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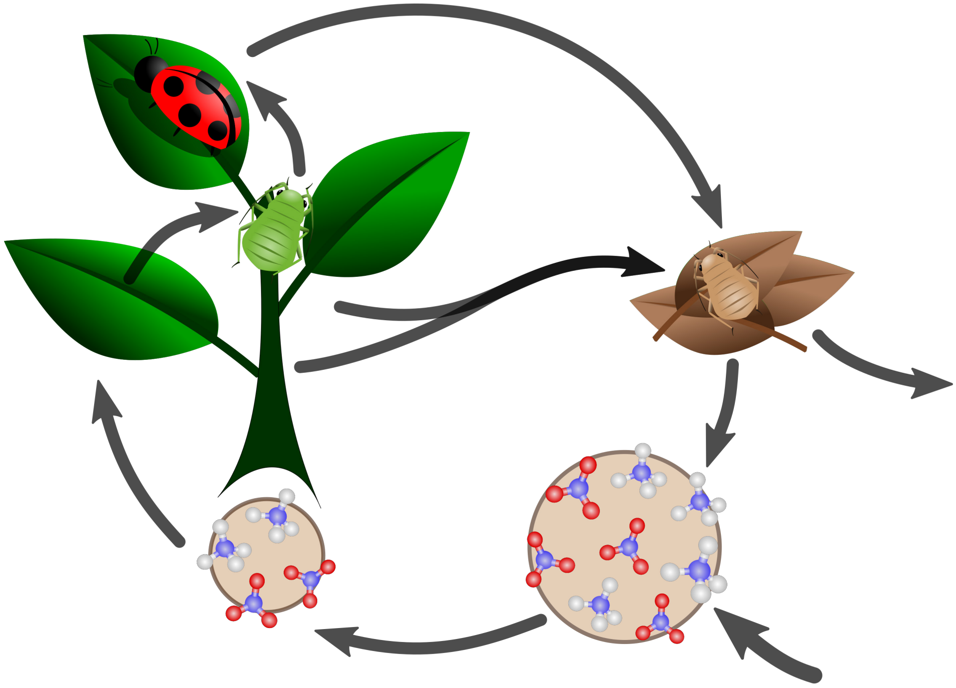
# Love (eating) thy neighbour?

## Understanding and predicting food-web structure and dynamics

Kate Wootton



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Doctoral Thesis
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Cover: An illustration of the food-web soil-nutrient model used in Paper V.
Illustration: Kate Wootton

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## Abstract

Food webs are networks of feeding interactions that provide the backbone of ecological communities. The structure - who eats whom - and dynamics - how population abundances fluctuate as a result - of food webs depend on the traits of the species present. The exchange of individuals or material between food webs can have further consequences for the structure and dynamics of both the donor and recipient communities. Increasing our insight into how species traits constrain both structure and dynamics of food webs, and how this is affected by exchanges with other communities, will advance both the theory and predictive capacity of food-web ecology.

In this thesis, I make a multifaceted foray into the factors behind food-web structure and dynamics. To provide a general framework for selecting and applying traits to food-web interactions, I show how a trophic interaction can be broken into steps and, combined with traits, used to parameterize dynamic food-web models. The resulting framework is sufficiently general and flexible to be applied to any community and to guide comparison across diverse interaction types and ecosystems. Using this framework, I developed a dynamic model parameterized by body size and microhabitat use and applied it in a mesocosm experiment. I found that different versions of the model fit the data equally well, but generated vastly different predictions for interactions with a hypothetical new species. With data from a tritrophic *Salix*-galler-parasitoid network, I used a suite of statistical approaches to reveal different facets of the relationship between traits and network structure, finding that traits explained more of the galler-parasitoid than *Salix*-galler network, and that the relationship between traits and network structure was non-linear. Finally, I returned to dynamic models to address the question of how coupled food webs affect each other. I simulated food-web and soil-nutrient dynamics in adjacent habitats differing in fertility and plant diversity. The foraging movement of consumers between habitats affected all elements of ecosystem function. This was especially evident in low fertility habitats coupled to high fertility habitats, with considerable applied and theoretical implications.

In total, I show that a trait-based approach to food webs has great promise for understanding food-web structure and dynamics and our ability to make accurate predictions, but that there are still a number of challenges to address. I lay out a framework and ground-work experiments for addressing some of these challenges, and show how the iteration between theory, empirical experiments, and analysis is ultimately required to reach the promise that trait-based approaches hold.

*Keywords:* Species traits, ecological network, trophic interactions, habitat use, allometric trophic network model, foraging movement, trait-matching

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# Att äta eller inte äta - hur kan vi förstå och förutsäga näringsvävars struktur och dynamik?

## Sammanfattning

Näringsvävar beskriver nätverk av födointeraktioner som bildar stommen i ekologiska samhällen. Strukturen - vem äter vem - och dynamiken - hur populationerna fluktuerar till följd av näringsvävsstrukturen beror på egenskaperna hos de närvarande arterna. Utbyte av individer eller material mellan näringsvävar kan få ytterligare konsekvenser för strukturen och dynamiken för både givar- och mottagarsystemet. Att öka vår insikt om hur artsegenskaper påverkar och begränsar födovävars struktur och dynamik, och hur detta påverkas av utbyte med andra samhällen, kommer att främja både teori och prediktionskapacitet för näringsväv-ekologin som forskningsområde.

I den här avhandlingen gör jag en mångfacetterad analys av faktorerna bakom näringsvävars struktur och dynamik. För att skapa en allmän ram för att välja och tillämpa arters egenskaper på näringsvävar interaktioner visar jag först hur en trofisk interaktion kan delas upp i steg och, i kombination med egenskaper, användas för att parametrera dynamiska näringsvävs-modeller. Med hjälp av detta ramverk utvecklade jag sedan en dynamisk modell, parameteriserad efter arters kroppsstorlek och mikrohabitat-användning och applicerade den på resultaten från ett mesokosm-experiment. Jag fann att olika versioner av modellen passar de obsererade resultaten i stort sett lika bra, men genererade väldigt olika förutsägelser för interaktioner med en hypotetisk ny art. Med data från ett tritrofiskt *Salix*-galler-parasitoid nätverk, använde jag därefter en serie statistiska metoder för att avslöja olika aspekter av förhållandet mellan egenskaper och nätverksstruktur, och fann att arters egenskaper förklarade mer av galler-parasitoid än strukturen på *Salix*-galler nätverketAvslutningsvis återvände jag till dynamiska modeller för att ta upp frågan om hur kopplade näringsvävar påverkar varandra. Jag simulerade näringsvävar och marknäringsdynamiken i intilliggande livsmiljöer som skilde sig åt i fertilitet och växtdiversitet. Rörelse av konsumenter mellan livsmiljöer påverkade alla delar av ekosystemets funktion med både tillämpade och teoretiska konsekvenser.

Sammantaget visar jag att ett artegenskapsbaserat tillvägagångssätt för energi- och materialflöden har en stor potential för att öka förståelsen för näringsvävars struktur och dynamik och vår förmåga att göra mer användbara förutsägelser, men att det fortfarande finns ett antal utmaningar att ta itu med för att nå dit. Jag presenterar ett ramverk och och förslag på experiment för att ta itu med några av dessa utmaningar och visar hur iterationen mellan teori, empiriska experiment och analys i slutändan krävs för att realisera den potential som egenskapsbaserade tillvägagångssätt utlovar.

*Nyckelord:* Artegenskaper, ekologiskt nätverk, trofiska interaktioner, användning av livsmiljöer, allometriskt trofiskt nätverk modell, foderrörelse, dragmatchning

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# Dedication

To the friends and family I left behind in New Zealand,
and to the friends who became family in Sweden.

*Anything that can be put in a nutshell should remain there*
- Bertrand Russell (Gregory David Roberts, Shantaram )

**Ma tini ma mano ka rapa te whai**
*By many, by thousands, the work will be completed*

- Māori proverb
(And a thousand thanks to the many who made this thesis possible!!)

# Contents

# List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Kate Wootton, Alva Curtsdotter, Tomas Roslin, Riccardo Bommarco and Tomas Jonsson (2020). Predicting trophic interactions using species' traits: a conceptual framework. (manuscript)

II A. N. Laubmeier*, Kate Wootton*, J. E. Banks, Riccardo Bommarco, Alva Curtsdotter, Tomas Jonsson, Tomas Roslin, H. T. Banks (2018). From theory to experimental design: Quantifying a trait-based theory of predator-prey dynamics. *PLoS ONE* 13(4): e0195919.

III Kate Wootton, A.N. Laubmeier, Alva Curtsdotter, Tomas Jonsson, H.T. Banks, Riccardo Bommarco and Tomas Roslin (2020). From theory to experiment and back again — Challenges in quantifying a trait-based theory of predator-prey dynamics. (manuscript)

IV Kate Wootton, Dominque Gravel, Guillaume Blanchet, Laura Riggi, Tommi Nyman, Andrew Liston, Jens-Peter Kopelke and Tomas Roslin (2020). Differential imprints of trait matching within a single tritrophic network: complementary insights from complementary methods. (manuscript)

V Kate Wootton*, Alva Curtsdotter*, Tomas Roslin, Riccardo Bommarco and Tomas Jonsson (2020). Food webs coupled in space: Consumer foraging movement affects both stocks and fluxes. (manuscript)

* Co-first authors

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The contribution of Kate Wootton to the papers included in this thesis was as follows:

I Conceived the project together with TR, developed the mathematical framework with TJ and AC, led the writing of the manuscript with contribution from co-authors.

