

# INCREASING REALISM IN MODELS OF BIOTIC INTERACTIONS:

*ecological and evolutionary consequences*



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Different abstractions from the same wholes capture different aspects of the reality but also leave us with different blindnesses. Therefore it is always necessary to recognize that our abstractions are intellectual constructs, that an “object” kicks and screams when it is abstracted from its context and may take its revenge in leading us astray.

– Richard Levins



## GENERAL INTRODUCTION

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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 models that describe 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 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 predominant 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 modelers' particular school of thought and mathematical convince (Bascompte, Jordano, and Olesen, 2006b; Holland, Okuyama, and DeAngelis, 2006).

### *The perils of simple models*

Always favoring 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 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 Tscharrntke, 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 predictions 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 allele's 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 to understand 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

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

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## 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 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

## CONCLUSION

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 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 abiotic and biotic 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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