

INCREASING REALISM IN MODELS OF BIOTIC INTERACTIONS:

ecological and evolutionary consequences



ALBA CERVANTES LORETO

*A thesis submitted in fulfillment of the requirements
for the degree of Doctor of Philosophy*

School of Biological Sciences
College of Science
University of Canterbury

Alba Cervantes Loreto. *Increasing realism in models of biotic interactions: ecological and evolutionary consequences* ; Doctoral thesis, November 2021

SUPERVISOR:

Daniel B. Stouffer

CO-SUPERVISORS:

Margaret M. Mayfield

Andrew Letten

Christchurch, New Zealand

Con amor a mis padres, Rosalva Loreto y Francisco Cervantes

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 visitation” 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

Deputy Vice-Chancellor's Office
Postgraduate Research Office



Co-Authorship Form

This form is to accompany the submission of any thesis that contains research reported in co-authored work that has been published, accepted for publication, or submitted for publication. A copy of this form should be included for each co-authored work that is included in the thesis. Completed forms should be included at the front (after the thesis abstract) of each copy of the thesis submitted for examination and library deposit.

Please indicate the chapter/section/pages of this thesis that are extracted from co-authored work and provide details of the publication or submission from the extract comes:

Chapters 2, 3 and 4 in this dissertation are extracted from co-authored work. Chapter 2 has been published in the journal *Ecology Letters* in volume 24, no. 7, pages 1443–1454.

Please detail the nature and extent (%) of contribution by the candidate:

For Chapter 2, the candidate contributed to the development of the theoretical framework (80%), wrote the code (100%), analysed all data (100%), and wrote the manuscript's first draft (100%).

For Chapter 3, the candidate contributed to the development of the theoretical framework (80%), wrote the code (100%), analysed all data (100%), and wrote the manuscript's first draft (100%).

For Chapter 4, the candidate contributed to the development of the theoretical framework (60%), wrote the code (80%), analysed all data (100%), and wrote the manuscript's first draft (100%).

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:

If there is more than one co-author then a single co-author can sign on behalf of all

The undersigned certifies that:

- 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

Name: Daniel B. Stouffer

Signature:

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

Date: 2021-11-22

ACKNOWLEDGEMENTS

Here go my aknowledgments

CONTENTS

I INTRODUCTION

- 1 GENERAL INTRODUCTION 3

II FRAMEWORKS FOR INCLUDING BIOTIC AND ABIOTIC COMPLEXITY IN MODELS OF BIOTIC INTERACTIONS

- 2 THE CONTEXT DEPENDENCY OF POLLINATOR INTERFERENCE:
HOW ENVIRONMENTAL CONDITIONS AND CO-FORAGING SPECIES
IMPACT FLORAL VISITATION 19
- 3 THE INTERPLAY OF ENVIRONMENTAL CONDITIONS, PARAMETER
SENSITIVITY AND STRUCTURAL SENSITIVITY IN PREDICTIONS
OF SPECIES COEXISTENCE 45
- 4 COEXISTENCE OF ALLELES 47

III FINAL WORDS

- 5 CONCLUSION 51

IV APPENDICES

- 6 APPENDIX A 63

LIST OF FIGURES

- Figure 2.1 Visualizing the mathematical relationship between visitation rate and time between visits. 23
- Figure 2.2 Model predictions of how the time between floral visits changed as the number of co-foragers increased and under different environmental conditions 31
- Figure 2.3 Model predictions of the effect an individual co-forager had on the time between visits of *Bombus* as resource availability increased 33
- Figure 2.4 The effect an individual co-forager had on the time between floral visits 34
- Figure 6.1 Posterior distribution of ϵ parameters from Eq. 6.1. Each parameter estimates the mean energetic gain per visit (in kilojoules), per flower type. We have also indicated the maximum gains per visit of the different flower types with an x. 64
- Figure 6.2 Relationship between the total number of visits made by an individual bee and its total energy gains during an experiment trial. In the top panel, the total energy consumed per trial is clearly an increasing function of the number of floral visits an individual makes during the trial. Each point corresponds to observations at the individual level. In the bottom panel, we show the same relationship with log-log axes. 65

LIST OF TABLES

Table 2.1	Model comparison table	30
Table 6.1	Maximum energy gains per visit	64
Table 6.2	Single-species foraging trials	67
Table 6.3	Multi-species foraging trials	68
Table 6.4	Statistical models fitted to the data	70

Part I

INTRODUCTION

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.

BIBLIOGRAPHY

- Abrams, Peter A (1983). 'Arguments in favor of higher order interactions.' In: *The American Naturalist* 121.6, pp. 887–891.
- (2001). 'Describing and quantifying interspecific interactions: a commentary on recent approaches.' In: *Oikos* 94.2, pp. 209–218.
- Adler, Peter B, Danielle Smull, Karen H Beard, Ryan T Choi, Tucker Furniss, Andrew Kulmatiski, Joan M Meiners, Andrew T Tredennick, and Kari E Veblen (2018). 'Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition.' In: *Ecology letters* 21.9, pp. 1319–1329.
- Aldebert, Clement and Daniel B Stouffer (2018). 'Community dynamics and sensitivity to model structure: towards a probabilistic view of process-based model predictions.' In: *Journal of the Royal Society Interface* 15.149, p. 20180741.
- Bascompte, Jordi, Pedro Jordano, and Jens M Olesen (2006a). 'Asymmetric coevolutionary networks facilitate biodiversity maintenance.' In: *Science* 312.5772, pp. 431–433.
- (2006b). 'Response to Comment on "Asymmetric Coevolutionary Networks Facilitate Biodiversity Maintenance".' In: *Science* 313.5795, pp. 1887–1887.
- Bimler, Malyon D., Daniel B. Stouffer, Hao Ran Lai, and Margaret M. Mayfield (2018). 'Accurate predictions of coexistence in natural systems require the inclusion of facilitative interactions and environmental dependency.' In: *Journal of Ecology* 106.5, pp. 1839–1852.
- Box, George EP, Alberto Luceño, and Maria del Carmen Paniagua-Quinones (2011). *Statistical control by monitoring and adjustment*. Vol. 700. John Wiley & Sons.
- Briggs, Heather M, Stuart Graham, Callin M Switzer, and Robin Hopkins (2018). 'Variation in context-dependent foraging behavior across pollinators.' In: *Ecology and evolution* 8.16, pp. 7964–7973.
- Briggs, Heather Mae (2016). 'Competitive context drives pollinator behavior: linking foraging plasticity, natural pollen deposition, and plant reproduction.' PhD thesis. UC Santa Cruz.
- Brosi, Berry J. and Heather M. Briggs (Aug. 2013). 'Single pollinator species losses reduce floral fidelity and plant reproductive function.' In: *Proceedings of the National Academy of Sciences* 110.32, pp. 13044–13048.

- Capdevila, Pol, Iain Stott, Imma Oliveras Menor, Daniel B Stouffer, Rafael LG Raimundo, Hannah White, Matthew Barbour, and Roberto Salguero-Gómez (2021). *Reconciling resilience across ecological systems, species and subdisciplines*.
- Chase, Jonathan M and Mathew A Leibold (2009). *Ecological niches*. University of Chicago Press.
- Chesson, Peter (2000). 'Mechanisms of maintenance of species diversity.' In: *Annual review of Ecology and Systematics* 31.1, pp. 343–366.
- Classen, Alice, Connal D Eardley, Andreas Hemp, Marcell K Peters, Ralph S Peters, Axel Ssymank, and Ingolf Steffan-Dewenter (2020). 'Specialization of plant–pollinator interactions increases with temperature at Mt. Kilimanjaro.' In: *Ecology and evolution* 10.4, pp. 2182–2195.
- Cnaani, Jonathan, James D. Thomson, and Daniel R. Papaj (2006). 'Flower Choice and Learning in Foraging Bumblebees: Effects of Variation in Nectar Volume and Concentration.' In: *Ethology* 112.3, pp. 278–285.
- Connallon, Tim and Andrew G Clark (2012). 'A general population genetic framework for antagonistic selection that accounts for demography and recurrent mutation.' In: *Genetics* 190.4, pp. 1477–1489.
- Connallon, Tim, Shefali Sharma, and Colin Olito (Jan. 2019). 'Evolutionary Consequences of Sex-Specific Selection in Variable Environments: Four Simple Models Reveal Diverse Evolutionary Outcomes.' In: *The American Naturalist* 193.1, pp. 93–105.
- Crick, F (1988). 'What Mad Pursuit: A Personal View of Scientific Discovery. Basic Books, New York.' In:
- D'Andrea, Rafael, Annette Ostling, and James P O'Dwyer (2018). 'Translucent windows: How uncertainty in competitive interactions impacts detection of community pattern.' In: *Ecology Letters* 21.6, pp. 826–835.
- Evans, Matthew R, Volker Grimm, Karin Johst, Tarja Knuuttila, Rogier De Langhe, Catherine M Lessells, Martina Merz, Maureen A O'Malley, Steve H Orzack, Michael Weisberg, et al. (2013). 'Do simple models lead to generality in ecology?' In: *Trends in ecology & evolution* 28.10, pp. 578–583.
- Flora, Cordoleani, Nerini David, Gauduchon Mathias, Morozov Andrew, and Poggiale Jean-Christophe (Aug. 2011). 'Structural sensitivity of biological models revisited.' In: *Journal of Theoretical Biology* 283.1, pp. 82–91.
- Freckleton, RP and AR Watkinson (2001). 'Predicting competition coefficients for plant mixtures: reciprocity, transitivity and correlations with life-history traits.' In: *Ecology Letters* 4.4, pp. 348–357.

- Gause, Georgii Frantsevitch (1934). 'Experimental analysis of Vito Volterra's mathematical theory of the struggle for existence.' In: *Science* 79.2036, pp. 16–17.
- Glaser-Schmitt, Amanda, Meike J Wittmann, Timothy JS Ramnarine, and John Parsch (2021). 'Sexual antagonism, temporally fluctuating selection, and variable dominance affect a regulatory polymorphism in *Drosophila melanogaster*.' In: *Molecular Biology and Evolution* 38.11, pp. 4891–4907.
- Godoy, Oscar, Lorena Gómez-Aparicio, Luis Matías, Ignacio M Pérez-Ramos, and Eric Allan (2020). 'An excess of niche differences maximizes ecosystem functioning.' In: *Nature communications* 11.1, pp. 1–10.
- Godoy, Oscar, Nathan J. B. Kraft, and Jonathan M. Levine (2014). 'Phylogenetic relatedness and the determinants of competitive outcomes.' In: *Ecology Letters* 17.7, pp. 836–844.
- Godoy, Oscar and Jonathan M. Levine (2014). 'Phenology effects on invasion success: insights from coupling field experiments to coexistence theory.' In: *Ecology* 95.3, pp. 726–736.
- Heinrich, Bernd (Aug. 1976). 'Resource Partitioning Among Some Eusocial Insects: Bumblebees.' In: *Ecology* 57.5, pp. 874–889.
- HilleRisLambers, Janneke, Peter B Adler, W Stanley Harpole, Jonathan M Levine, and Margaret M Mayfield (2012). 'Rethinking community assembly through the lens of coexistence theory.' In: *Annual review of ecology, evolution, and systematics* 43, pp. 227–248.
- Holland, J Nathaniel, Donald L DeAngelis, and Judith L Bronstein (2002). 'Population dynamics and mutualism: functional responses of benefits and costs.' In: *The American Naturalist* 159.3, pp. 231–244.
- Holland, J Nathaniel, Toshinori Okuyama, and Donald L DeAngelis (2006). 'Comment on "Asymmetric Coevolutionary Networks Facilitate Biodiversity Maintenance".' In: *Science* 313.5795, pp. 1887–1887.
- Holling, Crawford S (1959). 'Some characteristics of simple types of predation and parasitism1.' In: *The Canadian Entomologist* 91.7, pp. 385–398.
- (1966). 'The strategy of building models of complex ecological systems.' In: *Systems analysis in ecology*, pp. 195–214.
- Holt, Robert D (1977). 'Predation, apparent competition, and the structure of prey communities.' In: *Theoretical population biology* 12.2, pp. 197–229.
- Inouye, David W. (1978). 'Resource Partitioning in Bumblebees: Experimental Studies of Foraging Behavior.' In: *Ecology* 59.4, pp. 672–678.