II Co-first author. Designed the experiment together with co-authors. Developed the model together with AL, AC and TJ. Wrote the manuscript together with AL, with input from other co-authors.

III Conceived the project with RB, TJ, AC, and TR, performed the experiment, developed experimental design, contributed to analysis (led by AL), wrote manuscript with input from co-authors.

IV Designed the study together with TR, performed the field work together with LR, collected supplementary data with support from AL and TN, performed statistical analysis with support from GB and DG. Wrote the manuscript with input from all co-authors.

V Developed experimental design with co-authors, contributed to writing matlab code for simulations (led by TJ), ran computer simulations, analysed data, wrote manuscript together with AC.

# 1 Introduction

One cannot study a species in isolation and hope to understand its dynamics (i.e. fluctuations in its population abundance). To know whether it will persist, one needs to understand what the focal species is eating (its resources) and their dynamics, and what else is also eating them. One may also need to know what the focal species is eaten by (its consumers), what effect they have on the focal species, and their dynamics. In short, one needs in many cases to study an entire food web.

A food web maps feeding interactions within an ecological community in terms of both who eats whom (food-web structure) and the consequences those interactions have for the interacting populations (food-web dynamics). As such, food webs make a valuable tool for understanding the impacts of, for example, land-use change (e.g. Gagic et al., 2011; Tylianakis, Tscharntke, & Lewis, 2007), invasive species (e.g. Pearse & Altermatt, 2013), and climatic changes (e.g. Carscallen & Romanuk, 2012; Sentis, Hemptinne, & Brodeur, 2014). The particular value of food webs for approaching such questions is that they can capture indirect effects and non-intuitive responses as impacts propagate throughout the network (e.g. Montoya et al., 2009; Sanders, Sutter, & van Veen, 2013; K. L. Wootton & Stouffer, 2016b; Zarnetske, Skelly, & Urban, 2012).

The difficulty in using or studying a food web lies in actually establishing what it looks like. One needs to know not only who interacts with whom, but also how strong those interactions are (J. T. Wootton & Emmerson, 2005). Ob-

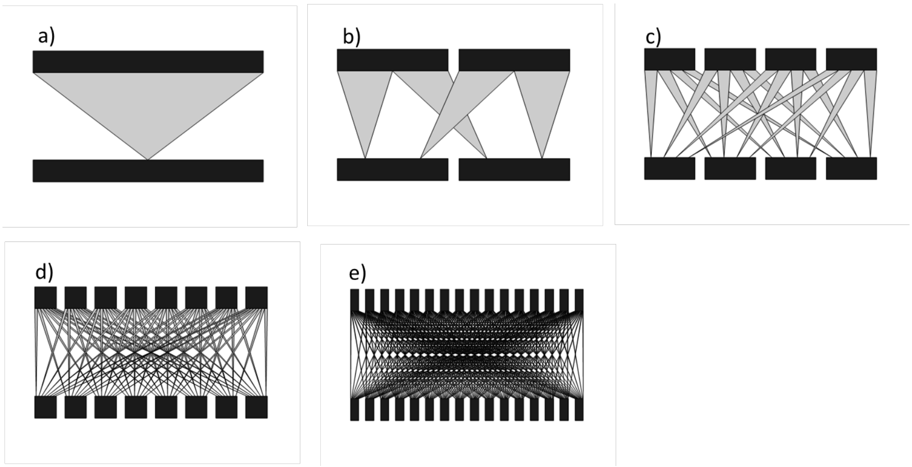


Figure 1: As the number of species in the network increases, the number of interactions increases much more rapidly. The figure shows all possible interactions between just a) two, b) four, c) eight, d) 16 and e) 32 species in a bipartite network.

taining this information empirically is difficult, expensive, and time consuming (Roslin & Majaneva, 2016).

An alternative, repeatedly mooted, is to use species traits to predict who will interact with whom (e.g. Bartomeus et al., 2016; Boukal, 2014; Morales-Castilla et al., 2015). For example, many interactions can be predicted based on body size (large things generally eat small things) (e.g. Gravel et al., 2013; Jonsson, 2014; Jonsson et al., 2018), while more specific traits such as barbel length (Nagelkerke & Rossberg, 2014) or biting strength (Brousseau, Gravel, & Handa, 2018b; Deraison et al., 2015) are more important in certain contexts. The advantage of using species traits — well-defined characteristics that can be evaluated at the individual level (Pey et al., 2014; Violle et al., 2007) — is two-fold; the effect of traits on an interaction can yield important insight into the mechanisms underlying the interaction, and predicting interactions from traits could be a significant time savings relative to characterizing all interactions individually (Roslin & Majaneva, 2016). Ideal traits in this regard are easily measured and, by doing so on a per-species basis, such traits can be used to predict interactions between all species in the community. As the number of possible interactions between species increases with the square of the number of species (Fig. 1), this rapidly becomes a significant savings.

There is abundant research on the impact of species' traits on interactions (e.g. Bartomeus et al., 2016; Brousseau et al., 2018b; Eklöf et al., 2013; Laigle et al., 2018) and an increasing number of models use species traits to predict food-web structure and dynamics (e.g. Gravel et al., 2013; Laubmeier et al., 2018; Schneider, Scheu, & Brose, 2012; Williams & Martinez, 2000). I give an overview of both in **Paper I**. Unfortunately, although there are a number of cases where species traits have predicted interactions well (particularly using body size), there is no one trait that can explain interactions across all ecosystems.

To progress with the goal of using species traits to explain and predict food-web structure and dynamics, we need a framework for using species traits to parameterize dynamic food-web models that can accommodate whichever traits are most important for a particular ecosystem. This I develop and describe in **Paper I**. We also require empirical experiments to investigate the effect of specific traits and integrate them into mathematical models — an example of this is **Paper III**, with pre-experimental simulations and model development laid out in **Paper II**. To understand which traits are likely to be important requires comparing a wide range of traits within a well-sampled ecosystem — this I do in **Paper IV**.

Although food webs are frequently conceptualized in isolation, ecosystems regularly exchange material and/or individuals with other communities and such exchanges can be crucial for food-web dynamics and ecosystem function (Loreau, Mouquet, & Gonzalez, 2003; Lovett et al., 2005; Polis, Anderson, & Holt, 1997). Just as one cannot study a single species in isolation and hope to truly understand its dynamics, one can also not study a food web in isolation and expect to truly understand its dynamics. In **Paper V**, I explore the impact of consumer foraging movement between adjacent habitats differing in fertility and plant diversity on food-web and soil-nutrient stocks and fluxes. To explore a wide range of scenarios, I used computer simulations driven by a dynamic model such as those used in **Paper I**, **Paper II** and **Paper III**. Together, **Paper I**-**Paper V** develop our understanding of food-web structure and dynamics, both in isolation and when coupled to other webs.

# 2 Theoretical perspectives

My thesis centers on the role of traits in structuring food webs and their dynamics and how these dynamics play out across habitats. To approach my research questions, outlined in section 3, I build on theory related to trophic interactions, including dynamic predator-prey models; functional traits; food-web theory, specifically theories and models related to food-web structure and food-web dynamics; and the effect of exchanging material or organisms with other ecosystems.

## 2.1 A trophic interaction

To survive, an organism must interact with its environment in a multitude of ways. One of the most fundamental interactions is the trophic, i.e. feeding, interaction. All organisms must consume resources to survive and the majority of consumers become resources to other consumers. The need to eat, and to avoid being eaten, shapes the world. As a result, ecologists have been interested in trophic interactions since ecology's inception, with the first food chains described in the late 1600s (Egerton, 2007). Consumers clearly cannot exist without resources. As a result, consumer population size depends on the availability of their resources (Polis & Strong, 1996). In turn, a resource population may be controlled by its consumers (Estes et al., 2011; Marshall & Essington, 2011). There are many types of trophic interaction, and while they each have their specifics, the underlying principles are general to all. Herbivory, predation, and parasitoids all make an appearance in the pages of this thesis.

An ever-present question is to what extent a community is top-down controlled (by the consumer) versus bottom up controlled (by the resource) (e.g.

Brose, 2008; Elmhagen & Rushton, 2007; Gravel, Albouy, & Thuiller, 2016; Polis & Strong, 1996). The distinction is important, especially when it comes to exploring or predicting the effects of land-use change (bottom-up) (e.g. Gagic et al., 2011; Tylianakis et al., 2007) and species extinctions (Estes et al., 2011). For example, the loss of top predators in a wide range of ecosystems has led to catastrophic effects including multiple secondary extinctions as the top-down control provided by the predators is lost and the ecosystem restructures (Estes et al., 2011). The strength of a trophic interaction influences not only the two species involved in the interaction, but also the rest of the community (Estes et al., 2011; J. T. Wootton, 1997; J. T. Wootton & Emmerson, 2005).

Dynamic models are an attempt to explore and understand how trophic interactions affect interacting populations (Berryman, 2011). The most simple and well-known dynamic predator-prey models are the Lotka-Volterra predator-prey models (Lotka, 1925; Volterra, 1926) which can be expressed as:

$$\begin{aligned} \frac{dR}{dt} &= rR - aRC \\ \frac{dC}{dt} &= eaRC - mC \end{aligned} \tag{1}$$

where the resource/prey population ($R$) increases due to its growth rate ($r$) and decreases depending on the attack rate ($a$) of the predator. The consumer/predator population ($C$) increases depending on its assimilation efficiency ($e$) and how much it attacks prey, and decreases dependent on its mortality rate ($m$).

