

INCREASING REALISM IN MODELS OF BIOTIC INTERACTIONS:

ecological and evolutionary consequences



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ABSTRACT

Interactions between organisms give rise to emergent properties of natural systems. This underpins the ubiquity of biotic interactions 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.

PREFACE

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*.

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.

Certification by Co-authors:

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- The above statement correctly reflects the nature and extent of the Doctoral candidate's contribution to this co-authored work
- In cases where the candidate was the lead author of the co-authored work he or she wrote the text

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Signature:

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

Date: 2021-11-22

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Here go my aknowledgments

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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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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 (briggs_variation_2018; 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 Tschamtkke, 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.

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

This is your bayesian competition manauscript

COEXISTENCE OF ALLELES

This is your coexistence of alleles manuscript

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 model realism. Furthermore, I provide direct evidence that many models used to describe biotic interactions are oversimplistic since 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

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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 effects 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 constants (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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