

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 in order to achieve general insights, we should favour 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). These belief is often rooted on a 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 modelled 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,

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

One of the impediments in comparing more complex models to simpler ones comes from the fact that there is no mathematical framework to include complexity.

A

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

62 happens when add biological, environmental and mathematical complexity to the study
63 of species interactions? Do they change our predictions?

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

References

- Adler, P.B., Smull, D., Beard, K.H., Choi, R.T., Furniss, T., Kulmatiski, A., Meiners, J.M., Tredennick, A.T. & Veblen, K.E. (2018). Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. *Ecology letters*, 21, 1319–1329.
- Bimler, M.D., Stouffer, D.B., Lai, H.R. & Mayfield, M.M. (2018). Accurate predictions of coexistence in natural systems require the inclusion of facilitative interactions and environmental dependency. *Journal of Ecology*, 106, 1839–1852.
- Box, G.E., Luceño, A. & del Carmen Paniagua-Quinones, M. (2011). *Statistical control by monitoring and adjustment*. vol. 700. John Wiley & Sons.
- Capdevila, P., Stott, I., Oliveras Menor, I., Stouffer, D.B., Raimundo, R.L., White, H., Barbour, M. & Salguero-Gómez, R. (2021). Reconciling resilience across ecological systems, species and subdisciplines.
- Chase, J.M. & Leibold, M.A. (2009). *Ecological niches*. University of Chicago Press.
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual review of Ecology and Systematics*, 31, 343–366.
- Evans, M.R., Grimm, V., Johst, K., Knuuttila, T., De Langhe, R., Lessells, C.M., Merz, M., O'Malley, M.A., Orzack, S.H., Weisberg, M. *et al.* (2013). Do simple models lead to generality in ecology? *Trends in ecology & evolution*, 28, 578–583.

85 Evans, M.R., Norris, K.J. & Benton, T.G. (2012). Predictive ecology: systems approaches.

86 Gause, G.F. (1934). Experimental analysis of vito volterra's mathematical theory of the
87 struggle for existence. 79, 16–17.

88 Godoy, O., Gómez-Aparicio, L., Matías, L., Pérez-Ramos, I.M. & Allan, E. (2020). An
89 excess of niche differences maximizes ecosystem functioning. *Nature communications*,
90 11, 1–10.

91 Godoy, O., Kraft, N.J.B. & Levine, J.M. (2014). Phylogenetic relatedness and the determi-
92 nants of competitive outcomes. *Ecology Letters*, 17, 836–844.

93 Godoy, O. & Levine, J.M. (2014). Phenology effects on invasion success: insights from
94 coupling field experiments to coexistence theory. *Ecology*, 95, 726–736.

95 Hart, S.P., Freckleton, R.P. & Levine, J.M. (2018). How to quantify competitive ability.
96 *Journal of Ecology*, 106, 1902–1909.

97 HilleRisLambers, J., Adler, P.B., Harpole, W.S., Levine, J.M. & Mayfield, M.M. (2012).
98 Rethinking community assembly through the lens of coexistence theory. *Annual review*
99 *of ecology, evolution, and systematics*, 43, 227–248.

100 Holland, J.N., DeAngelis, D.L. & Bronstein, J.L. (2002). Population dynamics and mutu-
101 alism: functional responses of benefits and costs. *The American Naturalist*, 159, 231–244.

102 Holling, C.S. (1959). Some characteristics of simple types of predation and parasitism1.
103 *The Canadian Entomologist*, 91, 385–398.

- 104 Holt, R.D. (1977). Predation, apparent competition, and the structure of prey communi-
105 ties. *Theoretical population biology*, 12, 197–229.
- 106 Lawton, J.H. (1999). Are there general laws in ecology? *Oikos*, pp. 177–192.
- 107 Levine, J.M. & HilleRisLambers, J. (2009). The importance of niches for the maintenance
108 of species diversity. *Nature*, 461, 254–257.
- 109 Levins, R. (2006). Strategies of abstraction. *Biology and Philosophy*, 21, 741–755.
- 110 MacArthur, R. & Levins, R. (1967). The limiting similarity, convergence, and divergence
111 of coexisting species. *The american naturalist*, 101, 377–385.
- 112 May, R.M. (1972). Will a large complex system be stable? *Nature*, 238, 413–414.
- 113 Maynard-Smith, J. (1978). *Models in ecology*. CUP Archive.
- 114 Orzack, S.H. (2012). The philosophy of modelling or does the philosophy of biology have
115 any use? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367, 170–180.
- 116 Saavedra, S., Rohr, R.P., Bascompte, J., Godoy, O., Kraft, N.J. & Levine, J.M. (2017). A
117 structural approach for understanding multispecies coexistence. *Ecological Monographs*,
118 87, 470–486.
- 119 Song, C. & Saavedra, S. (2018). Will a small randomly assembled community be feasible
120 and stable? *Ecology*, 99, 743–751.
- 121 Stouffer, D.B. (2019). All ecological models are wrong, but some are useful. *Journal of*
122 *Animal Ecology*, 88, 192–195.

- 123 Stouffer, D.B. & Novak, M. (2021). Hidden layers of density dependence in consumer
124 feeding rates. *Ecology Letters*, 24, 520–532.
- 125 Stouffer, D.B., Wainwright, C.E., Flanagan, T. & Mayfield, M.M. (2018). Cyclic population
126 dynamics and density-dependent intransitivity as pathways to coexistence between co-
127 occurring annual plants. *Journal of Ecology*, 106, 838–851.
- 128 Thompson, J.N. (1999). The evolution of species interactions. *Science*, 284, 2116–2118.
- 129 Turnbull, L.A., Levine, J.M., Loreau, M. & Hector, A. (2013). Coexistence, niches and
130 biodiversity effects on ecosystem functioning. *Ecology letters*, 16, 116–127.
- 131 Vázquez, D.P., Morris, W.F. & Jordano, P. (2005). Interaction frequency as a surrogate for
132 the total effect of animal mutualists on plants. *Ecology letters*, 8, 1088–1094.
- 133 Volterra, V. (1926). Fluctuations in the abundance of a species considered mathematically.
134 *Nature*, 118, 558–560.
- 135 Wood, S.N. & Thomas, M.B. (1999). Super-sensitivity to structure in biological models.
136 *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 266, 565–570.
- 137 Wootton, K. & Stouffer, D. (2016). Many weak interactions and few strong; food-web
138 feasibility depends on the combination of the strength of species' interactions and their
139 correct arrangement. *Theoretical Ecology*, 9, 185–195.