and eight *Bombus* individuals foraging under instantaneous floral refill and pesticide exposure. The third level of resource availability, intermediate floral refill time, was tested *only* for 16 *Bombus* individuals foraging at the same time, for the two levels of pesticide exposure (Table 6.2).

In multi-species trials, all but two of the factorial combinations of bee species richness, two levels of resource availability (instantaneous and delayed refill), and pesticide exposure had at least two replicates. The only exception was three foraging species with instantaneous refill and pesticide exposure. Furthermore, not all species of co-foragers were tested under all combinations of resource availability and pesticide exposure, making it impossible to fully disentangle their statistical interaction (Table 6.3).

In total, we tracked the time between floral visits and energy consumed by 735 *Bombus* individuals across 139 single-species trials and by 277 *Bombus* individuals across 112 multi-species trials. We excluded from the analysis the data from bumblebees that were completely inactive within trials (i.e. that did not record a single visit during the 75 minutes), since they do not provide information regarding visitation frequency or energy obtained per visit. Of the data collected from the active bees, we also excluded the first and last record of time and nectar consumption for every individual bumblebee within a trial, unless that individual only made one visit. We excluded those data points since previous research indicates that these points are less informative about foraging behavior and generate skewed data (Edwards et al., 2007). The number of observations we examined amounts to 33919 records of times between floral visits.

Table 6.2: Single-species foraging trials. We show the number of trials for different combinations of *Bombus* abundance, pesticide exposure and refill time. Pesticide exposure is a binary variable that equals to one when all individuals in the trial were subject to a sub-lethal doses of pesticide. Refill time is the time (in seconds) after which an artificial flower could dispense a new sucrose reward after a previous visit.

<i>Bombus</i> abundance	Pesticide exposure	Refill time	Number of trials
4	0	0	2
4	0	540	10
4	1	0	0
4	1	540	13
8	0	0	2
8	0	540	10
8	1	0	0
8	1	540	13
16	0	0	5
16	0	120	34
16	0	540	15
16	1	0	5
16	1	120	14
16	1	540	16

Table 6.3: Multi-species foraging trials. We show the number of trials for different combinations of species richness, pesticide exposure and two levels of resource availability. We also show the number of individuals of each species used in each trial as well as the number of trials per combination. Pesticide exposure and refill time have the same interpretation as in the single-species trials.

Richness	Pesticide exposure	Refill time	<i>Bombus</i> abundance	<i>Apis</i> abundance	<i>Osmia</i> abundance	<i>Megachile</i> abundance	Number of trials
2	0	0	8	0	8	0	7
2	0	0	8	0	0	8	5
2	0	0	8	8	0	0	5
2	1	0	8	0	8	0	2
2	0	540	8	0	8	0	7
2	0	540	8	0	0	8	5
2	0	540	8	8	0	0	5
2	1	540	8	0	8	0	6
2	1	540	8	0	0	8	4
2	1	540	8	8	0	0	6
3	0	0	5	5	6	0	3
3	0	0	6	5	5	0	1
3	0	0	5	6	5	0	1
3	0	0	5	0	6	5	3
3	0	0	6	0	5	5	2
3	0	0	6	5	0	5	2
3	0	0	5	5	0	6	1
3	0	540	6	5	5	0	1
3	0	540	5	5	6	0	3
3	0	540	5	6	5	0	1
3	0	540	5	0	6	5	3
3	0	540	6	0	5	5	3
3	0	540	6	5	0	5	3
3	1	540	6	5	5	0	5
3	1	540	5	5	6	0	2
3	1	540	6	0	5	5	4
3	1	540	5	0	6	5	1
3	1	540	6	5	0	5	1
4	0	0	4	4	4	4	5
4	1	0	4	4	4	4	5
4	0	540	4	4	4	4	5
4	1	540	4	4	4	4	5

## STATISTICAL ANALYSIS

We used hierarchical models to fit the data to the models described in the main text (Eqs. 9-11) because we have multiple observations from the same *Bombus* individuals and to allow each of these individuals to deviate from the parameter's grand mean. For example, predicted times between floral visits for an individual  $b$  of species  $i$  given by the *interference* model would be:

$$\rho_{i,b} = (\alpha + \Delta\alpha_b) + (\beta_i + \Delta\beta_{ib})(P_i - 1) + \sum_j (\beta_j + \Delta\beta_{jb})P_j \quad (6.6)$$