- Jørgensen, Sven Erik and Giuseppe Bendoricchio (2001). *Fundamentals of Ecological Modelling*. Vol. 21. Elsevier.
- Kokko, Hanna and Andrés López-Sepulcre (2007). 'The ecogenetic link between demography and evolution: can we bridge the gap between theory and data?' In: *Ecology Letters* 10.9, pp. 773–782.
- Kraft, Nathan JB, Oscar Godoy, and Jonathan M Levine (2015). 'Plant functional traits and the multidimensional nature of species coexistence.' In: *Proceedings of the National Academy of Sciences* 112.3, pp. 797–802.
- Lai, Hao Ran, Kwek Yan Chong, Alex Thiam Koon Yee, Margaret M Mayfield, and Daniel B Stouffer (2021). 'Non-additive biotic interactions improve predictions of tropical tree growth and impact community size structure.' In: *bioRxiv*, pp. 2020–09.
- Lässig, Michael, Ville Mustonen, and Aleksandra M Walczak (2017). 'Predicting evolution.' In: *Nature ecology & evolution* 1.3, pp. 1–9.
- Lawton, John H (1999). 'Are there general laws in ecology?' In: *Oikos*, pp. 177–192.
- Levine, Jonathan M and Janneke HilleRisLambers (2009). 'The importance of niches for the maintenance of species diversity.' In: *Nature* 461.7261, pp. 254–257.
- Levins, Richard (1966). 'The strategy of model building in population biology.' In: *American scientist* 54.4, pp. 421–431.
- (1993). 'A response to Orzack and Sober: formal analysis and the fluidity of science.' In: *The Quarterly Review of Biology* 68.4, pp. 547–555.
- (2006). 'Strategies of abstraction.' In: *Biology and Philosophy* 21.5, pp. 741–755.
- Levins, Richard and Richard Lewontin (Jan. 1980). 'Dialectics and reductionism in ecology.' In: *Synthese* 43.1, pp. 47–78.
- Lewontin, Richard C (1963). 'Models, mathematics and metaphors.' In: *Synthese*, pp. 222–244.
- MacArthur, Robert H (1962). 'Some generalized theorems of natural selection.' In: *Proceedings of the National Academy of Sciences of the United States of America* 48.11, p. 1893.
- MacArthur, Robert and Richard Levins (1967). 'The limiting similarity, convergence, and divergence of coexisting species.' In: *The american naturalist* 101.921, pp. 377–385.
- Marquet, Pablo A, Andrew P Allen, James H Brown, Jennifer A Dunne, Brian J Enquist, James F Gillooly, Patricia A Gowaty, Jessica L Green, John Harte, Steve P Hubbell, et al. (2014). 'On theory in ecology.' In: *BioScience* 64.8, pp. 701–710.

- Martyn, Trace E, Daniel B Stouffer, Oscar Godoy, Ignasi Bartomeus, Abigail I Pastore, and Margaret M Mayfield (2021). 'Identifying "Useful" Fitness Models: Balancing the Benefits of Added Complexity with Realistic Data Requirements in Models of Individual Plant Fitness.' In: *The American Naturalist* 197.4, pp. 415–433.
- May, Robert M (1972). 'Will a large complex system be stable?' In: *Nature* 238.5364, pp. 413–414.
- (2019). *Stability and complexity in model ecosystems*. Princeton university press.
- Mayfield, Margaret M and Daniel B Stouffer (2017). 'Higher-order interactions capture unexplained complexity in diverse communities.' In: *Nature ecology & evolution* 1.3, pp. 1–7.
- Maynard-Smith, John (1978). *Models in ecology*. CUP Archive.
- Morse, D. H. (Aug. 1977). 'Resource Partitioning in Bumble Bees: The Role of Behavioral Factors.' In: *Science* 197.4304, pp. 678–680.
- Odenbaugh, Jay (2005). 'Idealized, inaccurate but successful: A pragmatic approach to evaluating models in theoretical ecology.' In: *Biology and Philosophy* 20.2–3, pp. 231–255.
- Orzack, Steven Hecht and Elliott Sober (1993). 'A critical assessment of Levins's The strategy of model building in population biology (1966).' In: *The Quarterly Review of Biology* 68.4, pp. 533–546.
- Pickett, Steward TA (1980). 'Non-equilibrium coexistence of plants.' In: *Bulletin of the Torrey Botanical Club*, pp. 238–248.
- Rossberg, Axel G, György Barabás, Hugh P Possingham, Mercedes Pascual, Pablo A Marquet, Cang Hui, Matthew R Evans, and Géza Meszén (2019). 'Let's train more theoretical ecologists—here is why.' In: *Trends in ecology & evolution* 34.9, pp. 759–762.
- Roughgarden, Jonathan, Aviv Bergman, Sharoni Shafir, and Charles Taylor (2018). 'Adaptive Computation in Ecology and.' In: *Adaptive Individuals In Evolving Populations: Models And Algorithms*, p. 25.
- Saavedra, Serguei, Rudolf P Rohr, Jordi Bascompte, Oscar Godoy, Nathan JB Kraft, and Jonathan M Levine (2017). 'A structural approach for understanding multispecies coexistence.' In: *Ecological Monographs* 87.3, pp. 470–486.
- Schoener, Thomas W (1974). 'Some methods for calculating competition coefficients from resource-utilization spectra.' In: *The American Naturalist* 108.961, pp. 332–340.
- Servedio, Maria R, Yaniv Brandvain, Sumit Dhole, Courtney L Fitzpatrick, Emma E Goldberg, Caitlin A Stern, Jeremy Van Cleve, and D Justin Yeh (2014). 'Not just a theory—the utility of mathematical models in evolutionary biology.' In: *PLoS biology* 12.12, e1002017.

- Simberloff, Daniel (2004). 'Community Ecology: Is It Time to Move On? (An American Society of Naturalists Presidential Address).' In: *The American Naturalist* 163.6, pp. 787–799.
- Song, Chuliang and Serguei Saavedra (2018). 'Will a small randomly assembled community be feasible and stable?' In: *Ecology* 99.3, pp. 743–751.
- Stouffer, Daniel B (2019). 'All ecological models are wrong, but some are useful.' In: *Journal of Animal Ecology* 88.2, pp. 192–195.
- Stouffer, Daniel B and Mark Novak (2021). 'Hidden layers of density dependence in consumer feeding rates.' In: *Ecology Letters* 24.3, pp. 520–532.
- Sutherland, William J (2006). 'Predicting the ecological consequences of environmental change: a review of the methods.' In: *Journal of Applied Ecology* 43.4, pp. 599–616.
- Thompson, Andrew R., Roger M. Nisbet, and Russell J. Schmitt (Nov. 2006). 'Dynamics of mutualist populations that are demographically open.' In: *Journal of Animal Ecology* 75.6, pp. 1239–1251.
- Thompson, John N (1999). 'The evolution of species interactions.' In: *Science* 284.5423, pp. 2116–2118.
- (2014). *Interaction and coevolution*. University of Chicago Press.
- Thomson, Diane M and Maureen L Page (Apr. 2020). 'The importance of competition between insect pollinators in the Anthropocene.' In: *Current Opinion in Insect Science* 38, pp. 55–62.
- Thomson, J. D., S. C. Peterson, and L. D. Harder (Jan. 1987). 'Response of traplining bumble bees to competition experiments: shifts in feeding location and efficiency.' In: *Oecologia* 71.2, pp. 295–300.
- Turnbull, Lindsay Ann, Jonathan M Levine, Michel Loreau, and Andy Hector (2013). 'Coexistence, niches and biodiversity effects on ecosystem functioning.' In: *Ecology letters* 16, pp. 116–127.
- Vázquez, Diego P, William F Morris, and Pedro Jordano (2005). 'Interaction frequency as a surrogate for the total effect of animal mutualists on plants.' In: *Ecology letters* 8.10, pp. 1088–1094.
- Volterra, Vito (1926). 'Fluctuations in the abundance of a species considered mathematically.' In: *Nature* 118.2972, pp. 558–560.
- Weisberg, Michael (2006). 'Forty years of 'the strategy': Levins on model building and idealization.' In: *Biology and Philosophy* 21.5, pp. 623–645.
- Westphal, Catrin, Ingolf Steffan-Dewenter, and Teja Tscharntke (Aug. 2006). 'Bumblebees experience landscapes at different spatial scales: possible implications for coexistence.' In: *Oecologia* 149.2, pp. 289–300.

- Wood, Simon N and Matthew B Thomas (1999). 'Super-sensitivity to structure in biological models.' In: *Proceedings of the Royal Society of London. Series B: Biological Sciences* 266.1419, pp. 565–570.
- Wootton, KL and DB Stouffer (2016). 'Many weak interactions and few strong; food-web feasibility depends on the combination of the strength of species' interactions and their correct arrangement.' In: *Theoretical Ecology* 9.2, pp. 185–195.

Part II

FRAMEWORKS FOR INCLUDING BIOTIC AND ABIOTIC COMPLEXITY IN MODELS OF BIOTIC INTERACTIONS

THE CONTEXT DEPENDENCY OF POLLINATOR INTERFERENCE: HOW ENVIRONMENTAL CONDITIONS AND CO-FORAGING SPECIES IMPACT FLORAL VISITATION

Alba Cervantes-Loreto¹, Carolyn A. Ayers ², Emily K. Dobbs², Berry J. Brosi³,
Stouffer Daniel B.¹

1. Centre for Integrative Ecology, School of Biological Sciences, University of Canterbury, New Zealand
2. Department of Environmental Sciences, Emory University, Atlanta, Georgia USA
3. University of Washington, Department of Biology, Seattle USA

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 (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 Tschardt, 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.

METHODS

A functional response framework of times between floral visits

To understand the effect of varying abundances of plants and pollinators, as well as different environmental conditions, we build upon a classical framework to quantify consumption rates in consumer–resource systems. First, to mathematically describe how frequently a focal individual from pollinator species i visits flowers as floral abundance changes, we assumed the per capita visitation rate takes the form of a Type II functional response (Holling, 1959) as this is the predominant form assumed in various studies employing functional responses for mutualists (Bastolla et al., 2009; Holland, DeAngelis, and Bronstein, 2002; Rohr, Saavedra, and Bascompte, 2014; Valdovinos et al., 2013). Second, to describe how floral visits change with varying abundances of pollinators, we developed an analogue to the Beddington–DeAngelis functional response (Beddington, 1975; DeAngelis, Goldstein, and O'Neill, 1975). This function assumes that the instantaneous per capita flower visitation rate of

a focal pollinator from species i on focal flowers of the species m , $\lambda_{i,m}$, is a non-linear function with the form:

$$\lambda_{i,m} = \frac{a_m N_m}{1 + a_m h_m N_m + \sum_n a_n h_n N_n + c_i (P_i - 1) + \sum_j c_j P_j} , \quad (2.1)$$

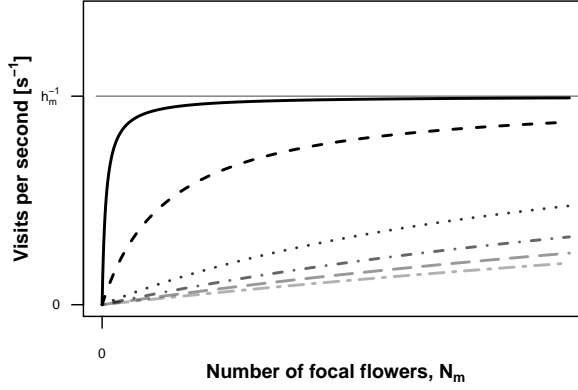
where N_m and N_n are the abundances of focal and non-focal flowers. The encounter rate of bee individuals with focal flowers is described by a_m , while a_n describes the encounter rate with non-focal flowers. Similarly, h_m and h_n denote the handling times of focal and non-focal flowers, respectively. The variables P_i and P_j represent the conspecific and heterospecific pollinator abundances, respectively, and their effects on visitation are captured by c_i and c_j . Note that for conspecific interactions between pollinators, we used $P_i - 1$ to account for the fact that focal individuals do not interact with themselves.

