IS SIMPLE ALWAYS BETTER?

The consequences of relaxing simplifying assumptions in models of biotic interactions

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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

ABSTRACT

Interactions between organisms have a central role in the study of ecological and evolutionary dynamics. The study of biotic interactions usually requires the use of models and simplifying assumptions about reality, since it is impossible to include every aspect of the real world in any model. Choices like the number of species that can alter the interaction between a focal pair, what abiotic variables constitute the environment, and even what type of mathematical formulation to use to capture the system's dynamics are common yet implicit in many ecological and evolutionary models. However, simplifying assumptions can lead to ignoring important heterogeneities at various levels, which could dramatically change model-based predictions. In this thesis, I explore with theoretical and empirical tools how relaxing simplifying assumptions in models of interactions between organisms change predictions related to diversity maintenance at ecological and evolutionary scales. Throughout my thesis, I focus on different types of interactions and organisms, and propose mathematical and statistical frameworks to incorporate biotic and abiotic variables, as well as different sources of uncertainty in our representations of biotic interactions.

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 roles of pollinator-pollinator interactions and abiotic conditions in altering the times between floral visits of a focal pollinator. I show that while density-dependent responses can substantially change the predicted number of visits a pollinator makes, they also strongly depend on the abiotic context pollinators experience. In Chapter 3 I explore how incorporating different sources of uncertainty changes our 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 an experimental system. I provide direct evidence that predictions of species coexistence are likely to change given the models used to quantify density-dependence as well as a theoretical framework to explore predictions made with different models. Finally, in Chapter 4 I adopted an ecological framework to examine evolutionary dynamics of sexually antagonistic alleles through the same lens as the coexistence of competing species. I show that incorporating environmental fluctuations can substantially increase the amount of genetic diversity in a population under sexually antagonistic selection. Overall, the results of this thesis show that the assumptions adopted by some ecological and evolutionary models tend to be oversimplifying. This thesis also provides the tools for ecologists and evolutionary biologists to explore a more complex representation of biotic interactions

PREFACE

This thesis is a collection of three stand alone 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 **??** I focus on summarising the results from each of my thesis chapters, their combined implications both in both how we study interactions and their consequences for diversity maintenance and 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 submission, each of these three articles are in different stages of the publication process and are formatted in the style of a journal article.

??: "The context dependency of pollinator interference: how environmental conditions and co-foraging species impact floral visitaion" was published on May 2021 in the journal of *Ecology Letters* in volume .

??: "The interplay of environmental conditions, parameter sensitivity and structural sensitivity in predictions of species coexistence" is in preparation for submission to *Ecology Letters*.

??: "Coexistence of sexually antagonistic alleles: insights of Modern Coexistence Theory into the maintenance of genetic diversity" is in preparation for submission to *The American Naturalist*.

Part I

GENERAL INTRODUCTION

1 INTRODUCTION

Interactions between organisms underpin the persistence of almost all life forms on Earth (Lawton, 1999). Furthermore, 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 reciprocal forces that organisms exert on each other (Chase and Leibold, 2009; Gause, 1934; HilleRisLambers et al., 2012; MacArthur and Levins, 1967; Thompson, 1999).

The study of biotic interactions often requires the use of mathematical models to represent them (Maynard-Smith, 1978). 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 reciprocally affect each other. Almost all known types of interactions can be accurately described in the form of mathematical expressions; mutualistic interactions, competition, parasitism, commensalism, and even the co-evolution of species. Second, they are practical tools with which to make predictions beyond the phenomena they describe. For instance.

However, models that capture the effect of biotic interactions, are abstractions of reality. It is rare that we know the exact equations governing a system or the full set of biotic and abiotic factors (song). Our abstractions always reflect choices. A common assumption in ecological en evolutionary models, is that in order to achieve general insight, we should favour simple models. Indeed there is a general belief in ecology and evolution that a good model should include as little as possible.

The simplifying assumptions made to represent biotic interactions can dramatically impact model-based predictions. For instance, the elementary pair-wise interactions between species have been studied extensively.

Thus, When is relaxing the simplifying assumptions in models of of biotic interactions necessary? Theoretical studies typically make two critical assumptions that do not hold in real communities, thus limiting their applicability.

In this thesis, I add another criteria to that, when it fundamentallyl.

INTRODUCING BIOTIC DRIVERS

I investigate precisely this and explore how

EXPLORING UNCERTAINTY

NON-CONSTANT ENVIRONMENTS

CONCLUDING REMARKS

The individual chapters of this thesis are thematically broad but all address in a different way the consequences of increasing complexity in models of biotic interactions. With the exception of **??** I explore the consequences in terms of the coexistence of species.

changes our understanding of the system. Through out this thesis I explored different ecological systems, with different types of interactions and species in them. However, the fundamental questions remains : what happens when add biological, environmental and mathematical complexity to the study of species interactions? Do they change our predictions?

As scientists, narrative reasoning allows us to explore, at a high level, the possible trajectories that evolution may take.

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COLOPHON

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