The three deviations from the grand means ( $\Delta\alpha_b$ ,  $\Delta\beta_{ib}$ ,  $\Delta\beta_{jb}$ ) capture the individual specific response and are incorporated in a comparable manner to how random effects are included in mixed-effects models. This way to parameterize our models allowed us to estimate how each individual responded to the treatments, helped to control for pseudo-replication across individual



bees, and pooled information across individual bees to still inform the grand mean when sample size was low. We show how we incorporated the random effects in each model in Table 6.4.

Across all models, we assumed that the times between floral visits followed an exponential distribution that has a rate parameter  $\rho_{i,b}$ . We also required the density-independent rate of all models to be positive, as a “negative” time would be unfeasible as a baseline. Thus we constrained the density independent parameters to be positive. Consequently, we fit non-linear models using the exponential family and the “identity” link. Again, using the *interference* model as an example, our Bayesian one-level hierarchical model of times between floral visits for an individual  $b$  may be written as:

$$t_{i,b} \sim \text{Exponential}(\rho_{i,b}) \quad (6.7)$$

$$\rho_b = e^{(\alpha + \Delta\alpha_b)} + (\beta_i + \Delta\beta_{ib})(P_i - 1) + \sum_j (\beta_j + \Delta\beta_{jb})P_j \quad (6.8)$$

$$\alpha, \beta_i, \beta_j \sim \text{Normal}(0, 10) \quad (6.9)$$

$$\Delta\alpha_b, \Delta\beta_{ib}, \Delta\beta_{jb} \sim \text{Multivariate Normal}(\sigma, \gamma) \quad (6.10)$$

$$\sigma \sim \text{Student-t}(3, 0, 70) \quad (6.11)$$

$$\gamma \sim \text{LKJcorr}(1) \quad (6.12)$$

Table 6.4: Statistical models fitted to the data. Each model includes fixed and random effects that together determine the time between floral visits. The *null* model assumes that neither co-foraging species nor environmental conditions change the times between floral visits. The *interference* model allows the number of visits to change only due to the number of co-foraging bees (i.e. it treats interference as constant across environmental conditions). Finally, the *treatments* model allows the environmental conditions to have an effect on both the density-independent and density-dependent parameters.

Model	Eqn. in main text	Parameter class	Fixed effects	Random effects
<i>null</i>	2.9	density-independent	$\alpha$	$\Delta\alpha_b$
<i>interference</i>	2.10	density-independent	$\alpha$	$\Delta\alpha_b$
		conspecific-dependent	$\beta_i$	$\Delta\beta_{ib}$
		heterospecific-dependent	$\beta_j$	$\Delta\beta_{jb}$
<i>treatments</i>	2.11	density-independent	$\alpha, \alpha_r, \alpha_e$	$\Delta\alpha_b, \Delta\alpha_{rb}, \Delta\alpha_{eb}$
		conspecific-dependent	$\beta_i, \beta_{ir}, \beta_{ie}$	$\Delta\beta_{ib}, \Delta\beta_{irb}, \Delta\beta_{ieb}$
		heterospecific-dependent	$\beta_j, \beta_{jr}, \beta_{je}$	$\Delta\beta_{jb}, \Delta\beta_{jrb}, \Delta\beta_{jeb}$

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## APPENDIX B

THE BIOLOGICALLY-CONSTRAINED FEASIBILITY DOMAIN,  $\beta$ 

We used Monte-Carlo integration methods to estimate the size of the biologically-constrained feasibility domain ( $\beta$ ); that is, the area where both species can have positive abundances given competitive, abundance, and model-based constraints. We performed this integration on the growth-rate parameter space. First, we determined the maximum possible value of the radius ( $R$ ) to integrate over given the abundance constraints under consideration. To do this, we first defined a radius  $R$ , as a function of both species' intrinsic growth rates:

$$R = \sqrt{r_i^2 + r_j^2}, \quad (7.1)$$

where  $r_i$  and  $r_j$  are the growth rates of species  $i$  and  $j$  defined by each model, respectively. We know that, for all of the models used, the vector of species growth rates can be expressed as a linear function of species densities such that:

