

# Introduction

Alba Cervantes-Loreto

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; Wootton & Stouffer, 2016; Song & Saavedra, 2018), resilience (Capdevila *et al.*, 2021), ecosystem functioning (Turnbull *et al.*, 2013; Godoy *et al.*, 2020), 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 (Gause, 1934; MacArthur & Levins, 1967; Thompson, 1999; HilleRisLambers *et al.*, 2012; Chase & Leibold, 2009).

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 *et al.*, 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 described in the form of mathematical expressions that reproduce the observed data faithfully (Volterra, 1926; Holling, 1959; Holt, 1977; Adler *et al.*, 2018; Wood & Thomas, 1999; Holland *et al.*, 2002; Vázquez *et al.*, 2005; Stouffer & Novak,

2021) . For example, the effect neighboring plants have on each other can be accurately described in various natural systems with functions that include solely the densities of the interacting species as well as a form of negative density dependence (Adler *et al.*, 2018; Hart *et al.*, 2018). 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 (Evans *et al.*, 2012; Stouffer, 2019). For instance, models that describe competitive interactions between plants have been extensively used to demonstrate the mechanisms that maintain diversity when species compete for the same pool of resources (Levine & HilleRisLambers, 2009; Godoy *et al.*, 2014; Godoy & Levine, 2014; Stouffer *et al.*, 2018; Bimler *et al.*, 2018).

However useful, models that capture the effect of biotic interactions are abstractions of reality and abstractions always reflect choices (Levins, 2006). Including all aspects of reality in a model 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 (Evans *et al.*, 2012). 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 good model should include as little as possible (Evans *et al.*, 2013; Orzack, 2012). This belief is often rooted in an implicit philosophical stance that one can not 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, 2006; Evans *et al.*, 2012).

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 a model is built for. Models of biotic interactions often fall into the category of “demonstration models”. 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 produce the phenomena of interest (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 what are the necessary principles and thus the answer to the question of when is a model realistic enough becomes the responsibility of the modeler. In many cases, the answer to this question can appear arbitrary or solely determined by the predominant paradigm regarding the studied system (Holland *et al.*, 2006; Bascompte *et al.*, 2006; AlAdwani & Saavedra, 2019; Martyn *et al.*, 2021).

Always favoring simple models in ecological and evolutionary contexts can be problematic from two perspectives.

## 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 organisms. 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

62 of species interactions? Do they change our predictions?

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