There are many ways this simple model can, and has been, improved to make it more realistic. One of the most fundamental is the functional response, which describes the way in which the predator population responds to the size of the prey population (Holling, 1959). In the equation above, $a$ is the parameter that changes depending on the functional response. Holling (1959) described three such functional responses (Fig. 2) which continue to be used today (e.g. Barrios-O'Neill et al., 2016; Brose, 2010; Koen-Alonso, 2007). A type I response is the simplest, where predators respond linearly to the prey population size. With a type II response, predators become saturated and their attack rate plateaus as the prey population increases. Finally, a type III response also takes into account the cost associated with learning to identify

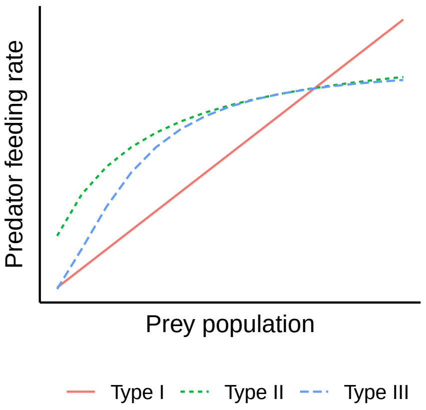


Figure 2: An overview of the relationship between prey population and predator feeding rate for Holling's functional responses (Holling, 1959). For a type I response, the predator's feeding rate increases linearly with the prey's abundance. In a type II response, the predator reaches saturation and cannot increase its feeding rate as the prey population increases. A type III response is similar to type II, but takes into account that finding and identifying prey at very low biomasses may be limiting which decreases attack rates.

and capture prey, so the per capita attack rate is highest at intermediate prey population sizes (Fig. 2). Although the type I response has frequently been used because of its computational simplicity, the most appropriate functional response depends on the species being modeled.

In studying trophic interactions, many researchers have implicitly or explicitly divided the predation process into steps (e.g. Bateman, Vos, & Anholt, 2014; Boukal, 2014; Griffiths, 1980; Holling, 1959; O'Brien, Browman, & Evans, 1990; Portalier et al., 2019). For example, Holling in his type II response recognizes the importance of both the attack stage and the time to handle and consume prey (Holling, 1959). From a trait-based perspective, the advantage of breaking a trophic interaction into steps is that traits have different impacts (or no impact) on each step. The division into steps allows a clearer understanding of where the trait is having an impact and what that means for the species involved (further discussed in **Paper I**). The most commonly recognized steps include search, attack (pursuit and/or subjugation), and handling (Bateman et al., 2014; Boukal, 2014; Griffiths, 1980; Portalier et al., 2019). Upon closer inspection, however, different studies draw the lines between steps in different places. For example, Griffiths (1980) only recognises the steps search, pursuit, and subjugation, while Bateman et al. (2014) describes the steps encounter, detection, pursuit, capture, handling and consumption, but then groups them simply as 'pre-attack' versus 'post-attack'. Barrios-O'Neill et al. (2016) bundles subjugation, ingestion, and digestion together as 'handling time'. This can be problematic when attempting to understand species' traits and model parameters in relation to steps - a consideration that I raise in **Paper I**. I therefore first define in **Paper I** eight steps which clearly break up any trophic interaction into its components; location, detection, decision, pursuit, subjugation, ingestion, digestion, allocation of resources. This division into steps can then aid understanding of how species' traits affect both food-web structure and dynamics.

## 2.2 Species' traits and trait-based modeling

Life is a constant battle to eat and avoid being eaten. The methods and traits species develop in response to this battle have both costs and benefits (Bateman et al., 2014). As a result, the traits a species exhibits can tell us a great deal about whom it eats or is eaten by, a topic which forms the substance of this thesis.

A "trait" is a characteristic of an organism which is well defined and measurable at an individual level (Pey et al., 2014; Violle et al., 2007). Those traits that influence an organism's performance are termed "functional traits", a term coined by Calow (1987). Functional traits can be further divided into response traits - those that govern a species' response to the environment, other species, or disturbances - and effect traits - which determine a species' effect on ecosystem properties and processes (Díaz & Cabido, 2001; Nock, Vogt, & Beisner, 2016). The concepts of response and effect traits were originally designed for plants or plant-herbivore interactions (Lavorel & Garnier, 2002). Gravel et al. (2016) proposed instead that in food webs traits should be categorized into *topological traits*, which determine pairwise interactions, *consumption traits*, which impact *per capita* interaction strength, and *life history traits* which influence *per population* interaction strengths.

Trait-based approaches to understanding community structure and dynamics began in the seventies and were first applied to plants (e.g. Cornelissen et al., 2003; Garnier & Navas, 2012). More recently, the use of traits in modeling is becoming increasingly popular (Zakharova, Meyer, & Seifan, 2019). Trait-based models hold promise over species-based methods for understanding the mechanisms underlying interactions, decreasing the amount of data required, and applying more generally across systems. This means that the interactions of novel species or the impacts of change can be better predicted (Morales-Castilla et al., 2015).

Traits affect many aspects of an organism's performance (Nock et al., 2016; Zakharova et al., 2019). When it comes to trophic interactions, it is often the "match" between predator and prey traits which is important (Bartomeus et al., 2016; Boukal, 2014; Schleuning, Fründ, & García, 2015), such as the match between prey cuticular toughness and predator biting force in ground beetle communities (Brousseau et al., 2018b). The concept of trait-matching dates back to Darwin's finches (Darwin, 1859), and has been a central component of coevolution studies (Cook & Rasplus, 2003). More recently, food-web ecology has turned to trait-matching as a way to explain food-web structure and dynamics (e.g. Bartomeus et al., 2016; Eklöf et al., 2013; Peralta et al., 2020; Rohr et al., 2016; Rossberg, Brännström, & Dieckmann, 2010). Such matching can be conceptualized as a lock and key, where a predator's foraging traits are the "key" that unlocks the "lock" that is a prey's vulnerability traits (Boukal, 2014). Some keys are applicable to many locks and some locks are easily opened. Others require more specialized keys (e.g. Pouilly et al., 2003).

Body size has been by far the most well-studied trait in the context of trophic interactions, with good reason. An organism's metabolic rate is closely related to its body size (Brown et al., 2004; Gillooly et al., 2001), which affects, among other things, how much it needs to consume. Especially in aquatic systems, many predators are also gape-limited (Brose et al., 2006). The ratio of predator to prey body size determines relative strength, energy gain, and energetic costs from an encounter (Portalier et al., 2019). As a result, the predator-prey body-size ratio is a strong predictor of interaction strength in many ecosystems (e.g. Brose, 2010; Brose et al., 2006; Nakazawa, Ohba, & Ushio, 2013; Riede et al., 2011; Schneider et al., 2012), however the nature of the relationship can vary among systems (Jonsson, 2014). Body size has been used in models predicting food-web structure (e.g. Cohen, 1977; Gravel et al., 2013; Petchey et al., 2008; Williams & Martinez, 2000) and dynamics (e.g. Berlow et al., 2009; Portalier et al., 2019; Schneider et al., 2012).

While body size can be effective in certain contexts, particularly aquatic systems, it cannot tell us everything (Nakazawa, 2017). Other traits are also important, to the point that body size has no predictive effect in some cases (e.g. Eitzinger et al., 2019). There is an increasingly large body of research on the relationship between species' traits and interactions (Brousseau, Gravel, & Handa, 2018a; Gravel et al., 2016; Zakharova et al., 2019), and a number of attempts (of varying success) at using traits to predict food-web structure and dynamics (e.g. Boit et al., 2012; Gravel et al., 2013; Jonsson et al., 2018; Peralta et al., 2020; Pichler et al., 2020; Rossberg et al., 2010; Schneider et al., 2012). Despite the successes and promise that relatively few traits are required to fully characterize a food web (Eklöf et al., 2013), we still lack the ability to predict interactions from traits in most ecosystems. Very few traits have been studied across more than one or a small handful of studies, greatly hindering our ability to make generalizations or uncover mechanisms (Brousseau et al., 2018a; Zakharova et al., 2019). Very few traits other than body size have received much attention, and of the 156 traits reviewed by Brousseau et al. (2018a), only 31 had been studied in at least 5 studies with at least two taxa.

To increase our understanding of the mechanisms underlying trophic interactions and apply trait-based methods to quantify interaction strength, food-web structure and food-web dynamics more widely, we need to be able to understand, compare, and generalize where and how diverse traits affect interactions. I address this issue in **Paper I**. We need empirical experiments and field studies exploring the effect of a variety of traits across multiple taxa - a task which I undertake in **Paper III** and **Paper IV**.

## 2.3 Food webs

Trophic interactions are frequently studied at the level of two species - a single predator species interacting with a single prey species. Rare, however, is the predator-prey pair that occurs in isolation from the wider context of other interactions. The vast majority of species interact with multiple prey, multiple predators, and/or must balance the conflicting roles of being both predator and prey. The network of who-eats-whom within a given community is called a food web. Charles Elton first introduced the concepts of food chains and food cycles (later known as food webs) in 1927 (Elton, 1927). Already here, at their very inception, Elton emphasized the role of body size in food webs, noting that predators tend to be larger than their prey (Elton, 1927). Food webs can be viewed as the flow of mass or material from one trophic level to another, or the flow of energy. The latter began with Lindeman's (1942) "Trophic-dynamic aspect" of ecology. Lindeman conceived food webs in terms of energy or nutrient flow, using the efficiency of energy transfer to calculate how much biomass could be sustained at higher trophic levels. This perspective therefore included abiotic compartments and created a common currency for studying disparate systems. Since Elton and Lindeman, food webs have grown to be a central thematic framework within ecology and have yielded insights into areas as diverse as population dynamics and nutrient cycling (Layman et al., 2015).