$$\begin{bmatrix} r_i \\ r_j \end{bmatrix} = \begin{bmatrix} \alpha_{ii} & \alpha_{ij} \\ \alpha_{ji} & \alpha_{jj} \end{bmatrix} \begin{bmatrix} g_i N_i^* \\ g_j N_j^* \end{bmatrix}, \quad (7.2)$$

where the elements of the interaction matrix denote the change in per capita growth rate of species  $i$  under a small change in the density of species  $j$ , and  $g_i N_i^*$  and  $g_j N_j^*$  define the vector of abundances for species  $i$  and  $j$ . Species growth rates can therefore be expressed as:

$$r_i = \alpha_{ii} g_i N_i^* + \alpha_{ij} g_j N_j^* \quad (7.3)$$

$$r_j = \alpha_{ji} g_i N_i^* + \alpha_{jj} g_j N_j^* \quad (7.4)$$

We must therefore find the maximum value of  $R$  given constraints on the maximum abundance of species  $i$  ( $g_i N_{i,max}^*$ ) and of species  $j$  ( $g_j N_{j,max}^*$ ). In the following sections, we show 9 scenarios that describe all the possible values  $R$  can take under such constraints, and how to determine if they can be a maximum.

*Scenario 1: Both species are absent*

If both  $g_i N_i^*$  and  $g_j N_j^*$  have a value of zero, then  $R = 0$ .

*Scenario 2: Species  $i$  is at its maximum abundance and species  $j$  is absent*

Then, the value of  $R$  is:

$$R = \sqrt{(\alpha_{ii} g_i N_{i,max}^*)^2 + (\alpha_{ji} g_i N_{i,max}^*)^2}. \quad (7.5)$$

*Scenario 3: Species  $i$  is absent and species  $j$  is at its maximum abundance*

Then the value of  $R$  is:

$$R = \sqrt{(\alpha_{ij} g_j N_{j,max}^*)^2 + (\alpha_{jj} g_j N_{j,max}^*)^2}. \quad (7.6)$$

*Scenario 4: Both species are at their maximum abundance*

If both species are at their maximum abundance then:

$$R = \sqrt{(\alpha_{ii} g_i N_{i,max}^* + \alpha_{ij} g_j N_{j,max}^*)^2 + (\alpha_{ji} g_i N_{i,max}^* + \alpha_{jj} g_j N_{j,max}^*)^2}. \quad (7.7)$$

*Scenario 5: Species  $j$  is absent*

When species  $j$  is absent, then:

$$R = \sqrt{(\alpha_{ii} g_i N_i^*)^2 + (\alpha_{ji} g_i N_i^*)^2} \quad (7.8)$$

To find the maximum, for mathematical simplicity we can differentiate  $R^2$ :

$$\frac{\partial R^2}{\partial g_i N_i^*} = \alpha_{ii}^2 2g_i N_i^* + \alpha_{ji}^2 2g_i N_i^*, \quad (7.9)$$

and the value of  $g_i N_i^*$  that corresponds to a maximum:

$$\alpha_{ii}^2 2g_i N_i^* + \alpha_{ji}^2 2g_i N_i^* = 0 \quad (7.10)$$

$$g_i N_i^* (2\alpha_{ii}^2 + 2\alpha_{ji}^2) = 0 \quad (7.11)$$

$$g_i N_i^* = 0 \quad (7.12)$$

which inevitably implies  $R = 0$ . Thus when species  $j$  is absent, the maximum of  $R$  is at zero and the maximum value of  $R$  is at the boundary of the constraints.

*Scenario 6: Species  $i$  is absent*

By symmetry, when species  $i$  is absent, the maximum value of  $R$  is at the boundary of the constraints.