Though they are rarely studied in this way due to the typical data available, an alternative and equivalent approach to characterize functional responses is to examine the time between feeding events instead of feeding rates themselves (Coblentz and DeLong, 2020). This approach has the advantage of allowing inference of a consumer's functional response using one or a few trials per individual (Coblentz and DeLong, 2020). Returning to the functional response given by Eq. 2.1, we can estimate time between floral visits, $\rho_{i,m}$, as the inverse of the per capita visitation rate:

$$\rho_{i,m} = \frac{1}{\lambda_{i,m}} = \frac{1}{a_m N_m} + h_m + \frac{1}{a_m N_m} \sum_n a_n h_n N_n + \frac{c_i}{a_m N_m} (P_i - 1) + \frac{1}{a_m N_m} \sum_j c_j P_j. \quad (2.2)$$

Written this way, the times between floral visits become the sum of the time each focal pollinator spends between visiting focal flowers, the time between visiting other flowers, and the time “added” by interactions with conspecific and heterospecific co-foragers. Importantly, the effects of pollinator–pollinator interactions can be quantified as increases or decreases to the times between floral visits. Note that conversion of times between visits to visitation rates can be done for either when the number of flowers or the number of pollinator vary (Fig. 2.1).

a)



b)

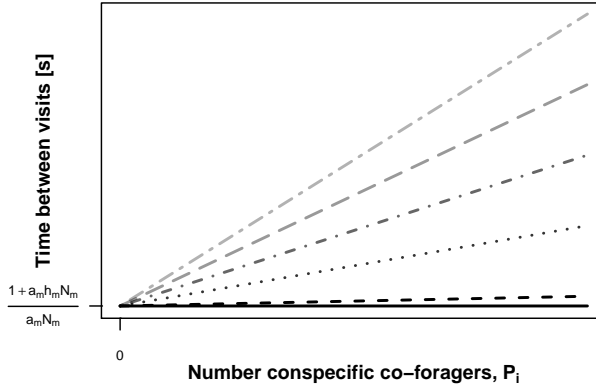


Figure 2.1: Visualizing the mathematical relationship between visitation rate and time between visits. a) Visitation rate as a function of the number of flowers N_m (Eq .2.1). For a fixed number of co-foraging conspecific pollinators P_i with no interference ($c_i = 0$), no heterospecific pollinators present ($P_j = 0$), and no other plants ($N_n = 0$), the visitation rate saturates at $1/h_m$ (solid black line). As c_i increases (dashed and dotted lines in lighter colours), the rate at which visitation rate reaches saturation decreases. b) Time between visits to a fixed number of focal flowers N_m as a function of conspecific co-foragers P_i , also with $P_j = 0$ and $N_n = 0$ (Eq .2.2). When $c_i = 0$, the time between floral visits does not change with increasing pollinator abundance (solid black line). As c_i increases, each co-foraging pollinator contributes more time to the time between floral visits (dashed and dotted lines in lighter colours as in a).

This general functional response framework allows us to quantify visitation rates under several experimental designs that might include scenarios (i) where floral abundances vary, (ii) where pollinator abundances vary, and (iii) under different environmental conditions. For example, when there are observations of a focal pollinator and conspecific co-foragers visiting varying abundances of two plants, Eq. 2.2 reduces to:

$$\rho_{i,m} = \frac{1}{a_m N_m} + h_m + \frac{a_n h_n N_n}{a_m N_m} + \frac{c_i}{a_m N_m} (P_i - 1). \quad (2.3)$$

Note that to parameterize Eq. 2.3, we require independent variations of the abundances of both flowers *and* of pollinators. However, it is also possible to adapt and fit a model based on our framework when only *some* abundances change. For instance, if the number of conspecific co-foragers P_i is fixed, Eq. 2.3 becomes:

$$\rho_{i,m} = h_m + \left(\frac{1}{a_m} + \frac{c_i(P_i - 1)}{a_m} \right) \frac{1}{N_m} + \left(\frac{a_n h_n}{a_m} \right) N_n \frac{1}{N_m} \quad (2.4)$$

which can be further simplified to:

$$\rho_{i,m} = h_m + \gamma_{i,m} \frac{1}{N_m} + \delta_{i,n} N_n \frac{1}{N_m}. \quad (2.5)$$

Here the composite parameter $\gamma_{i,m}$ scales the impact of changes in focal floral abundances in the time between floral visits while $\delta_{i,n}$ scales the relative impact of changes in non-focal floral abundances. Since $\gamma_{i,m}$ includes encounter rates with flowers as well as the implicit impact of pollinator interference, these cannot be disentangled statistically without variation in P_i . Similarly, $\delta_{i,n}$ is a term that includes both the encounter rates with focal and with non-focal flowers.

On the other hand, when there are observations of different abundances of co-foragers visiting a fixed number of flowers of a single species, then Eq. 2.2 becomes:

$$\rho_{i,m} = \frac{1 + a_m h_m N_m}{a_m N_m} + \frac{c_i}{a_m N_m} (P_i - 1) + \frac{c_j}{a_m N_m} P_j, \quad (2.6)$$

which can be further simplified to:

$$\rho_{i,m} = \alpha_m + \beta_{i,m} (P_i - 1) + \beta_{j,m} P_j, \quad (2.7)$$

where the composite parameter α_m sets a baseline of time between visits when there are no pollinator-pollinator interactions (i.e. the pollinator density-independent foraging outcomes), and the composite parameters $\beta_{i,m}$ and $\beta_{j,m}$ capture the density-dependent changes to the time between visits to focal flowers. As above, both $\beta_{i,m}$ and $\beta_{j,m}$ incorporate both pollinator interference and encounter rates with flowers. Thus, an increase of times between floral

visits (i.e. a decrease in floral visitation rates) could be the outcome of higher pollinator interference or decreasing encounter rates with flowers.

As a final example, both the density-dependent and density-independent terms can be inferred under different environmental conditions. For example, suppose we measure an environmental variable E , and there are observations similar to those of Eq. 2.6 but under different levels of the environmental condition. Then, Eq. 2.7 can be expanded into:

$$\rho_{i,m} = \alpha_m + \alpha_{m,e}E + (\beta_{i,m} + \beta_{i,m,e}E)(P_i - 1) + (\beta_{j,m} + \beta_{j,m,e}E)P_j, \quad (2.8)$$

where E is the value of the measured environmental variable (which can take continuous or discrete values), and the parameters with the subscript e capture changes driven by abiotic conditions. For example, if $\beta_{i,m}$ quantifies the effect of conspecific pollinators, then $\beta_{i,m,e}$ quantifies how much the effect of conspecific pollinators changes under a certain abiotic condition. Written this way, both pollinator abundances and the environmental conditions are the factors that determine the effect of pollinator–pollinator interactions.

Data

In the following sections, we use our framework to parameterize and compare different models of floral visits with a unique foraging experiment. To do so, we examined data from a set of experiments that allowed us to tightly monitor the time individual bumblebees spend between visits to artificial flowers, as well as the energy consumed per visit. During 2015 and 2016, we tracked the activity of commercial *Bombus impatiens* (henceforth *Bombus*) from Koppert Biological Systems (Howell, MI USA), inside a foraging chamber under (i) different richness and abundances of co-foragers and (ii) different levels of resource availability (iii) with and without pesticide exposure. These data belong the “Emory data set”, as described in Ayers, Armsworth, and Brosi (2018).

Experimental setup

To monitor the activity of our focal species, our enclosure consisted of an array of artificial flowers that recorded the presence of a visiting bee at the same time dispensed an automatic computer-controlled reward. The system was made up of 32 artificial flowers in four rows of eight flowers each distributed uniformly inside the chamber. The artificial flowers varied by color (blue, white, yellow, pink), scent, and sucrose concentrations (2.0 M, 1.5 M, 1.0 M, 0.5 M), in a way that yielded four distinct flower types. The automatic tracking of *Bombus* individuals and co-foragers was done using mic3-TAG RFID 16 kbit

tags (Microsensys GmbH, Erfurt, Germany) attached to each bee's thorax so as to not interfere with movement of flight.

Corresponding RFID tag readers embedded in each artificial flower recorded the presence of a bee (of any species) and activated an automatic reward of 10 μ l unless the same individual had been recorded in that flower in the last 30 seconds, in which case no reward was conferred. If a different individual, of any species, visited the same flower, then the granting of a new reward depended on the floral refill time, or the time after which artificial flowers would dispense a new sucrose reward after a previous visit, a condition that we manipulated throughout the trials (see *Foraging trials*). The sucrose reward was dispensed from a pipette tip embedded in the artificial flower, which was taken up by the bee's proboscis through capillary action. Data suggests that the bees were almost always consuming the full reward offered by the artificial flowers (Fig. 6.1 in Chapter 6). This system allowed us to closely monitor the time between floral visits and energy consumption at the individual-bee level as well as resource availability using Arduino MEGA 2560 R3 hardware (Arduino LLC) and Processing software.

Foraging trials

Foraging trials consisted of fasting the bees for one hour, transferring them to the foraging enclosure, and recording their behavior over 75 minutes. Before the experimental trials, we kept bees in separate training enclosures with artificial flowers identical to the ones in the experiment, except for the fact that training flowers were not computer controlled but delivered rewards *ad libitum*. We simultaneously manipulated the richness and abundance of co-foragers, floral refill time, and the sub-lethal exposure to a common dose of a neonicotinoid pesticide as follows.

We manipulated the richness and abundance of co-foragers through a series of single-species and multi-species trials. In single-species trials, we varied the abundance of *Bombus* to 4, 8 and 16 individuals foraging at the same time, with no other species present. In multi-species trials, we manipulated richness, or the number of species that were foraging at the same time as *Bombus*. We examined the combinations of one to three additional bee species foraging at the same time as *Bombus* while at all times holding total bee abundance constant at 16 individual bees. The three other species were another social bee species, *Apis mellifera* (henceforth *Apis*), and two solitary taxa, *Osmia lignaria* and *Megachile rotundata* (henceforth *Osmia* and *Megachile*). In multi-species trials, we used 8 *Bombus* individuals for 2-species trials, either 5 or 6 *Bombus* for 3-species trials, and 4 *Bombus* for 4-species trials. We present a detailed description of the abundances of the other species during the experiment in Table 6.1 in Chapter 6.

We also manipulated floral refill time to mimic different levels of resource availability since resource availability for the foraging bees decreases as refill time increases. The levels of floral refill time we examined were: instantaneous refill (0 seconds), intermediate refill (120 seconds), and delayed refill (540 seconds). We will refer to instantaneous refill (i.e. high resource availability) as the control condition.

Finally, we also manipulated bee exposure to a sub-lethal dose of neonicotinoid pesticide. While in the training enclosure, we fed individuals of all species subject to the pesticide treatment *ad libitum* on a sucrose solution with a sub-lethal concentration of 10 $\mu\text{g/L}$ of thiamethoxam ($\text{C}_8\text{H}_{10}\text{ClN}_5\text{O}_3\text{S}$, Sigma Aldrich); bees subject to the control condition were fed a sucrose solution without pesticide. For bees subject to pesticide treatment, the solution that contained pesticide was their only available sugar source. Thiamethoxam is applied to a wide range of crops (Maienfisch et al., 2001) and the concentration is consistent to what insects experience in the field (Blacqui re et al., 2012). We ran trials with either all exposed (of all species) or all unexposed bees to mimic exposure at the landscape level. We show a detailed description of the number of trials and replicates we performed in Tables 6.2 and 6.3 in Chapter 6, as well as an explicit account of how the data was cleaned for analysis.

Analysis

Models of times between floral visits

Given our framework and our very detailed data-set, we were able to contrast different hypotheses regarding how pollinators forage and interact, using *Bombus* as our focal species. Instead of testing *all* possible hypotheses of how co-foragers, resource availability and pesticide exposure influence the times between floral visits, we tested three relatively simple hypotheses: (i) *Bombus* individuals forage unaffected by the presence of co-foragers or by environmental conditions, (ii) only co-foragers modify how *Bombus* forages but environmental conditions do not, and (iii) environmental conditions modify how individuals forage alone and in the presence of other foragers. Our modelling aim was not to get a detailed prediction of the dynamics governing the experimental system, but rather to show that the modelled principles are sufficient to explain times between floral visits, following a demonstration modelling approach to reveal potential explanatory generalities (Evans et al., 2013).