The study of food webs allows the elucidation of indirect effects such as trophic cascades (Kitchell & Carpenter, 1993; Pace et al., 1999), where species $x$ consumes species $y$ who consumes species $z$. $x$ can indirectly affect the pop-

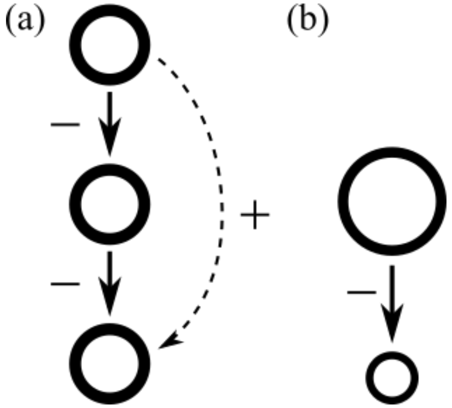


Figure 3: A representation of a trophic cascade. Arrows represent one species' effect on another, where a solid arrow represents a direct effect and a dashed arrow is an indirect effect. The top predator has a direct negative effect on the middle predator, and thereby an indirect positive effect on the basal resource. If the top predator is lost from the system as in (b), the middle predator can increase in biomass, having a negative effect on the basal resource.

ulation dynamics of species $z$ due to its effect on $y$ (Fig. 3). Omnivory, where one species feeds on multiple trophic levels, is also a key feature of food webs and, combined with trophic cascades, can lead to unexpected effects (Gellner & McCann, 2012). A striking example occurred on a small island in New Zealand, where cats were eradicated to increase breeding success of Cook's petrels, a bird that the cat predated on. Cats were the top predator, feeding on Cook's petrel as well as on rats. The rats, however, were also predators on the petrels, and removal of cats led to an increase in their population size and ultimately a *decrease* in petrel breeding success (Rayner et al., 2007). Keystone species are a similar such example, where a predator prevents one species becoming dominant across the community. The classic example is that of starfish maintaining biodiversity in inter-tidal zone habitats by controlling mussel populations that otherwise dominate (Paine, 1969). These indirect and often unexpected effects are crucial in ecological systems, particularly as human actions continue to change ecosystems and climate. For example, the loss of top predators globally, has led to trophic cascades and secondary extinctions as they no longer fill the keystone role (Estes et al., 2011). Studying both the structure and dynamics of food webs is important for understanding their effect on ecosystem functioning and ecosystem services (Dee et al., 2017; Hines et al., 2015), how they vary across space (e.g. Albouy et al., 2019; Poisot, Stouffer, & Gravel, 2015), how they respond to disturbances or change (reviewed by Ives & Carpenter, 2007; Tylianakis et al., 2008), and how we might manage ecological communities (e.g. Tylianakis, Laliberté, Nielsen, & Bascompte, 2010).

While there are diverse, valuable questions that are best addressed with food webs, food webs are not easily compiled. Determining who eats whom - the structure of the food web - requires large quantities of time, person-hours and money to observe, collect, dissect, or genetically determine each interaction (Roslin & Majaneva, 2016). As the number of species grows, the number of potential interactions grows as its square (Fig. 1). If one wishes to also study the dynamics of the food web, this requires determining the effect each species has on each of its interaction partners (J. T. Wootton & Emmerson, 2005). This task requires, at least, quantitative interaction data, but ideally manipulative experiments, and is further hampered by the fact that interaction strengths are often non-linear (Novak & Wootton, 2008). Assembling food webs is understandably the bottle neck in studying them.

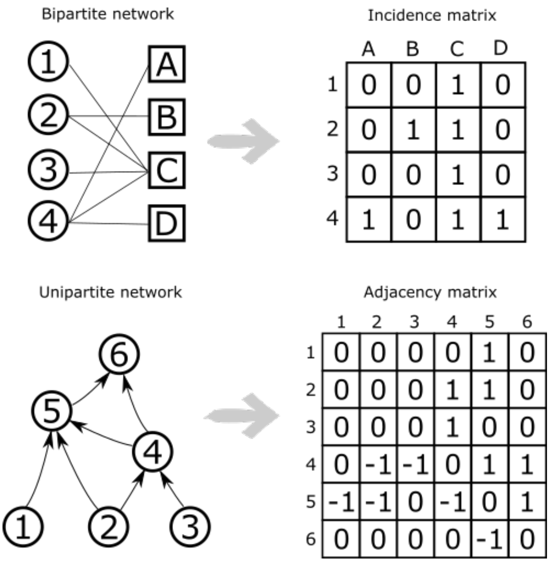
Additionally, once a food web is assembled, it is almost invariably either an aggregate over, or snapshot in, time and space (but see e.g. Knop et al., 2017; Woodward et al., 2010). Such aggregate networks gloss over important spatial and temporal variation, and may have limited ability to predict, for example, where an invasive species may fit into a network (Pearse & Altermatt, 2013). Food webs assembled based on species' traits offer the possibility to overcome such obstacles. Ideally the (few) relevant traits would be collected more easily than collecting all interactions (Lavorel et al., 2007; Zakharova et al., 2019); differences in food-web structure and dynamics across time and space could therefore be more easily explored, novel species could be placed based on their traits, novel food webs could be characterized based on relevant traits understood from previous communities, and effects of disturbances could be more easily predicted (Bartomeus et al., 2016; Morales-Castilla et al., 2015). While the potential benefit is considerable and the research in this area is continually building, there is still a great deal to be understood before the benefits can be realized.

## 2.4 Food-web structure

A food web's structure describes the network of interactions between species (Fig. 4). It can be visualized as a network (where arrows indicate interactions between species, shown as nodes) or as a matrix (Fig. 4) (Delmas et al., 2019). Food webs, where any species can (at least theoretically) interact with any other species, are described as 'unipartite'. Host-parasitoid, plant-pollinator, and plant-herbivore networks, in contrast, consist of two distinct groups of species that only interact with species in the other group, i.e. pollinators only interact with plants, not with other pollinators. Such networks have a ‘bipartite’ structure (Fig. 4).

A number of metrics have been developed to describe network structure. Early descriptions of food-web structure included trophic levels (the number of "levels" through which energy or matter passes before reaching a particular species) and the existence of both *generalists* (who consume many species) and *specialists* (who consume few) (Levine, 1980). At a more general level, a species’ *degree* is the number of species with whom it interacts (Cirtwill et al., 2018; Jordán, Benedek, & Podani, 2007). At an entire food-web level, *size* (the number of species), *connectance* (proportion of potential interactions that are realized), *modularity* (presence of sub groups within which species interact more frequently than with out), *nestedness* (species interact progressively with a subset of previous species interaction partners) and *degree distribution* (distribution of species’ degrees) are all metrics frequently calculated for food webs and related to their stability and function (Delmas et al., 2019). For example, more stable unipartite food webs often have a modular structure, which limits disturbances to one module rather than affecting the whole network (Stouffer & Bascompte, 2011; Thébault & Fontaine, 2010). More stable bipartite networks (e.g. pollination networks), on the other hand, tend to be more nested (Thébault & Fontaine, 2010). A nested structure means that loss of specialist species, which are often most vulnerable to extinction, does not result in extinction of their interaction partners, because their partners are generalists and still have other interaction partners (Baumgartner, 2020; Tylianakis et al., 2010). Food webs show a variety of different degree distributions, but generally show a distribution where most species have very few interactions and a few have many (Dunne, Williams, & Martinez, 2002; Montoya & Solé, 2003). This pattern, combined with a similar distribution in interaction strengths, where there are few strong interactions and many weak, is important for food-web stability (McCann, Hastings, & Huxel, 1998; K. L. Wootton & Stouffer, 2016a). In addition to the distribution of degree, the distribution of traits can affect the structure of the food web as a whole (Gravel et al., 2016; Laigle et al., 2018). This can be quantified as functional composition (Gravel et al., 2016). For example, the number of links, vulnerability (number of links to predators) generality (number of links to prey) and omnivory (feeding at more than one trophic level) all increase with the number of species using poison or webs to hunt (Laigle et al., 2018). This is because these traits allow predators to target a wider range of species.

A number of models have been developed to predict or simulate food-web structure based on traits. The majority of these models depend on the theory



Incidence matrix

| | A | B | C | D |
|---|---|---|---|---|
| 1 | 0 | 0 | 1 | 0 |
| 2 | 0 | 1 | 1 | 0 |
| 3 | 0 | 0 | 1 | 0 |
| 4 | 1 | 0 | 1 | 1 |

Adjacency matrix

| | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| 2 | 0 | 0 | 0 | 1 | 1 | 0 |
| 3 | 0 | 0 | 0 | 1 | 0 | 0 |
| 4 | 0 | -1 | -1 | 0 | 1 | 1 |
| 5 | -1 | -1 | 0 | -1 | 0 | 1 |
| 6 | 0 | 0 | 0 | 0 | -1 | 0 |

Figure 4: A simple representation of a bipartite versus unipartite network and how these correspond to an incidence matrix (for a bipartite network) or an adjacency matrix (for a unipartite network). In the incidence matrix, a “1” indicates an interaction between two species while a 0 indicates no interaction. In the adjacency matrix, a “1” indicates that the species in the row consumes the species in the column. A “-1” indicates that the species in the row is consumed by the species in the column, and a “0” indicates no interaction.