*Scenario 7: Species  $j$  is at its maximum abundance*

We can redefine  $R^2$  as:

$$R^2 = (\alpha_{ii}g_iN_i^* + \alpha_{ij}g_jN_{j,max}^*)^2 + (\alpha_{ji}g_iN_i^* + \alpha_{jj}g_jN_{j,max}^*)^2, \quad (7.13)$$

and find the value of  $g_iN_i^*$  where there is a maximum of  $R$ :

$$\frac{\partial R^2}{\partial g_iN_i^*} = 0 = \alpha_{ii}^2 2g_iN_i^* + 2\alpha_{ii}\alpha_{ij}g_jN_{j,max}^* + \alpha_{ji}^2 2g_iN_i^* + 2\alpha_{ji}\alpha_{jj}g_jN_{j,max}^* \quad (7.14)$$

$$g_iN_i^* = \frac{-\alpha_{ii}\alpha_{ij}g_jN_{j,max}^* - \alpha_{ji}\alpha_{jj}g_jN_{j,max}^*}{\alpha_{ii}^2 + \alpha_{ji}^2}. \quad (7.15)$$

Then the value of  $R$  that corresponds to this scenario is:

$$R = \sqrt{\left(\frac{-\alpha_{ii}\alpha_{ij}g_jN_{j,max}^* - \alpha_{ji}\alpha_{jj}g_jN_{j,max}^*}{\alpha_{ii}^2 + \alpha_{ji}^2}\alpha_{ii} + \alpha_{ij}g_jN_{j,max}^*\right)^2 + \left(\frac{-\alpha_{ii}\alpha_{ij}g_jN_{j,max}^* - \alpha_{ji}\alpha_{jj}g_jN_{j,max}^*}{\alpha_{ii}^2 + \alpha_{ji}^2}\alpha_{ji} + \alpha_{jj}g_jN_{j,max}^*\right)^2} \quad (7.16)$$

*Scenario 8: Species i is at its maximum abundance*

Similar to the previous scenario, the value of  $R$  that corresponds to this scenario is:

$$R = \sqrt{\left(\alpha_{ii}g_iN_{i,max}^* + \frac{-\alpha_{ii}\alpha_{ij}g_iN_{i,max}^* - \alpha_{ji}\alpha_{jj}g_iN_{i,max}^*}{\alpha_{ij}^2 + \alpha_{jj}^2}\alpha_{ij}\right)^2 + \left(\alpha_{ji}g_iN_{i,max}^* + \frac{-\alpha_{ii}\alpha_{ij}g_iN_{i,max}^* - \alpha_{ji}\alpha_{jj}g_iN_{i,max}^*}{\alpha_{ij}^2 + \alpha_{jj}^2}\alpha_{jj}\right)^2} \quad (7.17)$$

*Scenario 9: Neither species is at its maximum abundance*

If both species are present but neither of is at their maximum abundances, then:

$$R^2 = (\alpha_{ii}g_iN_i^* + \alpha_{ij}g_jN_j^*)^2 + (\alpha_{ji}g_iN_i^* + \alpha_{jj}g_jN_j^*)^2 \quad (7.18)$$

which can be expanded to:

$$R^2 = \alpha_{ii}^2g_i^2N_i^{*2} + 2\alpha_{ii}\alpha_{ij}g_iN_i^*g_jN_j^* + \alpha_{ij}^2g_j^2N_j^{*2} + \alpha_{ji}^2g_i^2N_i^{*2} + 2\alpha_{ji}\alpha_{jj}g_iN_i^*g_jN_j^* + \alpha_{jj}^2g_j^2N_j^{*2} \quad (7.19)$$

To find a maximum, we require:

$$\frac{\partial R_2}{\partial g_iN_i^*} = \alpha_{ii}^22g_iN_i^* + 2\alpha_{ii}\alpha_{ij}g_jN_j^* + \alpha_{ji}^22g_iN_i^* + 2\alpha_{ji}\alpha_{jj}g_jN_j^* \quad (7.20)$$

$$\frac{\partial R_2}{\partial g_jN_j^*} = 2\alpha_{ii}\alpha_{ij}g_iN_i^* + \alpha_{ij}^22g_jN_j^* + 2\alpha_{ji}\alpha_{jj}g_iN_i^* + \alpha_{jj}^22g_jN_j^* \quad (7.21)$$