If we map our functional response framework to our experimental setup, we can describe the functional response of the focal *Bombus* individuals with Eq. 2.7. Our hypotheses can then be tested across different foraging models that equate to further extensions or simplifications of Eq. 2.7. If the presence of co-foragers and environmental conditions have no effect on the times between

visits across experiments, then a density-independent rate will be sufficient to describe the data:

$$\rho_i = \alpha. \quad (2.9)$$

We call this our *null* model. Note that since in our experiment floral abundances remained constant, we did not explore how changes in densities of different flower types changed foraging rates. Rather, we modelled how long *Bombus* individuals would take between visits to all of the artificial flowers, regardless of the type of flower. Thus, for simplicity we dropped subscripts on terms that depended on flower types.

On the other hand, if co-foragers interact with each other but visitation is unaffected by the abiotic conditions, then an equation similar to Eq. 2.7 that only considers the effect of co-foragers would best describe the times between floral visits. We call this the *interference* model:

$$\rho_i = \alpha + \beta_i(P_i - 1) + \sum_j \beta_j P_j. \quad (2.10)$$

Finally, if the abiotic treatments modify how *Bombus* forages with and without co-foragers, similar to Eq. 2.8, we would expect the times between visits to be a function of the abundance of co-foragers, level of resource availability (R) and pesticide exposure (E), we call this the *treatments* model:

$$\rho_i = \alpha + \alpha_r R + \alpha_e E + \beta_i(P_i - 1) + \beta_{i,r}(P_i - 1)R + \beta_{i,e}(P_i - 1)E + \sum_j \beta_j P_j + \sum_j \beta_{j,r} P_j R + \sum_j \beta_{j,e} P_j E. \quad (2.11)$$

Here the subscripts r and e denote the parameters that estimate the effect of R and E , respectively. In our case, R is a continuous variable that corresponds to the floral refill time (i.e. goes from 0 to 540 seconds) and E is a dummy variable to indicate pesticide exposure (i.e. $E = 0$ when bees are subject to the control treatment, and $E = 1$ when bees were exposed to the pesticide treatment). The subscripts we used are consistent with the nomenclature of the density-independent and density-dependent terms described previously. Note that in our data, not all co-foraging species were tested under all experimental conditions (Table 6.3 in Chapter 6). Therefore, we did not model the three-way interaction between species identity, pesticide exposure and resource availability.

Statistical analysis

To infer the parameters of Eqs. (2.9-2.11), we fit non-linear hierarchical models with a Bayesian framework using Hamiltonian Monte Carlo (HMC) methods. We provide the details of our statistical analysis in Chapter 6. We fit our

models using the function *brm* from the package *brms* (Bürkner, 2017) in the statistical program R (version 3.4.2) (R Core Team, 2013). We ran four chains with a warm up of 3000 iterations and 2000 sampling iterations, using weakly informative priors and a maximum treedepth of 13 and an adapt delta of 0.99. We determined convergence when trace plots were well mixed and stationary and when the Gelman-Rubin convergence diagnostic (Rhat) was less than 1.05 for all parameters (Vehtari et al., 2020).

We compared the fits of Eqs. (2.9-2.11) to each other using the the Wanatabe-Akaike information criterion (WAIC) to determine which of the hypotheses encoded within the models best predicts out of sample times between floral visits. WAIC provides a measure for model fit that is penalized for the number of model parameters, and the best fit model in terms of out of sample predictions is the one with the lowest WAIC value. Additionally, we calculated Akaike weights for each model, which can be interpreted as an estimate of the probability that the model will make the best predictions of new data based on the the set of models considered. We did model comparisons using 500 samples from the posterior distribution, and we defined best-fit models as those with the lowest WAIC and an Akaike weight greater than 0.9 (McElreath, 2018).

RESULTS

Model comparison using Wanatabe-Akaike information criterion (WAIC) showed that the *treatments* model was the best-fit model for explaining the data by a wide margin (Table 2.1). The *treatments* model had the lowest WAIC score and received all of the Akaike weight, which means it had the highest probability to make the best predictions of new data compared to the two other models considered. Model comparison therefore showed not only that co-foraging pollinator abundances systematically modified the times between floral visits, but also that resource availability and pesticide exposure modified how bumblebees foraged alone and with other species present.

Density-independent effects

The parameters of the *treatments* model allowed us to make predictions beyond the pollinator densities manipulated during the trials since it estimated density-independent effects as the intercept. Without any co-foragers present, predictions using the *treatments* model confirmed that both low resource availability and sub-lethal exposure to pesticide increased the time between floral visits (Fig. 2.2). Predictions made at low resource availability and under pesticide exposure (Fig. 2.2d) showed that a bumblebee foraging alone would spend on average 90 seconds more between floral visits when compared to predictions made at high resource availability and under no pesticide exposure

(Fig. 2.2a); this equates to a near doubling of the amount of time between floral visits. Consequently, over the course of a 75 minute experiment, an average bumblebee foraging alone would make 15 fewer floral visits if there was low resource availability and it had been exposed to pesticide.

Table 2.1: Model comparison table. WAIC (Widely Applicable Information Criteria) penalizes models for parameters, and the lowest WAIC reflects the best-fit model. pWAIC is the effective number of parameters and provides information on how flexible each model is in fitting the sample. Akaike Weight for each model is an estimate of the probability that the model will make the best predictions of new data based on the the set of models considered.

model	WAIC	pWAIC	Akaike weight
<i>treatments</i>	413322.5	2386.6	1.00
<i>interference</i>	414462.5	2135.6	< .002
<i>null</i>	416063.6	1769.6	< .002

As shown in the intercepts of Fig. 2.2a and c, we also found that the time between floral visits decreased as resource availability increased (i.e. the time between floral refill decreased). Predictions made at high resource availability (0 seconds between floral refill) showed that an average bumblebee would make 7 more floral visits over the course of an experiment than it would at low resource availability (540 seconds between floral refill).

Density-dependent effects

We found that the time between floral visits for a focal pollinator changed consistently as a function of the identity and abundance of the co-foragers (Fig. 2.2). All of the species examined could potentially interfere with a focal *Bombus* individual by increasing the time between floral visits, but the extent of the interference effect depended on the environmental context bees experienced.

Under control conditions (i.e. no pesticide exposure and high resource availability), increasing abundances of *Bombus*, *Osmia*, and *Megachile* all increased the times between visits (and therefore decreased the visitation rate) to a similar extent (Fig. 2.2a). However, *Apis* had an opposite effect under control conditions as increasing its density *decreased* the times between floral visits. Thus, when there was high resource abundance and no pesticide exposure three of the species (including conspecifics) had an interference effect. However, as environmental conditions changed, so did these interference effects. For example, increasing abundances of *Apis* changed from decreasing times between visits to increasing them when there was either pesticide exposure or low resource availability (Fig. 2.2).

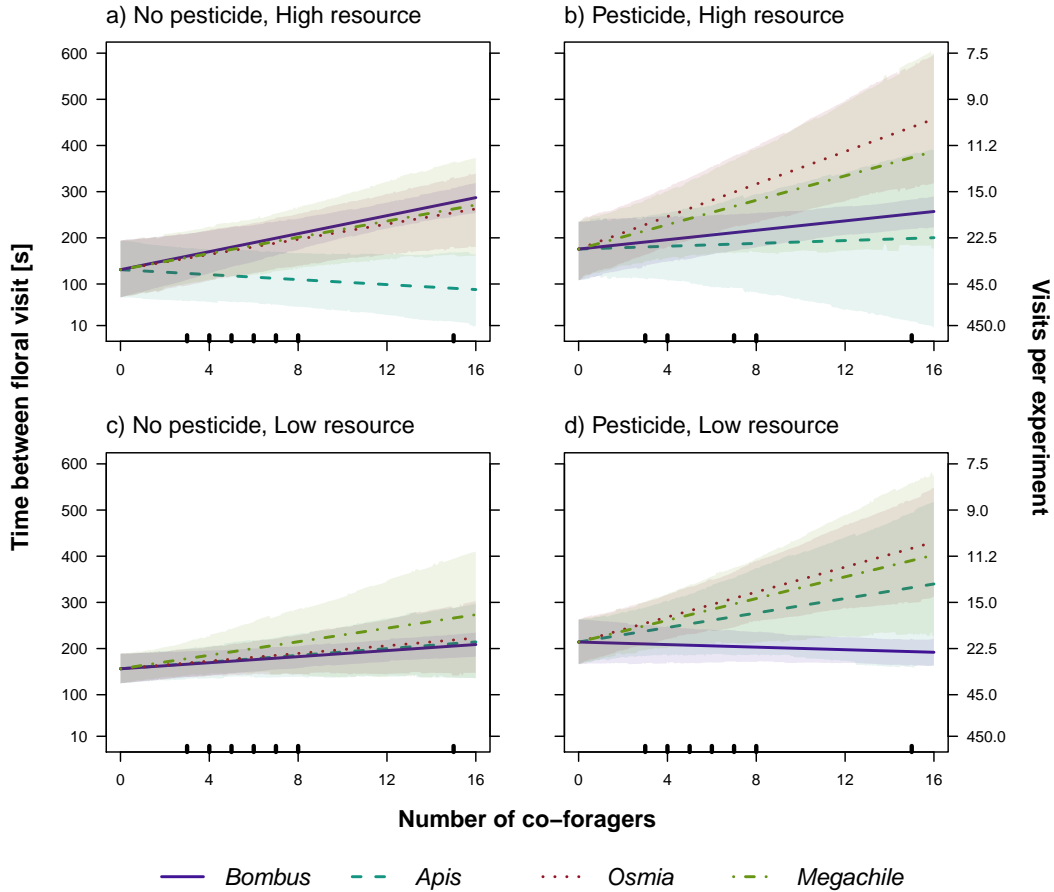


Figure 2.2: Model predictions of how the time between floral visits changed as the number of co-foragers increased and under different environmental conditions. Each color and line type correspond to a different co-forager. Lines represent predictions using the median parameter values of the *treatments* model for the average focal individual. The shaded areas correspond to the 90% highest posterior density interval (HPDI). High resource availability corresponds to 0 seconds between floral refill, and low resource availability to 540 seconds between floral refill (the maximum used during the experiments). Ticks along the x-axis indicate the actual co-forager abundances examined during the experimental trials. On the right y-axis and to help interpretation, we show how many visits per 75 minute experiment would be expected for the corresponding times between floral visits.

To better disentangle the species-specific response of interference to environmental variables, we estimated the time contributed by a single co-forager individual of each species to the total times between floral visits as resource availability increased (Fig. 2.3) and with the exposure to a neonicotinoid pesticide (Fig. 2.4). That is, given the posterior distribution of the fixed effects, we calculated how total times between floral visits changed due to the contribution of a single individual of each species under different environmental conditions. Note that due to the inverse relationship between time between floral visits and resource availability, Fig. 2.3 shows decreasing times between floral refill.

We found that, as resources became more abundant (or the time between floral refill decreased), interference by *Bombus*, *Osmia*, and *Megachile* increased (Fig. 2.3). In particular, the time contributed by a conspecific individual almost tripled when resource availability changed from low to high (Fig. 2.3a). For the majority of the species examined, interference was strongest when there was high resource availability, and its effect weakened as resources became more scarce. In contrast, as resources became more abundant, the contribution of an additional individual of *Apis* to the time between floral visits decreased. Indeed, our predictions using median parameter values showed that an individual of *Apis* went from creating net decreases in visitation rate at low resource availability to creating net increases in visitation rate at high resource availability (Fig. 2.3b). However, the predictions using the 90% highest posterior density interval (HPDI, or the narrowest interval containing the specified probability mass (McElreath, 2018)) for *Apis* included competitive and facilitative outcomes at all levels of resource availability. Thus, even though on average *Apis* individuals had a facilitative effect as resources became more abundant, we predicted some competitive effects as well when making predictions using the full posterior distribution.