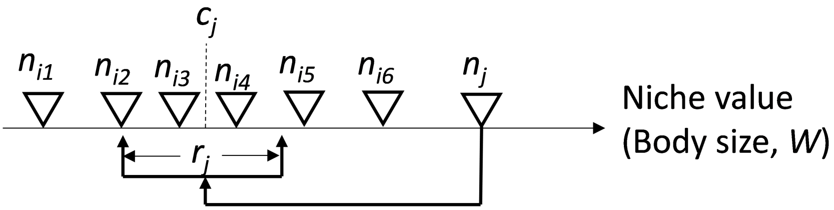


Figure 5: A representation of the niche model. Species (inverse triangles) are arranged along a niche axis (frequently body size, as in the example here) according to their niche value $n_j$. Species are able to consume other species that fall within their feeding range. The feeding range is defined by a center $c_j$ and a range $r_j$.

of trait-matching, where the match between consumer and resource traits define the limits of a possible interaction (Bartomeus et al., 2016; Boukal, 2014; Brousseau et al., 2018a; Rohr et al., 2016). The Cascade Model (Cohen, 1977) was an early model structuring food webs along a single axis, usually body mass. Predators fed on species below themselves on the axis. The Niche Model (Williams & Martinez, 2000) was an improvement on the Cascade model, recognizing that species fed not on *all* species below themselves in the continuum, but only those within a certain range, the center of which describes the "niche" of the predator (Fig. 5). Specifically, it is the *ratio* between predator and prey body mass which is important (Neubert et al., 2000). Gravel et al. (2013) illustrate a method to apply the niche model to real food webs, where species-specific parameters are determined by statistical analysis of the predator-prey body-mass ratio and allometric scaling of model parameters. They apply it to predict interactions among a meta web of Mediterranean fishes. A number of other models, including the nested hierarchy model (Cattin et al., 2004), Minimum potential model (Allesina, Alonso, & Pascual, 2008) and the Probabilistic niche model (Williams, Anandanadesan, & Purves, 2010), are all derived from the Niche Model (Stouffer et al., 2005). The allometric diet breadth model (ADBM) uses different assumptions to the niche model - using optimal foraging theory and allometric scaling as a basis - but generates comparable predictions (Petchey et al., 2008).

Extending the theory of trait-matching is the realization that some species are more likely to form interactions than others, thereby increasing their *centrality* in the network, for reasons also attributable to traits (Rohr et al., 2016). In the matching-centrality framework, species have traits that fall along a "matching" dimension and a "centrality" dimension (Rohr et al., 2016). The matching dimension describes *whom* a species will interact with (i.e. a match between predator and prey traits) while the centrality dimension describes how *many* species they interact with, i.e. a species with high centrality will have a higher degree than a species with low centrality. Two consumer species with the same matching traits will interact with the same resource species in the center of their matching range. If, however, the two consumer species have different centrality, the consumer with the larger centrality will interact with a wider range of resources around the optimal match. If the matching dimension is dominant, the network is more modular (where groups of species interact with each other), while if the centrality dimension is dominant, the network will be more nested. This method uses *latent* traits to describe where species fit along each dimension (Rohr et al., 2010). Latent traits are not real, but instead arrange species along an axis that explains as much structure in the data as possible (Rohr et al., 2010). In this way, it is possible to explore the potential importance of traits in structuring a food web even if the real traits driving that relationship are unknown or unmeasurable. It is then possible to compare latent traits to real traits (Rohr et al., 2016). Latent traits can also be used to calculate a food web's *dimensionality* or the number of trait dimensions needed to fully explain interactions within a food web (Eklöf et al., 2013). Again, it is possible to calculate dimensionality using real traits, but almost invariably more real than latent traits are required to describe the web (Eklöf et al., 2013), indicating we have either (i) measured the wrong traits, (ii) multiple traits are important for a dimension, or (iii) there may be unrecorded interactions within the network.

Encouragingly, while there are many models and methods for describing food-web structure from traits, it seems that we actually require relatively few traits as such to describe a food web. Eklöf et al. (2013) found that the structure of food webs can be explained with less than five 'dimensions', implying that a similar number of traits could, in theory, explain network structure. We are, however, still a long way from successfully predicting food-web structure from traits. We require more research comparing multiple traits across multiple species with multiple methods to disentangle the different elements of structure that different traits and methods can illuminate. I approach this in **Paper IV**.

## 2.5 Food-web dynamics

Food-web dynamics refer not only to who interacts with whom, but also how strong those interactions are and what the consequences of that are for the food web as a whole (Polis & Strong, 1996). The pair-wise dynamic models introduced in section 2.1 form the core of food-web dynamic models, but by modeling multiple species together we can explore, for example, indirect effects and the importance of diverse interaction strengths (e.g. Montoya et al., 2009; Otto, Rall, & Brose, 2007; K. L. Wootton & Stouffer, 2016a). The strength and distribution of interactions can have critical effects on the stability of a community (Berlow, 1999; McCann et al., 1998). Changes in the strength of even a single interaction can have far-reaching effects and one species can have severe impacts on species with whom it does not even interact (Watson & Estes, 2011; K. L. Wootton & Stouffer, 2016b).

Just as there are models predicting interaction structure from traits, so too are there models predicting interaction dynamics. Yodzis and Innes (1992) began by using body size and metabolic category to parameterize consumer-resource models. Currently, one of the most effective models using traits to predict food-web dynamics is the allometric trophic network (ATN) model (Berlow et al., 2009; Otto et al., 2007; Schneider et al., 2012). As an animal's metabolism is dependent on its body size, larger animals have a proportionally lower metabolic rate than smaller animals (Brown et al., 2004; Gillooly et al., 2001). This relationship is described as 'allometric scaling' and underlies, among other things, how much an individual needs to eat, their mobility, and their strength. The ATN model uses allometric scaling of attack rate and handling time to parameterize food-web models using predator and prey body masses (Berlow et al., 2009; Otto et al., 2007; Schneider et al., 2012). It has successfully explained a large portion of food-web dynamics in a number of cases (e.g. Curtsdotter et al., 2019; Jonsson et al., 2018; Schneider et al., 2012). The ATN model forms the basis of **Paper I**, **Paper III**, and **Paper V**.

It is also possible to calculate energy gain for a predator consuming prey based on mechanics. Portalier et al. (2019) develop a Newtonian, mechanical model to calculate the net energy gain to a predator on consumption of a prey item based on the mechanical costs associated with searching, capturing, and handling. At present, this model is restricted to pelagic or flying predator species and their prey, but its accuracy in predicting interactions is overall higher than the allometric niche model (Gravel et al., 2013) and by relying on the first principles of physics it can be applied across species when only the body mass of predator and prey are known. By extension, the model demonstrates energetic limits, where the energy gained from consuming the prey item is insufficient compared with the cost of search, capture, and/or handling, as well as mechanical limits, where the predator has insufficient muscular power to capture prey or to lift the prey during handling.

Unfortunately, as with structure, body size cannot always describe all dynamics and as trophic complexity (i.e. the number of species and interactions in the network) increases, predictive power decreases (Curtsdotter et al., 2019; Jonsson et al., 2018). Both Jonsson et al. (2018) and Schneider et al. (2012) hypothesize that the areas where the ATN model did not describe dynamics so well in their respective studies may be due to differences in habitat use between species. This I test explicitly in cage experiments in **Paper III**, in addition to the effects of increased trophic complexity and whether it can be explained by non-trophic predator-predator effects.

The ultimate goal of trait-based modeling of food webs, and especially of food-web dynamics, will be to understand the mechanisms underlying food-web dynamics and to make accurate predictions of the effects of change or management on ecological communities (Bartomeus et al., 2016; Morales-Castilla et al., 2015). We still have a long way to go to reach that goal, despite the rapidly increasing interest and research in this area (Zakharova et al., 2019). To ensure that we can synthesize and build from this research in an effective and efficient manner, we require a way to conceptualize and compare diverse traits across diverse ecosystems and diverse trophic interaction types. In **Paper I**, I develop a candidate framework to do this. I apply the framework in **Paper II** and **Paper III**, incorporating the trait of overlap in habitat use, in addition to non-trophic predator-predator effects, into a dynamic model and parameterize it using time-series prey abundances from mesocosm experiments. Once we have such models we can begin running simulations across diverse scenarios to explore the effect on food web dynamics. In **Paper V**, I explore one such scenario using computer simulations. There, I look at the impacts of food webs coupled by the movement of foraging consumers.

## 2.6 Food webs in space

Although we tend to conceptualize food webs in isolation, in reality they exchange material and/or individuals with other systems (Polis et al., 1997). Such exchanges can take the form of subsidies from one ecosystem to another, supporting species or trophic levels in the recipient system that could not otherwise exist (Nakano & Murakami, 2001; Sabo & Power, 2002). Individuals can disperse (i.e. move away from their birth place) from one system to another, giving rise to the field of metacommunity ecology (Holyoak, Leibold, & Holt, 2005; Leibold et al., 2004). Such flows of individuals or nutrients can fundamentally alter food-web stability and function. For example, dispersal among multiple ‘patches’ can increase overall stability; if one or multiple species are lost from one patch they can be recolonized from another patch (Loreau, Mouquet, & Gonzalez, 2003; Polis et al., 1997). Meta*ecosystem* ecology additionally integrates the flow of resources between ecosystems (Gounand et al., 2017, 2018; Loreau, Mouquet, & Holt, 2003; McCann et al., 2020). This allows the integration of landscape ecology, effects of productivity, and understanding of source-sink dynamics.