If we solve for the abundance of species  $i$  in the second equation at a maximum:

$$\alpha_{ii}\alpha_{ij}g_iN_i^* + \alpha_{ij}^2g_jN_j^* + \alpha_{ji}\alpha_{jj}g_iN_i^* + \alpha_{jj}^2g_jN_j^* = 0 \quad (7.22)$$

$$N_i = -g_jN_j^* \frac{\alpha_{ij}^2 + \alpha_{jj}^2}{\alpha_{ii}\alpha_{ij} + \alpha_{ji}\alpha_{jj}} \quad (7.23)$$



and for species  $j$  in the first equation:

$$\alpha_{ii}^2 - g_j N_j^* \frac{\alpha_{ij}^2 + \alpha_{jj}^2}{\alpha_{ii}\alpha_{ij} + \alpha_{ji}\alpha_{jj}} + \alpha_{ii}\alpha_{ij}g_j N_j^* + \alpha_{ji}^2 - g_j N_j^* \frac{\alpha_{ij}^2 + \alpha_{jj}^2}{\alpha_{ii}\alpha_{ij} + \alpha_{ji}\alpha_{jj}} + \alpha_{ji}\alpha_{jj}g_j N_j^* = 0 \quad (7.24)$$

$$g_j N_j^* = 0 \quad (7.25)$$

This implies that there is no maximum for when both species are present but neither of them is at their maximum abundance. As a result of these nine scenarios, the maximum value of  $R$  can be found only where one or both of the species are at their maximum abundances, which correspond to only five possible scenarios (Eqns. 7.5, 7.6, 7.7, 7.16, 7.17). In our framework, given an interaction matrix and the constraints on species abundances, we calculated the value of  $R$  for each one of the five possible scenarios and chose the value that was the highest.

### Integration methods

Once we determined the range of  $R$  to integrate over, we performed a Monte Carlo Integration to determine the size of the biologically-constrained feasibility domain. We did this by generating random points within a circle of radius  $R$ . We discarded points that did not correspond to positive abundances of both species given their interaction matrix (i.e., we kept only feasible growth rates). We further discarded points that corresponded to abundances greater than  $g_i N_{i,max}^*$  and  $g_j N_{j,max}^*$ . Finally, we discarded all of the points that fell outside the model-based constraints for each species (Table 1 of the main text). This method allowed us to sample points that were feasible *and* biologically plausible. We set our integration to sample random points until we had at least 500 points inside the feasible and biologically-plausible space, or when it reached 200,000 total samples. We also kept track of all of the points that were discarded. All calculations were done in the programming language *R* (R Core Team, 2013).

Once we had a sample of feasible and biologically plausible points, we determined the points that comprise the convex hull around them using the function *chull* from the package *grDevices*. To determine the vertices of the convex hull, we required a sample of at least 4 points. If the sample of the MC integration was lower than 4 points, we did not perform further calculations and determined that the biologically-constrained feasibility domain could not be detected and was effectively of size  $\beta \approx 0$ . To determine if the vertices were in fact describing a convex hull, we also kept track if any of the discarded points could be inside the area described by the vertices using the function *point.in.polygon* from the package *sp*. Finally, we determined the size of the area described by the convex hull using the function *Polygon* from the package *sp*.

MINIMUM DISTANCE FROM THE EDGE,  $\delta$ 

To calculate the minimum euclidean distance from the observed growth rates to the edge of the biologically-constrained feasibility domain, we used the set of vertices describing that domain's boundaries. For every two adjacent vertices, we calculated the distance between species' growth rates  $r_i$  and  $r_j$ , and the perpendicular projection of the line between the vertices using the function *pointLineD* from the package *SpatialGraph*. We also calculated the euclidean distance between the observed growth rates and the two adjacent vertices. From those three measures, we determined the shortest distance. We performed these calculations for every set of adjacent vertices, and determined  $\delta$  as the minimum of all of the values we obtained.

AREA IN MONOCULTURE,  $\gamma$ 

To determine the parameter space where both species can grow in monoculture given abundance and model-based constraints, we first determined the constrained values of species growth rates  $r_{i,c}$  and  $r_{j,c}$ . Note that empirical values of species growth rates  $r_i$  and  $r_j$  can take negative values if competition coefficients are negative, which would imply facilitative interactions. Necesarily, the parameter space where both species can grow in monoculture includes the coordinate 0,0. Thus, from this coordinate, we calculated the maximum value each species' growth rates could take given abundance and model constraints.