In contrast to resource availability, pesticide exposure tended to increase the strength of pollinator interference for all species except *Bombus* (Fig. 2.4). That is, when all of the bees had been exposed to pesticide, increasing heterospecific abundances of pollinators generally decreased floral visitation rate because individuals contributed positively to the times between floral visits. Conspecifics, however, had the opposite effect: pesticide exposure decreased the strength of pollinator interference (Fig. 2.4).

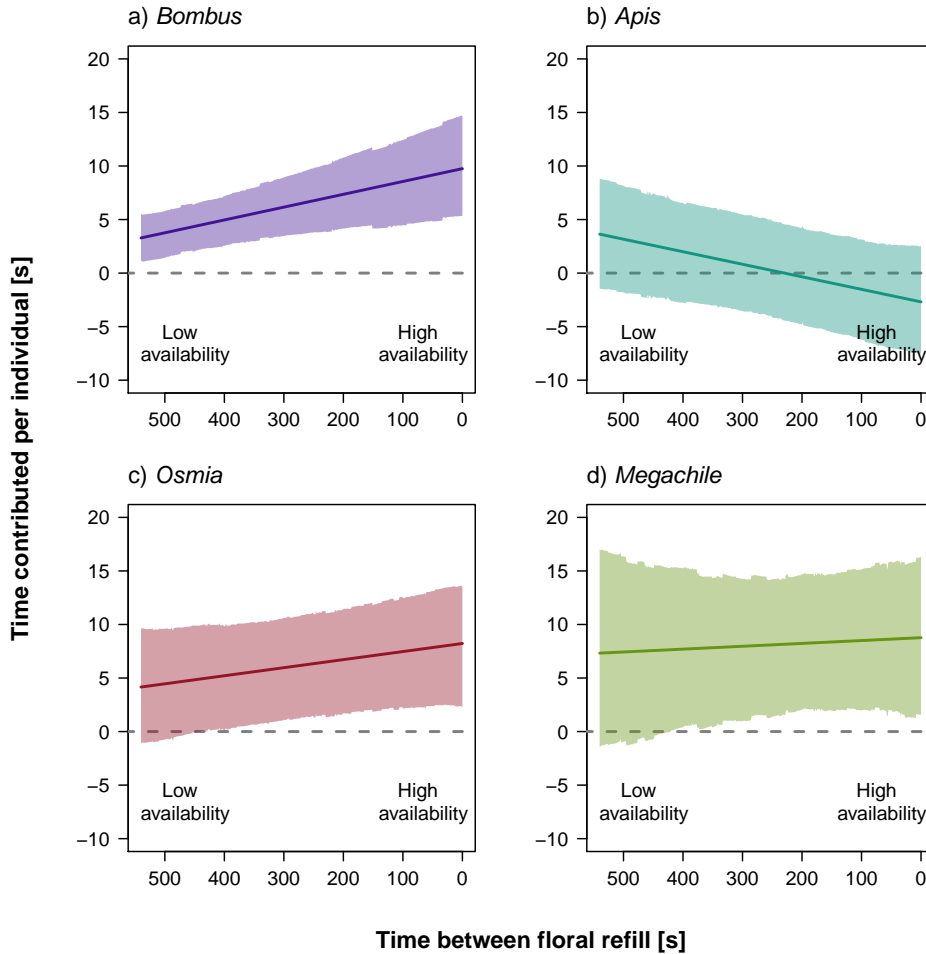


Figure 2.3: Model predictions of the effect an individual co-forager had on the time between visits of *Bombus* as resource availability increased and when there was no pesticide exposure. Each panel estimates the contribution of an individual co-forager from each of the four co-foraging species from our study. Solid lines represent the predictions made with the median parameter values of the *treatments* model for the average focal individual whereas the shaded areas correspond to the 90% highest posterior density interval (HPDI). To help interpretation, we provide the mapping between low and high resource availability and time between floral refill in each panel.

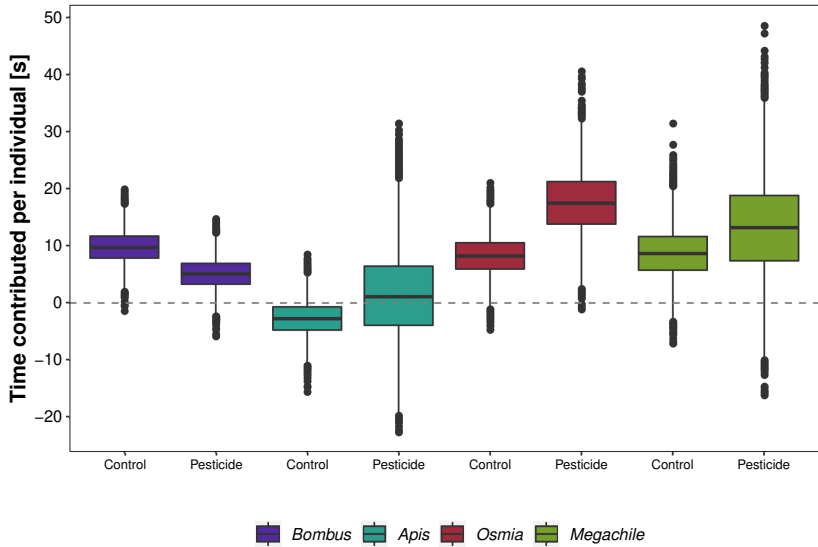


Figure 2.4: The effect an individual co-forager had on the time between floral visits when it had not been exposed to pesticide at high resource availability (Control), and when it had been exposed to a sub-lethal dose of neonicotinoid pesticide and at high resource availability (Pesticide). Each color corresponds to the different species of co-foragers. Each box plot extends from the first to third quantiles of the corresponding posterior distribution of parameter values, and the line inside the box indicates the median. The upper whisker extends to the largest value no further than 1.5 times the inter-quantile range (IQR, or the distance between the first and third quantiles); the lower whisker extends to the smallest value at most 1.5 times the IQR. Data beyond the end of the whiskers are determined to be outliers and are plotted individually with solid black points.

DISCUSSION

We applied our functional response framework to illustrate how both environmental context and pollinator–pollinator interactions can substantially change the number of visits a pollinator will make. Our model predictions showed that when a pollinator was foraging alone, conditions such as low resource availability and exposure to a sub-lethal dose of pesticide decreased the visits made to flowers. However, the same environmental conditions could have opposite effects on pollinator–pollinator interactions; for most species examined, interference was strongest when there was high resource abundance, and

pollinator interference decreased as resources became scarcer (except for *Apis*). Finally, we found a density-dependent response to pesticide exposure since, for all co-foraging species except *Bombus*, exposure to pesticide increased the sensitivity to individuals of other co-foraging species. On the whole, our results make clear that the question is not whether or not pollinators interfere with each other, but under what conditions they do so.

Resource abundance

When resources are scarce, it has been previously documented that bumblebees make fewer visits to flowers than in rich-resource areas (Heinrich, 2004; Westphal, Steffan-Dewenter, and Tschardtke, 2006). Our predictions agreed on the effect of low resource availability when a pollinator is foraging *alone* (Fig. 2.2). For bumblebees, high resource availability can be associated with mass-flowering (Westphal, Steffan-Dewenter, and Tschardtke, 2003), and other studies have shown that net benefits are increased when bumblebees concentrate their efforts in areas of rich nectar resources while moving rapidly through depleted areas (Heinrich, 1979).

In contrast, the role of resources was reversed when a bumblebee foraged at the same time as other species. For most of the species examined, interference was strongest when resources were most abundant (Fig. 2.3). Recall that in our modeling framework an increase of times between floral visits can be caused by many different mechanisms. For example, we found with $\beta_{i,r}$ that the effect of conspecifics decreased as resources became more scarce. This decrease could be due to a decrease in overt interference, c_i , or to a lower encounter rates with flowers a_m . However, observations of bees during the experiments offer some potential insights into this question. First and foremost, we never observed obvious aggressive interactions between bee individuals in the foraging arena. Instead, interference appears to have been driven by avoidance of flowers due to visual and/or olfactory cues presented by other bee individuals. The response to these cues was clearly context dependent. For example, while we did not specifically test learning within individual bees, they may have learned within the course of a trial that a visual or olfactory cue of another individual at a flower signaled that the flower was unlikely to be rewarding (in the case of delayed floral refill) or that the cues were not related to rewards (in the case of instantaneous floral refill). Indeed, overt interference has not been observed in bumblebees (Heinrich, 1976, 2004), but bumblebees have been documented to have avoidance behavior when foraging with other species (Inouye, 1978; Morse, 1977) and are able to detect and reject flowers which have been visited by other *Bombus* species using scent (Goulson, 1999).

Additionally, different bee species behaved differently in the experiments and the contribution to the times between floral visits we found (positive and negative) was also reflective of competitor species identities. For example,

Apis individuals generated net increases in floral visits by decreasing the time between floral visits under high resource availability. This may be because honey bees were not particularly active in foraging and may have spent more time outside of flowers, which could have led to essentially an overall decrease in competition for *Bombus*. Previous studies have found that interspecific interactions between honeybees and other species can sometimes result in an increase in pollination efficiency (Greenleaf and Kremen, 2006). In contrast, *Megachile* individuals also had low foraging rates, but based on observations may have spent more time in and near flowers, potentially leading *Bombus* individuals to avoid those flowers and increasing interference despite low foraging rates. Changes in bee foraging behavior have been shown to be species-specific before (Briggs, 2016), and it remains an exciting and open challenge to fully understand how they explicitly depend on environmental conditions.

Pesticide exposure

Our results were also consistent with previous studies that saw a decrease in floral visits when pollinators are exposed to a sub-lethal dose of neonicotinoid pesticide (Gill and Raine, 2014; Henry et al., 2012; Mommaerts et al., 2009; Stanley and Raine, 2016). Neonicotinoid pesticides bind strongly to nicotinic acetylcholine receptors in the central nervous system of insects (Goulson, 2013). At sub-lethal doses, this creates difficulties for memory and learning (Henry et al., 2012), as well as compromises navigation skills (Desneux, Decourtye, and Delpuech, 2007). Unsurprisingly, exposure to thiamethoxam increased the times between floral visits when a bumblebee was foraging alone and with the addition of individuals of all of the heterospecific pollinators (Fig. 2.2 & 2.4). For conspecifics, pesticide exposure weakened the effect of conspecific interference. That is, relative to the control conditions, foraging with conspecific individuals still resulted in a net decrease of floral visits but to a lesser extent. Thus, the general effect of sub-lethal exposure to a neonicotinoid pesticide is to decrease floral visits via both by density-dependent and density-independent mechanisms.

Experimental limitations

In our study, the highly controlled experimental setup allowed us to tightly monitor bee behavior and thus explicitly quantify pollinator interference and its relationship with experimental treatments. However, the artificial environment might not accurately capture how bees forage in the wild. For example, bumblebees could not leave low resource areas and concentrate their efforts in less depleted areas as they are prone to do (Heinrich, 2004). Furthermore, the non-focal species were not as active as *Bombus* during the trials, which

might further change how interference operates. Thus, the results presented here should be considered in the context of a controlled foraging experiment. This notwithstanding, we directly quantified behavioral changes driven by the presence of other pollinator species into pollinator functional responses, which has rarely been done.

Consequences of pollinator–pollinator interactions

In this study we focused on the functional responses of pollinators, and did not quantify their numerical responses (Morris, Vázquez, and Chacoff, 2010). Without knowing the numerical responses of the populations involved, we can not fully understand the dynamic consequences of pollinator–pollinator interactions (Revilla, 2015). However, our results do provide insights of how interference might affect mutualistic communities. Empirical and theoretical studies suggest that how often pollinators visit plants is a good predictor of the strength of the interaction, for both pollinators and plants involved (Vázquez et al., 2012; Vázquez, Morris, and Jordano, 2005). Indeed, in our experimental system the number of floral visits was a good predictor of the energetic gains for bees, since bees seemed to almost always consume the full reward offered by artificial flowers (Fig. 6.1, Supporting Information). Thus, from the point of view of pollinators, foraging with other species can be disadvantageous under certain conditions. For example, if high resource abundance made the other species more active, *Bombus* individuals might spend longer between flower visits because they are trying to avoid flowers that have already been visited. However, from the plant’s perspective, receiving visits from a diverse pollinator assemblage can produce more stable plant reproduction (Sahli and Conner, 2006), and greater competition tends to make bees increase floral fidelity, which also enhances plant fitness (Brosi and Briggs, 2013). Much like plant diversity (Bruninga-Socolar, Crone, and Winfree, 2016), our results show that pollinator diversity does not always have straightforward consequences on the populations involved.