In addition to exchanges between clearly distinct or separated ecosystems, the question of scale is important. Large, mobile consumers cover a wider area than smaller species and couple habitats by foraging in both (Polis et al., 1997; Rooney & McCann, 2012). Such coupling can be essential for stabilizing the dynamics of the linked systems by relieving pressure on one ecosystem if resources are scarce and focusing instead on the other ecosystem (McCann & Rooney, 2009; Rooney & McCann, 2012; Warfe et al., 2013). This is one reason why the loss of top predators can have such catastrophic and wide reaching effects (Estes et al., 2011). I explore the importance of habitat use for food-web dynamics on a micro scale in **Paper III**, looking at the importance of differences in microhabitat use for predator-prey interactions and food-web dynamics. In **Paper V**, I look at a much larger scale, using computer simulations to explore how the foraging movement of consumer species between adjacent but dissimilar habitats affects ecosystem functions in terms of both stocks (i.e. levels of biomass and nutrients) and fluxes (i.e. movement between the stocks) in each habitat.

# 3 Objectives

The main aim of my thesis was increasing understanding of food-web structure and dynamics. I took a trait-based approach in **Paper I**-**Paper IV**, and in **Paper V** explore the effects of adjacent food webs on each other. To this aim, I first developed a general framework for understanding which traits are most important in a given food web and using these traits to parameterize dynamic food-web models. Second, I applied the framework by developing a dynamic model parameterized by specific traits and fitting it to experimental data. Third, I explored which traits were most important for both structuring food webs and driving their dynamics, and whether this varied across different systems. Finally, I applied such dynamic models to *in silico* experiments to explore the impact of consumer foraging movement between adjacent food webs on ecosystem function.

## Specifically, my research questions were:

1. How can we develop a general framework for selecting whichever traits are most important for a given community and using them to parameterize a dynamic food-web model? (**Paper I**)

2. Can we apply a dynamic model parameterized by traits to experimental data? (**Paper I**, **Paper II**, **Paper III**)

3. What can species traits tell us about food-web structure? (**Paper IV**)

4. Which species traits have the biggest influence on interactions, food-web structure and food-web dynamics? (**Paper I**, **Paper II**, **Paper III**, and **Paper IV**)

5. How do food webs coupled in space affect each other? (**Paper V**)

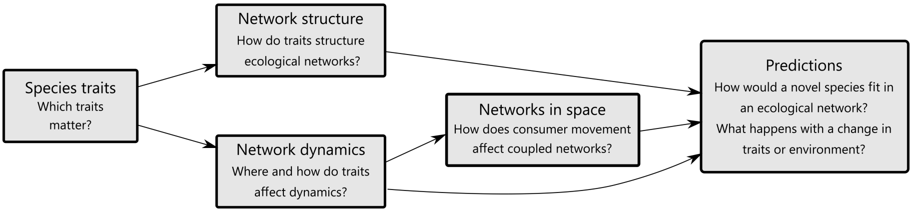


Figure 6: The different elements approached in my thesis and how they relate to one another. Arrows indicate how the lessons or results from one element can influence or inform our understanding and ability to ask the questions of another element.

I approached these questions from multiple perspectives by using conceptual, statistical, empirical, experimental, and computational approaches in the following projects.

## Project 1: Predicting trophic interactions using species' traits: a conceptual framework

Here, I developed a framework to allow the effective parameterization of a dynamic food-web model using species traits. This framework is applicable to trophic interactions of all types and in all ecosystems (**Paper I**). I briefly reviewed the development of trait-based models, and then outlined how a trophic interaction can be broken into eight component steps. Deriving the overall approach from first principles, I described how the eight steps make up the functional and numerical response terms of a dynamic food-web model, and how these may be parameterized using species traits. In this project, I addressed the questions of how species' traits have been used to predict food-web structure and dynamics in the literature and how we can develop a general framework to accommodate the parameterization of a dynamic food-web model by whichever traits are most important for a given food web.

## Project 2: Adding microhabitat use and non-consumptive predator effects to a dynamic food-web model and fitting to mesocosm data.

Here, I used a small food web consisting of two aphid species and their arthropod predators to investigate the importance of overlap in microhabitat use and non-consumptive predator-predator effects on food-web dynamics. I used body size and microhabitat use to parameterize a dynamic food-web model and fitted it to the data using the inverse method.

In **Paper II**, I first described the development of the model and a series of pre-experimental simulations. Here I addressed the question of how we incorporate overlap in microhabitat use and non-consumptive predator-predator effects into a dynamic food-web model. Once the model was developed, I and my collaborators used pre-experimental simulations to determine the optimal design of an experiment testing the model.

In **Paper III** I carried out the experiment designed in **Paper II** and fitted the data to the model. I addressed the questions of whether the strength of a trophic interaction depends on the amount of time predators and prey spend in the same habitat and whether food-web dynamics are influenced by non-consumptive effects of predators on each other.

## Project 3: The importance of traits for network structure in a tritrophic *Salix*-galler-parasitoid network

This project used a tritrophic *Salix*-galler-parasitoid network to compare the importance of species' traits for food-web structure (**Paper IV**). I collected a range of traits that I predicted were important for trophic interactions, including body size, phenology, gall-wall thickness, glycoside levels and ovipositor length. I used a set of five different statistical approaches to analyse the data. By comparing the results from the different methods, I could obtain a deeper ecological understanding than each method could provide alone. Together I used these methods to ask whether similar species were more likely to share interactions; whether current food-web theory, including trait-matching, was appropriate to represent the structure of this network; how well the measured traits or phylogeny explained trait-matching; whether the relationship was linear or complex; and which approaches are most appropriate for predicting missing interactions.

## Project 4: Food webs coupled in space: The effect of consumer foraging movement on habitats differing in fertility and plant diversity

Here, I scaled up from the effects of microhabitat (**Paper III**) to look at the effect of consumer foraging movement between neighbouring habitats. Using a hybrid food-web nutrient-cycling dynamic model, I simulated food webs in habitats varying in fertility and plant diversity, coupled by the foraging movement of consumers between habitats (**Paper V**). I first explored the effect of plant diversity and fertility on isolated food webs in terms of ecosystem function, i.e. stocks of biomass and nutrients in different components of the ecosystem and the fluxes between them. I then allowed some consumers to feed in both habitats and investigated how low versus high consumer foraging movement impacted the same ecosystem functions. I answered the questions of how fertility and plant diversity affected ecosystem function in isolated ecosystems and how this was modulated by the foraging movement of consumers between habitats.

# 4 Material and Methods

My aim was to increase understanding of food-web structure and dynamics, largely from a trait-based perspective. The difficulty with this is that different traits are important in different systems and affect interactions in different ways. To progress, therefore, requires a way to move beyond the particulars of specific traits and to instead move toward understanding the mechanisms of when and how traits affect interactions, thereby allowing comparison of how different traits act in similar or different ways in different communities or interaction types.

## 4.1 Developing a general framework

In **Paper I**, I developed the theory of trait-based trophic interactions by developing a general framework to facilitate comparison and generalization among communities. To build the framework, I first reviewed the literature to determine which traits have been studied before and how they affect trophic interactions. I then broke the interaction down into eight steps that underlie any trophic interaction; (1) encounter, (2) detection, (3) decision, (4) pursuit, (5) subjugation, (6) ingestion, (7) digestion and assimilation, and (8) allocation of resources (Fig. 7). Using these steps facilitates the effective use of traits to parameterize dynamic food-web models. I described the process of using these steps to select traits and decide the model structure, illustrated by an example using an insect community and the traits body size and temperature optima.

Dynamic food-web models, developed from the Lotka-Volterra (LV) framework (Lotka, 1925; Volterra, 1926) (see section 2.1), form a core part of this thesis. These models describe population dynamics in terms of increases due to growth or consumption and losses due to predation or mortality. I use the simple LV model as the backbone of the framework in **Paper I** and expand it to include terms for the eight steps of a trophic interaction (Fig. 11). It is not expected that all terms be used to build the model; rather that the few steps most important for the given community are included while the others are omitted. To build the mathematical framework, we re-derived functional and numerical response terms from first principles and explicitly examined the assumptions behind the parameterization of previous, similar models. Through decisions of which steps are or are not important for the system and how they are influenced by traits, one can build up a dynamic food-web model of appropriate complexity for the system of interest and state of knowledge about it.

## 4.2 Food-web dynamics

In **Paper II** and **Paper III**, I applied the framework developed in **Paper I**. I began by modifying the allometric trophic network (ATN) model (see section 2.5). The ATN model uses body size to parameterize trophic interactions and I modified it to also use microhabitat use. I hypothesized that predators and prey which spend more time in the same microhabitat should encounter (step 1 of the framework in **Paper I**) each other more frequently (Barrios-O'Neill, Kelly, & Emmerson, 2019), thereby leading to a stronger interaction. I developed a metric for overlap in microhabitat use that takes into account the proportion of time each species spends in each microhabitat and the area of the microhabitat to determine the likelihood of encounter between different species. Increasing the number of species present in the network has been shown to decrease the fit of the ATN model (Jonsson et al., 2018). This is likely due to non-consumptive effects of predators on each other, such as interference or a change in behaviour due to fear of predation. Such non-consumptive effects are not captured by the ATN model. To address this, I also added a term for non-consumptive predator-predator effects to my model. If a predator individual spends more time avoiding or interfering with other predators, it will have less time available for foraging, thereby decreasing trophic interaction strength with their prey.