When competition coefficients are positive, then the constrained values of species growth rates are:

$$r_{i,c} = \min \{0, r_i, r_{i,max}, upper_i\} \quad (7.26)$$

$$r_{j,c} = \min \{0, r_j, r_{j,max}, upper_j\} \quad (7.27)$$

where  $upper_i$  and  $upper_j$  are the upper limits of species growth rates given the models used to quantify density dependence for each species, and  $r_{i,max}$  and  $r_{j,max}$  are the growth rates that solve for the maximum abundances given abundance constraints for each species.

However, when competition coefficients are negative, then the constrained values of species growth rates are:

$$r_{i,c} = \max \{0, r_i, r_{i,max}, lower_i\} \quad (7.28)$$

$$r_{j,c} = \max \{0, r_j, r_{j,max}, lower_j\} \quad (7.29)$$

where  $lower_i$  and  $lower_j$  are the lower limits of species growth rates given models used to quantify density dependence for each species. Together,  $r_{i,c}$  and

$r_{j,c}$  describe the parameter space where both species can grow in monoculture, that is also within model-based and abundance constraints. To measure how big is that parameter space, we calculated  $\gamma$  as:

$$\gamma = |r_{i,c} \cdot r_{j,c}| \quad (7.30)$$

#### SURVIVAL, GERMINATION AND MAXIMUM ABUNDANCES

We relied on independent empirical measures of seed germination rate, seed survival rate, and maximum expected abundances for both species. We obtained values of seed survival rate and germination rate for each species from a previous study that looked at species-level metrics in our study system (Towers et al., 2021).

We determined the maximum abundance of seeds based on empirical observations of individual plants of both species within a 7.5 cm radius. Both *Vellia rosea* and *Trachymene cyanopetala* rarely exceed abundances larger than 100 plant individuals within a 7.5 cm radius (Trace E. Martyn, personal communications). However, we decided to use a more conservative, larger threshold than these empirical observations to impose conservative abundance constraints on the system. Therefore, we used a value 5 times higher than the maximum observed abundance for both species: 500 individuals. Since our model-based predictions are based on population dynamics of seeds and not plant individuals, however, we used the aforementioned germination rates to determine the number of seeds that we would expect to produce 500 individual plants of each species. The resulting seed survival rates, germination rates, and maximum abundances we used in our analyses were:

Table 7.1: Seed survival rates, germination rates, and maximum abundances we used in our analyses

Species	Germination rate	Seed survival rate	Maximum seed abundance
<i>Vellia rosea</i>	0.964	0.965	518
<i>Trachymene cyanopetala</i>	0.474	0.969	1054