Conclusion

The impact of interactions between pollinators in natural communities it is still poorly understood. In this study, we argue that in order to understand when and why those interactions change the course of plant and pollinator populations, we should also determine the environmental context in which they occur. Importantly, our study provides a theoretical framework to do so, coupled with a highly controlled foraging experiment to show how drastically abiotic conditions can change the outcomes of pollinator–pollinator interactions. By incorporating intra-guild interactions into pollinator functional responses, our study opens up an urgent avenue to study the consequences of species loss and environmental change in natural communities. It is critical to determine just how prevalent interference or facilitation between pollinator species is in

nature, in order to further understand how species loss could affect pollinator populations. We believe our study gives ecologists the theoretical and statistical tools to quantify the effects of other species both in experimental and observational studies, and contributes to closing the gap between the mutualistic and predator-prey literatures.

BIBLIOGRAPHY

- Abrams, Peter A. and Lev R. Ginzburg (Aug. 2000). 'The nature of predation: prey dependent, ratio dependent or neither?' In: *Trends in Ecology & Evolution* 15.8, pp. 337–341.
- Ayers, Carolyn A, Paul R Armsworth, and Berry J Brosi (July 2018). 'Statistically testing the role of individual learning and decision-making in trapline foraging.' In: *Behavioral Ecology* 29.4, pp. 885–893.
- Bastolla, Ugo, Miguel A Fortuna, Alberto Pascual-García, Antonio Ferrera, Bartolo Luque, and Jordi Bascompte (2009). 'The architecture of mutualistic networks minimizes competition and increases biodiversity.' In: *Nature* 458.7241, pp. 1018–1020.
- Beddington, J. R. (1975). 'Mutual Interference Between Parasites or Predators and its Effect on Searching Efficiency.' In: *Journal of Animal Ecology* 44.1, pp. 331–340.
- Blacqui re, Tjeerd, Guy Smagghe, Cornelis A. M. van Gestel, and Veerle Mommaerts (May 2012). 'Neonicotinoids in bees: a review on concentrations, side-effects and risk assessment.' In: *Ecotoxicology* 21.4, pp. 973–992.
- Briggs, Heather Mae (2016). 'Competitive context drives pollinator behavior: linking foraging plasticity, natural pollen deposition, and plant reproduction.' PhD thesis. UC Santa Cruz.
- Brosi, Berry J. and Heather M. Briggs (Aug. 2013). 'Single pollinator species losses reduce floral fidelity and plant reproductive function.' In: *Proceedings of the National Academy of Sciences* 110.32, pp. 13044–13048.
- Bruninga-Socolar, Bethanne, Elizabeth E Crone, and Rachael Winfree (2016). 'The role of floral density in determining bee foraging behavior: a natural experiment.' In: *Natural Areas Journal* 36.4, pp. 392–399.
- B rkner, Paul-Christian (Oct. 2017). 'Advanced Bayesian Multilevel Modeling with the R Package brms.' In: *arXiv:1705.11123*.
- Classen, Alice, Connal D Eardley, Andreas Hemp, Marcell K Peters, Ralph S Peters, Axel Ssymank, and Ingolf Steffan-Dewenter (2020). 'Specialization of plant–pollinator interactions increases with temperature at Mt. Kilimanjaro.' In: *Ecology and evolution* 10.4, pp. 2182–2195.

- Cnaani, Jonathan, James D. Thomson, and Daniel R. Papaj (2006). 'Flower Choice and Learning in Foraging Bumblebees: Effects of Variation in Nectar Volume and Concentration.' In: *Ethology* 112.3, pp. 278–285.
- Coblentz, Kyle E and John P DeLong (2020). 'Estimating predator functional responses using the times between prey captures.' In: *bioRxiv*.
- DeAngelis, D. L., R. A. Goldstein, and R. V. O'Neill (1975). 'A Model for Tropic Interaction.' In: *Ecology* 56.4, pp. 881–892.
- DeAngelis, Donald L. and J. Nathaniel Holland (Feb. 2006). 'Emergence of ratio-dependent and predator-dependent functional responses for pollination mutualism and seed parasitism.' In: *Ecological Modelling* 191.3, pp. 551–556.
- Desneux, Nicolas, Axel Decourtye, and Jean-Marie Delpuech (2007). 'The Sublethal Effects of Pesticides on Beneficial Arthropods.' In: *Annual Review of Entomology* 52.1, pp. 81–106.
- Evans, Matthew R, Volker Grimm, Karin Johst, Tarja Knuuttila, Rogier De Langhe, Catherine M Lessells, Martina Merz, Maureen A O'Malley, Steve H Orzack, Michael Weisberg, et al. (2013). 'Do simple models lead to generality in ecology?' In: *Trends in ecology & evolution* 28.10, pp. 578–583.
- Fründ, Jochen, Carsten F. Dormann, Andrea Holzschuh, and Teja Tscharrntke (2013). 'Bee diversity effects on pollination depend on functional complementarity and niche shifts.' In: *Ecology* 94.9, pp. 2042–2054.
- Gill, Richard J. and Nigel E. Raine (2014). 'Chronic impairment of bumblebee natural foraging behaviour induced by sublethal pesticide exposure.' In: *Functional Ecology* 28.6, pp. 1459–1471.
- Goulson, Dave (Jan. 1999). 'Foraging strategies of insects for gathering nectar and pollen, and implications for plant ecology and evolution.' In: *Perspectives in Plant Ecology, Evolution and Systematics* 2.2, pp. 185–209.
- (Aug. 2013). 'REVIEW: An overview of the environmental risks posed by neonicotinoid insecticides.' In: *Journal of Applied Ecology* 50.4. Ed. by David Kleijn, pp. 977–987.
- Greenleaf, Sarah S. and Claire Kremen (Sept. 2006). 'Wild bees enhance honey bees' pollination of hybrid sunflower.' In: *Proceedings of the National Academy of Sciences* 103.37, pp. 13890–13895.
- Heinrich, Bernd (Aug. 1976). 'Resource Partitioning Among Some Eusocial Insects: Bumblebees.' In: *Ecology* 57.5, pp. 874–889.
- (Jan. 1979). 'Resource heterogeneity and patterns of movement in foraging bumblebees.' In: *Oecologia* 40.3, pp. 235–245.

- (2004). *Bumblebee economics*. Harvard University Press.
- Heinrich, Bernd and Peter H. Raven (1972). 'Energetics and Pollination Ecology.' In: *Science* 176.4035, pp. 597–602.
- Henry, Mickaël, Maxime Béguin, Fabrice Requier, Orianne Rollin, Jean-François Odoux, Pierrick Aupinel, Jean Aptel, Sylvie Tchamitchian, and Axel Decourtye (Apr. 2012). 'A Common Pesticide Decreases Foraging Success and Survival in Honey Bees.' In: *Science* 336.6079, pp. 348–350.
- Holland, J. Nathaniel and Donald L. DeAngelis (Feb. 2001). 'Population dynamics and the ecological stability of obligate pollination mutualisms.' In: *Oecologia* 126.4, pp. 575–586.
- Holland, J Nathaniel, Donald L DeAngelis, and Judith L Bronstein (2002). 'Population dynamics and mutualism: functional responses of benefits and costs.' In: *The American Naturalist* 159.3, pp. 231–244.
- Holling, Crawford S (1959). 'Some characteristics of simple types of predation and parasitism1.' In: *The Canadian Entomologist* 91.7, pp. 385–398.
- Inouye, David W. (1978). 'Resource Partitioning in Bumblebees: Experimental Studies of Foraging Behavior.' In: *Ecology* 59.4, pp. 672–678.
- Lichtenberg, Elinor M., Michael Hrnčir, Izabel C. Turatti, and James C. Nieh (Apr. 2011). 'Olfactory eavesdropping between two competing stingless bee species.' In: *Behavioral Ecology and Sociobiology* 65.4, pp. 763–774.
- Maienfisch, Peter et al. (2001). 'Chemistry and biology of thiamethoxam: a second generation neonicotinoid.' In: *Pest Management Science* 57.10, pp. 906–913.
- Mallinger, Rachel E, Hannah R Gaines-Day, and Claudio Gratton (2017). 'Do managed bees have negative effects on wild bees?: A systematic review of the literature.' In: *PloS one* 12.12, e0189268.
- McElreath, Richard (Jan. 2018). *Statistical Rethinking : A Bayesian Course with Examples in R and Stan*. Chapman and Hall/CRC. ISBN: 978-1-315-37249-5.
- Mommaerts, Veerle, Sofie Reynders, Jana Boulet, Linde Besard, Guido Sterk, and Guy Smagghe (Sept. 2009). 'Risk assessment for side-effects of neonicotinoids against bumblebees with and without impairing foraging behavior.' In: *Ecotoxicology* 19.1, p. 207.
- Morris, William F., Diego P. Vázquez, and Natacha P. Chacoff (2010). 'Benefit and cost curves for typical pollination mutualisms.' In: *Ecology* 91.5, pp. 1276–1285.
- Morse, D. H. (Aug. 1977). 'Resource Partitioning in Bumble Bees: The Role of Behavioral Factors.' In: *Science* 197.4304, pp. 678–680.

- R Core Team (2013). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. Vienna, Austria.
- Revilla, Tomás A (2015). 'Numerical responses in resource-based mutualisms: a time scale approach.' In: *Journal of theoretical biology* 378, pp. 39–46.
- Rohr, Rudolf P., Serguei Saavedra, and Jordi Bascompte (July 2014). 'On the structural stability of mutualistic systems.' In: *Science* 345.6195, p. 1253497.
- Roubik, David W. (Sept. 1978). 'Competitive Interactions Between Neotropical Pollinators and Africanized Honey Bees.' In: *Science* 201.4360.
- Sahli, Heather F and Jeffrey K Conner (2006). 'Characterizing ecological generalization in plant-pollination systems.' In: *Oecologia* 148.3, pp. 365–372.
- Skalski, Garrick T. and James F. Gilliam (2001). 'Functional Responses with Predator Interference: Viable Alternatives to the Holling Type II Model.' In: *Ecology* 82.11, pp. 3083–3092.
- Stanley, Dara A. and Nigel E. Raine (2016). 'Chronic exposure to a neonicotinoid pesticide alters the interactions between bumblebees and wild plants.' In: *Functional Ecology* 30.7, pp. 1132–1139.
- Thomson, Diane M. (2006). 'Detecting the effects of introduced species: a case study of competition between *Apis* and *Bombus*.' In: *Oikos* 114.3, pp. 407–418.
- Thomson, Diane M and Maureen L Page (Apr. 2020). 'The importance of competition between insect pollinators in the Anthropocene.' In: *Current Opinion in Insect Science* 38, pp. 55–62.
- Thomson, J. D., S. C. Peterson, and L. D. Harder (Jan. 1987). 'Response of traplining bumble bees to competition experiments: shifts in feeding location and efficiency.' In: *Oecologia* 71.2, pp. 295–300.
- Thomson, James D. (Jan. 1988). 'Effects of variation in inflorescence size and floral rewards on the visitation rates of traplining pollinators of *Aralia hispida*.' In: *Evolutionary Ecology* 2.1, pp. 65–76.
- Valdovinos, Fernanda S., Pablo Moisset De Espanés, José D. Flores, and Rodrigo Ramos-Jiliberto (2013). 'Adaptive foraging allows the maintenance of biodiversity of pollination networks.' In: *Oikos* 122.6, pp. 907–917.
- Vehtari, Aki, Andrew Gelman, Daniel Simpson, Bob Carpenter, and Paul-Christian Bürkner (May 2020). 'Rank-normalization, folding, and localization: An improved R for assessing convergence of MCMC.' In: arXiv: 1903.08008.
- Vázquez, Diego P., Silvia B. Lomáscolo, M. Belén Maldonado, Natacha P. Chacoff, Jimena Dorado, Erica L. Stevani, and Nydia L. Vitale

- (2012). 'The strength of plant–pollinator interactions.' In: *Ecology* 93.4, pp. 719–725.
- Vázquez, Diego P., William F. Morris, and Pedro Jordano (2005). 'Interaction frequency as a surrogate for the total effect of animal mutualists on plants.' In: *Ecology Letters* 8.10, pp. 1088–1094.
- Westphal, Catrin, Ingolf Steffan-Dewenter, and Teja Tscharntke (2003). 'Mass flowering crops enhance pollinator densities at a landscape scale.' In: *Ecology Letters* 6.11, pp. 961–965.
- (2006). 'Foraging trip duration of bumblebees in relation to landscape-wide resource availability.' In: *Ecological Entomology* 31.4, pp. 389–394.