To test the modified model, I ran mesocosm experiments using small food-web modules of aphid prey and different predator species (Fig. 8). Using different combinations of predator and prey species, I collected time-series data of the aphid populations over eight days and then used the inverse method to determine the parameter values that give the closest fit to the data (see **Paper**

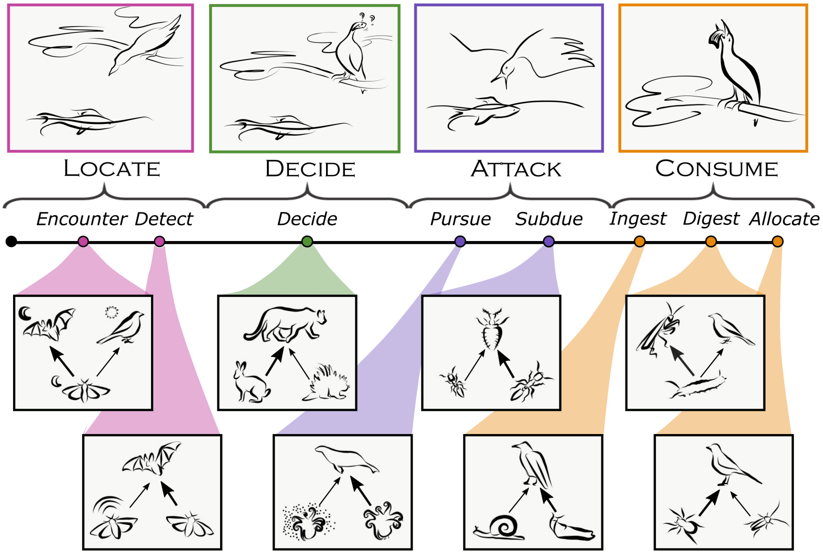


Figure 7: An overview of the steps making up a trophic interaction and of the four broader stages the steps can be grouped under. How traits may increase or decrease the probability of each of the eight steps occurring is illustrated by the examples in the lower boxes, comparing in each case an interaction with a higher probability of that step occurring (thicker arrow) versus lower probability (thinner arrow). *Encounter*: Moths are active at night, avoiding temporal overlap and therefore encounter with birds, but retaining it with nocturnal bats. *Detect*: Bats have developed sonar to help locate their prey in the dark, but some moths have developed methods of jamming sonar, essentially becoming invisible to the bat (Corcoran & Conner, 2012). *Decide*: Porcupines have spines that dissuade potential predators from attacking them, relative to unprotected prey such as hares (Mori et al., 2014). *Pursue*: Octopi release ink to distract and confuse their predators, making pursuit more difficult. *Subdue*: Ant lions have pits to capture their ant prey, enabling them to catch larger individuals than they otherwise would (Kuszewska et al., 2016). *Ingest*: The shell of a snail makes them more difficult to ingest than unprotected slugs. *Digest*: Monarch caterpillars are toxic, preventing most predators from successfully attacking them. Chinese praying mantises, however, remove the gut of the caterpillar and discard the toxic plant compounds, enabling them to digest and assimilate the otherwise toxic prey (Rafter et al., 2013). *Allocate*: By consuming prey of higher nutritional content, including protein, fat, and also micronutrients (e.g., spiders and Coleoptera rather than Blattodea), insectivorous birds allocate more nutrients to growth and reproduction per unit of consumed prey (Razeng & Watson, 2015). Figure reproduced from **Paper I**.

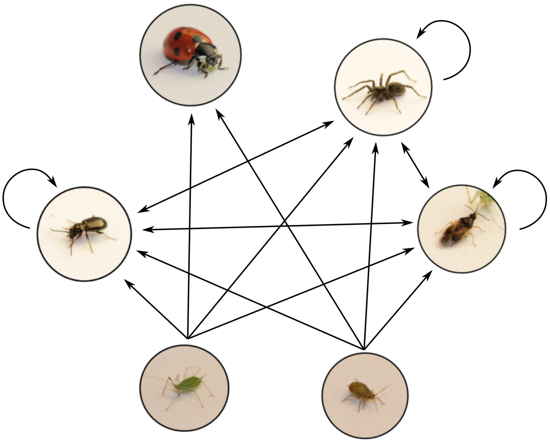


Figure 8: The food web used for the cage experiments in **Paper III**. Species are, from top left: lady beetle (*Coccinella septempunctata*); wolf spiders (*Pardosa* spp.); minute pirate bug (*Orius majusculus*); bird cherry-oat aphid (*Rhopalosiphum padi*); pea aphid (*Acyrthosiphon pisum*); and ground beetle (*Bembidion spp*). Arrows indicate potential feeding interactions which we then parameterized in **Paper III**. Arrows point from prey to predator, double headed arrows indicate that species could potentially eat each other and arrows beginning and ending with the same species indicate cannibalism. With the exception of *C. septempunctata*, we allowed all potential feeding interactions between predators. We modeled the dynamics of *C. septempunctata* slightly differently to the other predators for reasons outlined in **Paper III** and so omitted their interactions with other predators. Figure reproduced from **Paper III**.

**II** and **Paper III** for further details). Collecting enough time-series data is a time-consuming and expensive process. To ensure I had an optimal experimental design, I collaborated with applied mathematicians to run pre-experimental simulations (**Paper II**). Using data from a previous, similar experiment as a baseline, these pre-experimental simulations enabled us to determine optimal sampling time points and minimal sufficient sub-sampling.

To determine how important microhabitat use and non-consumptive predator-predator effects were to the model, I compared four different models: (i) a full model with both microhabitat use and non-consumptive predator-predator effects, (ii) a model with microhabitat use but without non-consumptive predator-predator effects, (iii) a model with non-consumptive predator-predator effects but without microhabitat use, and (iv) a model with neither term. The models were parameterized to fit the same data, but I also wanted to establish how they compared when predicting outside the data range. I therefore used each model to predict the population dynamics of a hypothetical prey species with a different body size and microhabitat use than either of the prey species in the experiment.

## 4.3 Food-web structure

In addition to food-web dynamics, I was also interested in what species traits can tell us about food-web structure. This I investigated in a *Salix*-galler-parasitoid tri-trophic network (**Paper IV**). This is a particularly interesting data set as it contains both plant-herbivore and host-parasitoid elements of the network, so I could compare how traits affected the structure of different network types. The interaction network came from Kopelke et al. (2017), which already contained some trait information, primarily about the parasitoids. I collected further trait data from the field as well as from the literature and from discussions with experts in the field.

I used a range of statistical inference methods to analyse the trait and interaction data in **Paper IV**, each method telling a different part of the story in terms of how traits structure interactions (Fig. 9). Each method described the relationship between species traits and network structure in a different way which, by comparison with the other methods, could answer a different question about how traits were related to food-web structure (visualized in subfigures i-v in Fig. 9, for further details refer to **Paper IV**). Based on this relationship, each method produced a matrix of interaction probabilities for each species pair (subfigures vi-x in Fig. 9), which I compared to the matrix of observed interactions to determine each method's performance. Some methods used species' traits to generate these interaction probability matrices, and others simply used the structure of the observed network. By comparing methods which used traits to those that did not, I could determine how much of the inherent network structure could be explained by traits and which theories of how traits structure interactions were most effective.

To compare the importance of different traits for structuring networks, I reran the statistical methods with subsets of only four traits at a time. Traits regularly occurring in subsets with higher performance were more important in structuring the network. This allowed me to see which traits gave the best model fits and whether this varied from model to model. Finally, I used the matrix of interaction probabilities produced by each method (subfigures vi-x in Fig. 9) to sample 100 networks for each method (subfigures xi-xv in Fig. 9). This would be analogous to sampling 100 new locations, where the com-

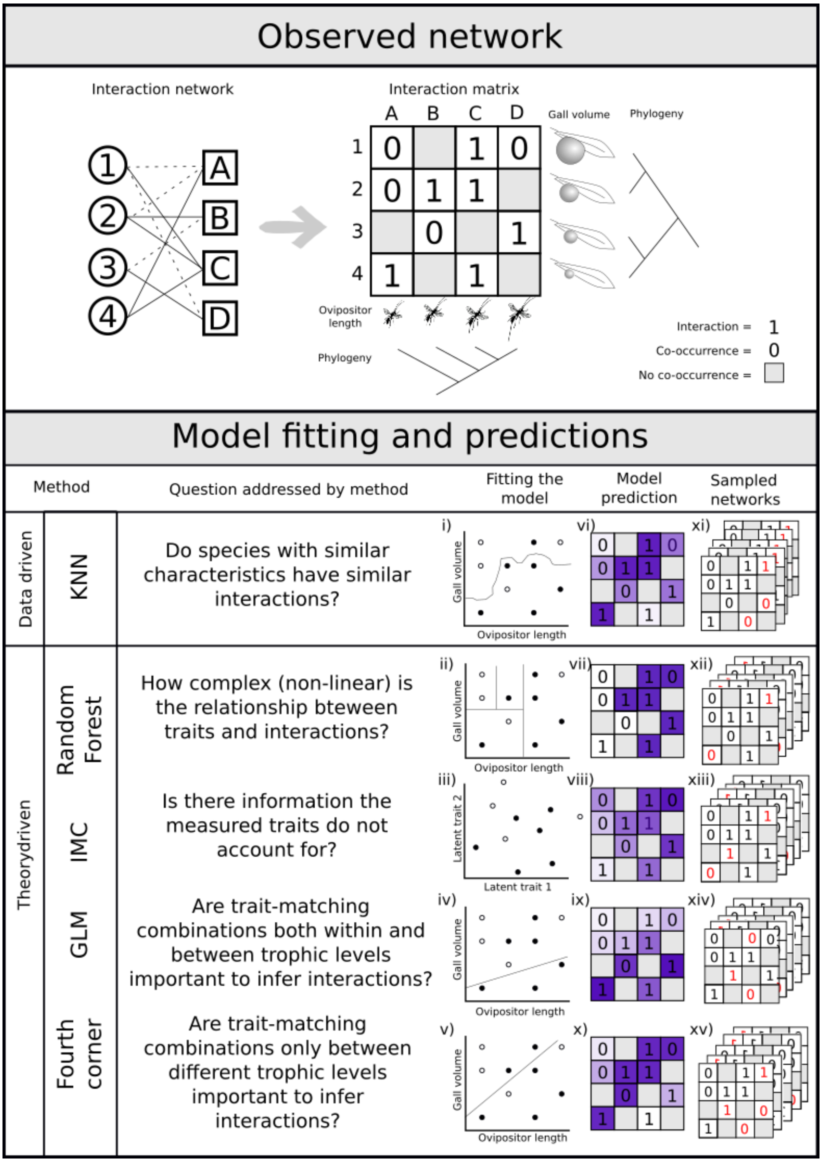


Figure 9: An overview of the type of network, trait, and phylogeny data used in **Paper IV** (‘Observed network’) and the different statistical methods used to analyze the data (‘Model fitting and predictions’). Each method addressed a different question due to the different ways in which the model assigned a relationship between traits and structure (subfigures i-v). Each method therefore produced different predictions (subfigures vi-x) which I could then use to sample new networks (subfigures xi-xv). For further details, please refer to **Paper IV**, where this figure is reproduced from.

munity was known, but not the interaction network underlying it. By looking at the distribution of structural metrics, such as connectance and modularity, produced by the sampled networks and comparing them to the observed network, I could see which approaches were most accurate in terms of different aspects of network structure.