## POSTERIOR DISTRIBUTIONS OF MODEL PARAMETERS

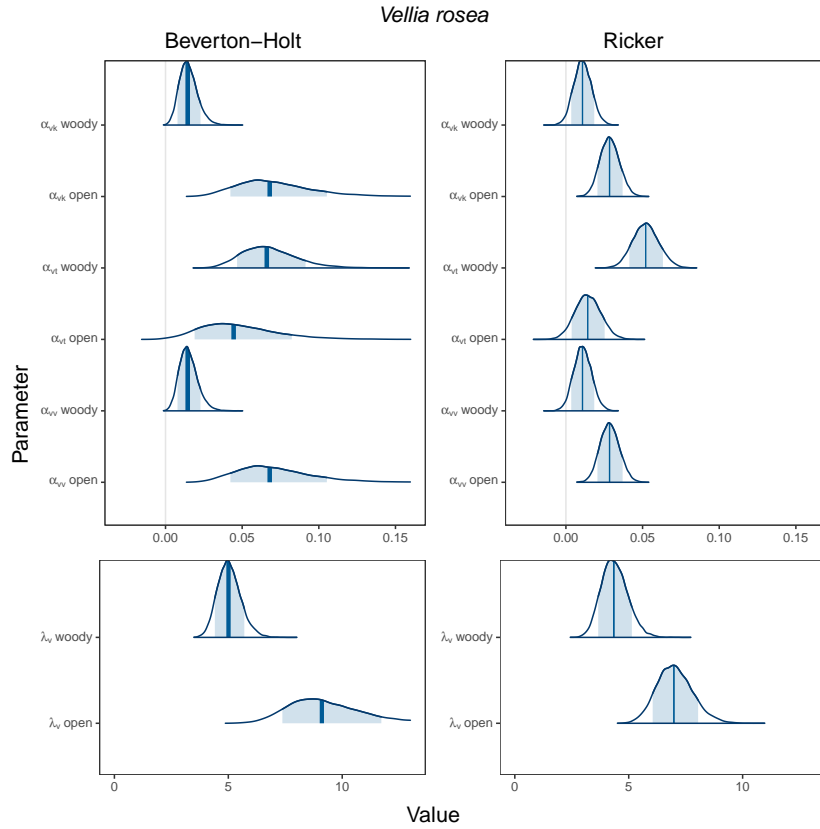


Figure 7.1: The posterior distributions of competition coefficients and intrinsic fecundity in the Beverton–Holt model and the Ricker model for *Vellia rosea*. The subscript  $v$  in parameter names denotes the species *Vellia rosea*, while the subscript  $t$  denotes the species *Trachymene cyanopetala*, and the subscript  $k$  other species that germinated in the system. Solid blue lines represent median estimates of parameter values, while shaded blue areas correspond to the 80% probability mass of the posterior distribution of each parameter. Finally, we denote the environment where interactions took place to estimate parameter values with *open* and *woody*, as we do in [Chapter 3](#)

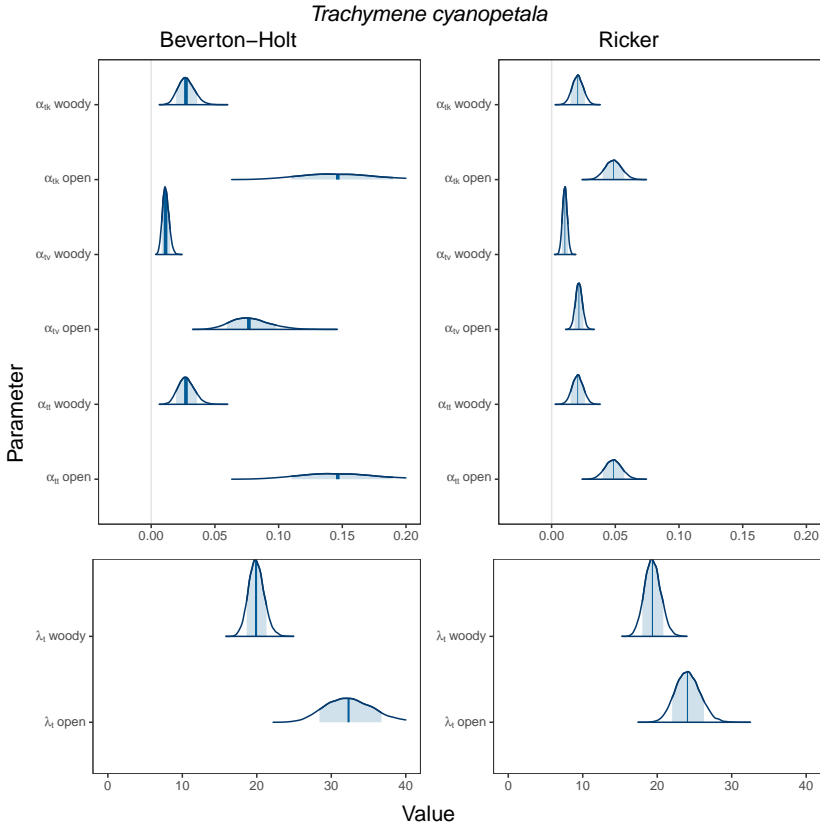


Figure 7.2: The posterior distributions of competition coefficients and intrinsic fecundity in the Beverton–Holt model and the Ricker model for *Trachymene cyanopetala*. The subscript  $v$  in parameter names denotes the species *Vellia rosea*, while the subscript  $t$  denotes the species *Trachymene cyanopetala*, and the subscript  $k$  other species that germinated in the system. Solid blue lines represent median estimates of parameter values, while shaded blue areas correspond to the 80% probability mass of the posterior distribution of each parameter. Finally, we denote the environment where interactions took place to estimate parameter values with *open* and *woody*, as we do in the [Chapter 3](#)



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## COLOPHON

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