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

Part III

FINAL WORDS

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

CONCLUSION

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

CONCLUSION

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.

BIBLIOGRAPHY

- Abrams, Peter A (1983). 'Arguments in favor of higher order interactions.' In: *The American Naturalist* 121.6, pp. 887–891.
- Abrams, Peter A. and Lev R. Ginzburg (Aug. 2000). 'The nature of predation: prey dependent, ratio dependent or neither?' In: *Trends in Ecology & Evolution* 15.8, pp. 337–341.
- Adler, Frederick R. and William F. Morris (Sept. 1994). 'A General Test for Interaction Modification.' In: *Ecology* 75.6, pp. 1552–1559.
- AlAdwani, Mohammad and Serguei Saavedra (2019). 'Is the addition of higher-order interactions in ecological models increasing the understanding of ecological dynamics?' In: *Mathematical Biosciences* 315, p. 108222.
- Amarasekare, Priyanga (2003). 'Competitive coexistence in spatially structured environments: a synthesis.' In: *Ecology letters* 6.12, pp. 1109–1122.
- Billick, Ian and Ted J. Case (1994). 'Higher Order Interactions in Ecological Communities: What Are They and How Can They be Detected?' In: *Ecology* 75.6, pp. 1529–1543.
- Bimler, Malyon D., Daniel B. Stouffer, Hao Ran Lai, and Margaret M. Mayfield (2018). 'Accurate predictions of coexistence in natural systems require the inclusion of facilitative interactions and environmental dependency.' In: *Journal of Ecology* 106.5, pp. 1839–1852.
- Callaway, Ragan M (2007). *Positive interactions and interdependence in plant communities*. Springer.
- Callaway, Ragan M. et al. (June 2002). 'Positive interactions among alpine plants increase with stress.' In: *Nature* 417.6891, pp. 844–848.
- Chamberlain, Scott A., Judith L. Bronstein, and Jennifer A. Rudgers (2014). 'How context dependent are species interactions?' In: *Ecology Letters* 17.7, pp. 881–890.
- Chesson, Peter (2000). 'Mechanisms of maintenance of species diversity.' In: *Annual review of Ecology and Systematics* 31.1, pp. 343–366.
- Connallon, Tim, Shefali Sharma, and Colin Olito (Jan. 2019). 'Evolutionary Consequences of Sex-Specific Selection in Variable Environments: Four Simple Models Reveal Diverse Evolutionary Outcomes.' In: *The American Naturalist* 193.1, pp. 93–105.

- D'Andrea, Rafael, Annette Ostling, and James P O'Dwyer (2018). 'Translucent windows: How uncertainty in competitive interactions impacts detection of community pattern.' In: *Ecology Letters* 21.6, pp. 826–835.
- Dean, Antony M (2005). 'Protecting haploid polymorphisms in temporally variable environments.' In: *Genetics* 169.2, pp. 1147–1156.
- Ellner, Stephen and Nelson G Hairston Jr (1994). 'Role of overlapping generations in maintaining genetic variation in a fluctuating environment.' In: *The American Naturalist* 143.3, pp. 403–417.
- Evans, Matthew R, Volker Grimm, Karin Johst, Tarja Knuuttila, Rogier De Langhe, Catherine M Lessells, Martina Merz, Maureen A O'Malley, Steve H Orzack, Michael Weisberg, et al. (2013). 'Do simple models lead to generality in ecology?' In: *Trends in ecology & evolution* 28.10, pp. 578–583.
- Freckleton, Robert P, Andrew R Watkinson, and Mark Rees (2009). 'Measuring the importance of competition in plant communities.' In: *Journal of ecology* 97.3, pp. 379–384.
- Hastings, Alan, James E Byers, Jeffrey A Crooks, Kim Cuddington, Clive G Jones, John G Lambrinos, Theresa S Talley, and William G Wilson (2007). 'Ecosystem engineering in space and time.' In: *Ecology letters* 10.2, pp. 153–164.
- Holling, Crawford S (1966). 'The strategy of building models of complex ecological systems.' In: *Systems analysis in ecology*, pp. 195–214.
- Kleinhesselink, Andrew R, Nathan JB Kraft, and Jonathan M Levine (2019). 'Mechanisms underlying higher order interactions: from quantitative definitions to ecological processes.' In: *bioRxiv*, p. 857920.
- Kneitel, Jamie M and Jonathan M Chase (2004). 'Trade-offs in community ecology: linking spatial scales and species coexistence.' In: *Ecology letters* 7.1, pp. 69–80.
- Kylafis, Grigoris and Michel Loreau (2008). 'Ecological and evolutionary consequences of niche construction for its agent.' In: *Ecology letters* 11.10, pp. 1072–1081.
- (Feb. 2011). 'Niche construction in the light of niche theory: Niche construction in light of niche theory.' In: *Ecology Letters* 14.2, pp. 82–90.
- Lai, Hao Ran, Kwek Yan Chong, Margaret M Mayfield, and Daniel B Stouffer (2020). 'The role of higher-order biotic interactions on tropical tree growth.' In: *bioRxiv*.
- Laland, Kevin N, F John Odling-Smee, and Marcus W Feldman (1999). 'Evolutionary consequences of niche construction and their implications for ecology.' In: *Proceedings of the National Academy of Sciences* 96.18, pp. 10242–10247.

- Lanuza, Jose B., Ignasi Bartomeus, and Oscar Godoy (2018). 'Opposing effects of floral visitors and soil conditions on the determinants of competitive outcomes maintain species diversity in heterogeneous landscapes.' In: *Ecology Letters* 21.6, pp. 865–874.
- Letten, Andrew D. and Daniel B. Stouffer (2019). 'The mechanistic basis for higher-order interactions and non-additivity in competitive communities.' In: *Ecology Letters* 22.3, pp. 423–436.
- Levine, Jonathan M., Jordi Bascompte, Peter B. Adler, and Stefano Allesina (June 2017). 'Beyond pairwise mechanisms of species coexistence in complex communities.' In: *Nature* 546.7656, pp. 56–64.
- Levins, Richard (1993). 'A response to Orzack and Sober: formal analysis and the fluidity of science.' In: *The Quarterly Review of Biology* 68.4, pp. 547–555.
- (2006). 'Strategies of abstraction.' In: *Biology and Philosophy* 21.5, pp. 741–755.
- Levins, Richard and Richard Lewontin (Jan. 1980). 'Dialectics and reductionism in ecology.' In: *Synthese* 43.1, pp. 47–78.
- Martyn, Trace E, Daniel B Stouffer, Oscar Godoy, Ignasi Bartomeus, Abigail I Pastore, and Margaret M Mayfield (2021). 'Identifying "Useful" Fitness Models: Balancing the Benefits of Added Complexity with Realistic Data Requirements in Models of Individual Plant Fitness.' In: *The American Naturalist* 197.4, pp. 415–433.
- May, Robert M (2019). *Stability and complexity in model ecosystems*. Princeton university press.
- Mayfield, Margaret M and Daniel B Stouffer (2017). 'Higher-order interactions capture unexplained complexity in diverse communities.' In: *Nature ecology & evolution* 1.3, pp. 1–7.
- Orzack, Steven Hecht (2012). 'The philosophy of modelling or does the philosophy of biology have any use?' In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 367.1586, pp. 170–180.
- Orzack, Steven Hecht and Elliott Sober (1993). 'A critical assessment of Levins's The strategy of model building in population biology (1966).' In: *The Quarterly Review of Biology* 68.4, pp. 533–546.
- Roughgarden, Jonathan, Aviv Bergman, Sharoni Shafir, and Charles Taylor (2018). 'Adaptive Computation in Ecology and.' In: *Adaptive Individuals In Evolving Populations: Models And Algorithms*, p. 25.
- Song, Chuliang, Sarah Von Ahn, Rudolf P. Rohr, and Serguei Saavedra (Jan. 2020). 'Towards a Probabilistic Understanding About the Context-Dependency of Species Interactions.' In: *Trends in Ecology & Evolution*.

- Stouffer, Daniel B and Mark Novak (2021). 'Hidden layers of density dependence in consumer feeding rates.' In: *Ecology Letters* 24.3, pp. 520–532.
- Tylianakis, Jason M, Raphael K Didham, Jordi Bascompte, and David A Wardle (2008). 'Global change and species interactions in terrestrial ecosystems.' In: *Ecology letters* 11.12, pp. 1351–1363.
- Vázquez, Diego P, William F Morris, and Pedro Jordano (2005). 'Interaction frequency as a surrogate for the total effect of animal mutualists on plants.' In: *Ecology letters* 8.10, pp. 1088–1094.
- Vázquez, Diego P., Silvia B. Lomáscolo, M. Belén Maldonado, Natacha P. Chacoff, Jimena Dorado, Erica L. Stevani, and Nydia L. Vitale (2012). 'The strength of plant–pollinator interactions.' In: *Ecology* 93.4, pp. 719–725.
- Weiss-Lehman, Christopher P, Chhaya M Werner, Catherine H Bowler, Lauren M Hallett, Margaret M Mayfield, Oscar Godoy, Lina Aoyama, György Barabás, Chengjin Chu, Emma Ladouceur, et al. (2021). 'Disentangling key species interactions in diverse and heterogeneous communities: A Bayesian sparse modeling approach.' In: *bioRxiv*.

Part IV

APPENDICES

APPENDIX A

ENERGY GAINS DURING THE EXPERIMENT

To evaluate the energy gains of *Bombus* individuals during the experiments, we first determined the maximum energy gains per floral visits (Table 6.1). Then, we fit a model to predict the energy gains per visit for species i , using flower types as predictors:

$$\kappa_i = \epsilon_p F_{pink} + \epsilon_b F_{blue} + \epsilon_w F_{white} + \epsilon_y F_{yellow}, \quad (6.1)$$

where κ_i is energy consumed per visit for species i , ϵ_j , are parameters that describe the energy gains, and F_j are dummy variables that represent the type of flower visited. The subscripts denote the type of flowers by colors. We fit the model from Eq. 6.1 to the data of energy per visit described in the main text. We fit this model using a Bayesian framework with Hamiltonian Monte Carlo (HMC) methods:

$$e_i \sim \text{Normal}(\mu_i, \sigma) \quad (6.2)$$

$$\mu_i = \epsilon_p F_{pink} + \epsilon_b F_{blue} + \epsilon_w F_{white} + \epsilon_y F_{yellow} \quad (6.3)$$

$$\epsilon_p, \epsilon_b, \epsilon_w, \epsilon_y \sim \text{Normal}(0, 10) \quad (6.4)$$

$$\sigma \sim \text{Student-t}(3, 0, 10) \quad (6.5)$$

We ran four chains with a warmup of 1000 iterations and 1000 sampling iterations and using weakly informative priors. We fit our model and determined convergence using the same approach as described in Chapter 2. Finally we used Bayes R^2 to estimate the proportion of variance explained by our model for new data.

The model of energy consumption with flower types as predictors had a value of Bayes R^2 of 0.847. That is, if we were to fit the energy model to new data, we would expect it to estimate around 85% of the variance. Furthermore, the parameter distribution of the energy mode yields estimates very similar to the maximum energy gains per visit Fig. 6.1. That is, each time a bee visited a flower, we would expect it to gain as much energy as the maximum a flower has to offer. Thus, the more visits an individual makes, the more energy gains it obtains.

Table 6.1: Maximum energy gains per visit, for each of the different flower types. Each visit triggered the automatic reward of $10\text{ }\mu\text{l}$, and each gram of sugar has 17 kilojoules of energy.

Flower type	Sucrose concentration	Max. kilojoules per visit
Blue	2.0 M	0.1165
White	1.5 M	0.0877
Yellow	1.0 M	0.0581
Pink	0.5 M	0.0290

Indeed, plots of total number of floral visits per bee per trial and total energy gains per trial (Fig. 6.2), show that energy gains are strongly correlated with the number of floral visits an individual makes. Thus, we can be confident that *Bombus* individuals were consuming close to the full reward each time they visited an artificial flower.

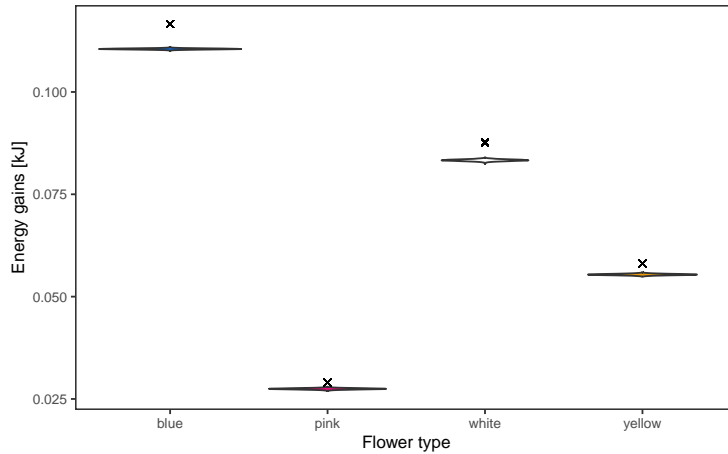


Figure 6.1: Posterior distribution of ϵ parameters from Eq. 6.1. Each parameter estimates the mean energetic gain per visit (in kilojoules), per flower type. We have also indicated the maximum gains per visit of the different flower types with an x.

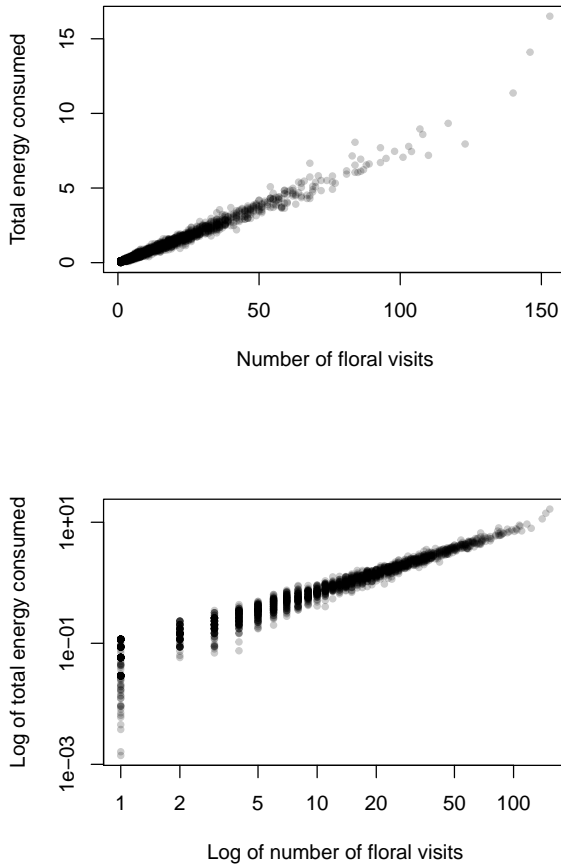


Figure 6.2: Relationship between the total number of visits made by an individual bee and its total energy gains during an experiment trial. In the top panel, the total energy consumed per trial is clearly an increasing function of the number of floral visits an individual makes during the trial. Each point corresponds to observations at the individual level. In the bottom panel, we show the same relationship with log-log axes.

FORAGING TRIALS AND DATA STRUCTURE

In single-species trials, all but one of the factorial combinations of conspecific co-foragers, pesticide exposure, and two levels of resource availability (instantaneous and delayed refill) had at least two replicates. The only exceptions were the combinations of four and eight *Bombus* individuals foraging under instantaneous floral refill and pesticide exposure. The third level of resource availability, intermediate floral refill time, was tested *only* for 16 *Bombus* individuals foraging at the same time, for the two levels of pesticide exposure (Table 6.2).

In multi-species trials, all but two of the factorial combinations of bee species richness, two levels of resource availability (instantaneous and delayed refill), and pesticide exposure had at least two replicates. The only exception was three foraging species with instantaneous refill and pesticide exposure. Furthermore, not all species of co-foragers were tested under all combinations of resource availability and pesticide exposure, making it impossible to fully disentangle their statistical interaction (Table 6.3).

In total, we tracked the time between floral visits and energy consumed by 735 *Bombus* individuals across 139 single-species trials and by 277 *Bombus* individuals across 112 multi-species trials. We excluded from the analysis the data from bumblebees that were completely inactive within trials (i.e. that did not record a single visit during the 75 minutes), since they do not provide information regarding visitation frequency or energy obtained per visit. Of the data collected from the active bees, we also excluded the first and last record of time and nectar consumption for every individual bumblebee within a trial, unless that individual only made one visit. We excluded those data points since previous research indicates that these points are less informative about foraging behavior and generate skewed data (Edwards et al., 2007). The number of observations we examined amounts to 33919 records of times between floral visits.

Table 6.2: Single-species foraging trials. We show the number of trials for different combinations of *Bombus* abundance, pesticide exposure and refill time. Pesticide exposure is a binary variable that equals to one when all individuals in the trial were subject to a sub-lethal doses of pesticide. Refill time is the time (in seconds) after which an artificial flower could dispense a new sucrose reward after a previous visit.

<i>Bombus</i> abundance	Pesticide exposure	Refill time	Number of trials
4	0	0	2
4	0	540	10
4	1	0	0
4	1	540	13
8	0	0	2
8	0	540	10
8	1	0	0
8	1	540	13
16	0	0	5
16	0	120	34
16	0	540	15
16	1	0	5
16	1	120	14
16	1	540	16

Table 6.3: Multi-species foraging trials. We show the number of trials for different combinations of species richness, pesticide exposure and two levels of resource availability. We also show the number of individuals of each species used in each trial as well as the number of trials per combination. Pesticide exposure and refill time have the same interpretation as in the single-species trials.

Richness	Pesticide exposure	Refill time	<i>Bombus</i> abundance	<i>Apis</i> abundance	<i>Osmia</i> abundance	<i>Megachile</i> abundance	Number of trials
2	0	0	8	0	8	0	7
2	0	0	8	0	0	8	5
2	0	0	8	8	0	0	5
2	1	0	8	0	8	0	2
2	0	540	8	0	8	0	7
2	0	540	8	0	0	8	5
2	0	540	8	8	0	0	5
2	1	540	8	0	8	0	6
2	1	540	8	0	0	8	4
2	1	540	8	8	0	0	6
3	0	0	5	5	6	0	3
3	0	0	6	5	5	0	1
3	0	0	5	6	5	0	1
3	0	0	5	0	6	5	3
3	0	0	6	0	5	5	2
3	0	0	6	5	0	5	2
3	0	0	5	5	0	6	1
3	0	540	6	5	5	0	1
3	0	540	5	5	6	0	3
3	0	540	5	6	5	0	1
3	0	540	5	0	6	5	3
3	0	540	6	0	5	5	3
3	0	540	6	5	0	5	3
3	1	540	6	5	5	0	5
3	1	540	5	5	6	0	2
3	1	540	6	0	5	5	4
3	1	540	5	0	6	5	1
3	1	540	6	5	0	5	1
4	0	0	4	4	4	4	5
4	1	0	4	4	4	4	5
4	0	540	4	4	4	4	5
4	1	540	4	4	4	4	5

STATISTICAL ANALYSIS

We used hierarchical models to fit the data to the models described in the main text (Eqs. 9-11) because we have multiple observations from the same *Bombus* individuals and to allow each of these individuals to deviate from the parameter's grand mean. For example, predicted times between floral visits for an individual b of species i given by the *interference* model would be:

$$\rho_{i,b} = (\alpha + \Delta\alpha_b) + (\beta_i + \Delta\beta_{ib})(P_i - 1) + \sum_j (\beta_j + \Delta\beta_{jb})P_j \quad (6.6)$$

The three deviations from the grand means ($\Delta\alpha_b$, $\Delta\beta_{ib}$, $\Delta\beta_{jb}$) capture the individual specific response and are incorporated in a comparable manner to how random effects are included in mixed-effects models. This way to parameterize our models allowed us to estimate how each individual responded to the treatments, helped to control for pseudo-replication across individual

bees, and pooled information across individual bees to still inform the grand mean when sample size was low. We show how we incorporated the random effects in each model in Table 6.4.

Across all models, we assumed that the times between floral visits followed an exponential distribution that has a rate parameter $\rho_{i,b}$. We also required the density-independent rate of all models to be positive, as a “negative” time would be unfeasible as a baseline. Thus we constrained the density independent parameters to be positive. Consequently, we fit non-linear models using the exponential family and the “identity” link. Again, using the *interference* model as an example, our Bayesian one-level hierarchical model of times between floral visits for an individual b may be written as:

$$t_{i,b} \sim \text{Exponential}(\rho_{i,b}) \quad (6.7)$$

$$\rho_b = e^{(\alpha + \Delta\alpha_b)} + (\beta_i + \Delta\beta_{ib})(P_i - 1) + \sum_j (\beta_j + \Delta\beta_{jb})P_j \quad (6.8)$$

$$\alpha, \beta_i, \beta_j \sim \text{Normal}(0, 10) \quad (6.9)$$

$$\Delta\alpha_b, \Delta\beta_{ib}, \Delta\beta_{jb} \sim \text{Multivariate Normal}(\sigma, \gamma) \quad (6.10)$$

$$\sigma \sim \text{Student-t}(3, 0, 70) \quad (6.11)$$

$$\gamma \sim \text{LKJcorr}(1) \quad (6.12)$$

Table 6.4: Statistical models fitted to the data. Each model includes fixed and random effects that together determine the time between floral visits. The *null* model assumes that neither co-foraging species nor environmental conditions change the times between floral visits. The *interference* model allows the number of visits to change only due to the number of co-foraging bees (i.e. it treats interference as constant across environmental conditions). Finally, the *treatments* model allows the environmental conditions to have an effect on both the density-independent and density-dependent parameters.

Model	Eqn. in main text	Parameter class	Fixed effects	Random effects
<i>null</i>	2.9	density-independent	α	$\Delta\alpha_b$
<i>interference</i>	2.10	density-independent	α	$\Delta\alpha_b$
		conspecific-dependent	β_i	$\Delta\beta_{ib}$
		heterospecific-dependent	β_j	$\Delta\beta_{jb}$
<i>treatments</i>	2.11	density-independent	$\alpha, \alpha_r, \alpha_e$	$\Delta\alpha_b, \Delta\alpha_{rb}, \Delta\alpha_{eb}$
		conspecific-dependent	$\beta_i, \beta_{ir}, \beta_{ie}$	$\Delta\beta_{ib}, \Delta\beta_{irb}, \Delta\beta_{ieb}$
		heterospecific-dependent	$\beta_j, \beta_{jr}, \beta_{je}$	$\Delta\beta_{jb}, \Delta\beta_{jrb}, \Delta\beta_{jeb}$

COLOPHON

This document was typeset using the typographical look-and-feel `classicthesis` developed by André Miede. The style was inspired by Robert Bringhurst’s seminal book on typography “*The Elements of Typographic Style*”. `classicthesis` is available for both \LaTeX and \LyX :

<https://bitbucket.org/amiede/classicthesis/>

Final Version as of November 23, 2021 (Version 1.0).