## 4.4 Coupled food webs

My final project extended the importance of habitat use from the microscale explored in **Paper III**, to the wider scale of mobile consumers coupling neighbouring habitats by feeding in both (**Paper V**). This project answered the research question of how coupled food webs affect each other. Here again I utilized dynamic models - specifically the ATN model combined with a dynamic nutrient-plant model (Thébault & Loreau, 2005) - to run computer simulations (Fig. 10). I simulated food webs in two separate habitats that differed in fertility level (i.e. nutrient availability) and plant diversity. I then allowed a proportion of herbivores and predators to forage in both habitats based on where their prey was (Fig. 10). This simulation allowed me to explore how foraging movement between habitats differing in fertility and diversity affected each habitat, in terms of both stocks (e.g. the amount of biomass or detritus) and fluxes (the amount of energy or material moving from one stock to another).

The advantages of using computer simulations include that I can strictly control all parameters, look at far more scenarios that I could empirically, and replicate extensively, as well as extrapolate to long-term dynamics. The disadvantage is that the outcome depends on the parameter values and set up. If these conditions then the output will be wrong too. While all models will be wrong to some extent - if only because the model is necessarily simplified relative to the real world - I tried to get this one as right as possible. I did so by using realistic models, exploring where all our parameter values came from and aiming for as much realism as possible, and introducing some stochasticity into most parameter values across replicates. This way, I tried to avoid cases where the results were due to a particular strange parameter value.

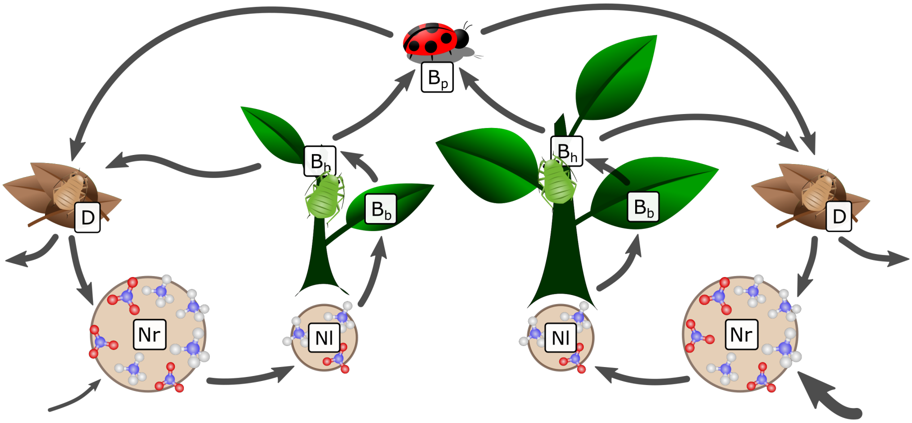


Figure 10: A visual overview of the model behind the computer simulations in **Paper V** showing the flow of nitrogen or biomass among the different components of the network. There were multiple plant, herbivore and predator species in each habitat which are not shown here. Figure reproduced from **Paper V**.

# 5 Results and Discussion

In this thesis, I first demonstrated how we may develop a general framework for selecting whichever traits are most important for a given community and use them to parameterize a dynamic food-web model. I did so by breaking the trophic interaction into eight steps. I then formulated a dynamic model where traits can be used to parameterize the relevant steps (**Paper I**).

I showed that we can apply a dynamic model parameterized by species traits to experimental data (**Paper II** and **Paper III**), but I also showed that alternative models using different terms (i.e. traits) all fit the data equally well. This meant I could not discern which traits were most important for food-web dynamics. The different models all fit the data equally well, but did so by having different values for key parameters. This lead to vastly different predictions when applied outside the data range and demonstrated the need for additional, more focused experiments to narrow down the reasonable range of parameter values in order to differentiate among models.

In terms of the effects of traits on network structure, I found that by using a suite of complementary statistical approaches, traits could explain a substantial portion of network structure. However, the traits and their predictive power can differ substantially between different network types, even within the same ecosystem (**Paper IV**).

I found that the specific traits affecting ecosystem dynamics and structure depended on the system and interaction type. For example, in **Paper IV**, I found that gall type was the most important trait structuring both plant-herbivore and host-parasitoid networks, but explained more of network structure in the host-parasitoid than plant-herbivore part of the network. A coarser grouping of gall types, based on how easy they are to access, was important for the host-parasitoid part of the network but not the plant-herbivore part. In **Paper III**, I developed a metric for calculating habitat overlap, but my results were inconclusive for how important this trait was for food-web dynamics.

With respect to the effect of food webs on each other, I found that coupled food webs can affect each other substantially due to the foraging movement of consumers (**Paper V**). This affected both the fluxes and stocks, and effects were strongest in low fertility habitats coupled with high fertility habitats.

Below, I investigate each finding in more detail.

## 5.1 How can we develop a general framework to select whichever traits are most important for a given community and use them to parameterize a dynamic food-web model?

Incorporating traits into dynamic models will help elucidate mechanisms underlying trophic interactions (e.g. Portalier et al., 2019) and facilitate predictions of how networks will respond to anthropogenic as well as natural stressors or disturbances, and mapping of novel networks (Bartomeus et al., 2016; Morales-Castilla et al., 2015; Pearse & Altermatt, 2013). In **Paper I**, I demonstrate a framework for determining how to incorporate traits into dynamic models of all interaction types. I do so by breaking an interaction into eight distinct steps. The particular steps which are most important for an interaction will depend on the system of interest, and this can be used to guide the selection of traits and their incorporation into dynamic models.

The steps comprising a trophic interaction are (1) encounter, (2) detection, (3) decision, (4) pursuit, (5) subjugation, (6) ingestion, (7) digestion, and (8) allocation of resources. These steps underlie trophic interactions of all types, but certain steps are more important for some interactions than others (Fig. 7). For example, step 4, pursuit, is generally not an important step for herbivores, as plants rarely flee. In contrast, steps 6, ingestion and 7, digestion, can be very important steps for herbivory; plants display a wide range of traits to make ingestion or digestion difficult (Agrawal & Fishbein, 2006) and herbivores show as many traits to overcome those defenses (Karban & Agrawal, 2002). The reason herbivorous interactions frequently center on steps 7 and 8 is because plants generally cannot flee or hide, but are also generally not killed outright as a result of herbivory. In predator-prey interactions, in contrast, traits relevant to predation generally focus on steps earlier in the interaction. Giving a predator indigestion is scant consolation to a prey individual that has lost its life to the predator. There are, of course, exceptions to this rule, such as the

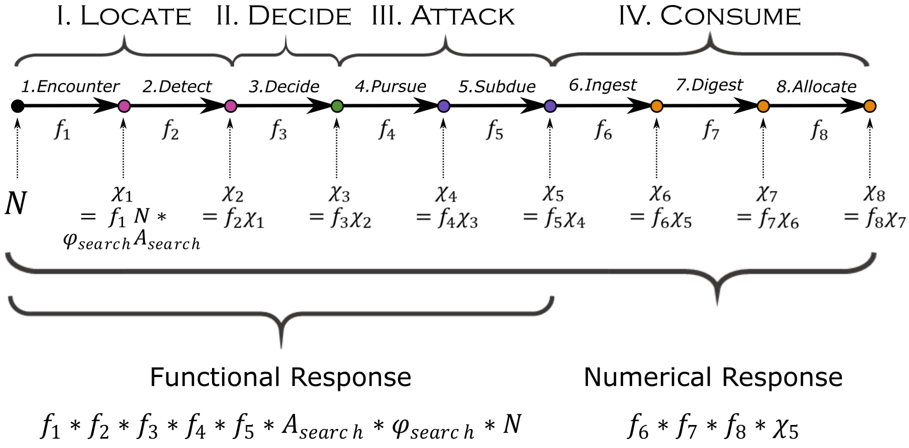


Figure 11: An outline of the steps making up a trophic interaction and how terms for each step combine into the functional and numerical response. Each $f_x$ term describes the conditional probability that step $x$ occurs successfully (from the consumers' perspective). Each $f_x$ term can be parameterized by traits and will take a different formulation depending on the relationship of that step to traits. $\chi_x$ therefore represents the portion of the prey population $N$ that is encountered, detected, etc., and depends on the proportion of the predator's time spent searching, $\varphi_{search}$ and the area searched by the predator $A_{search}$. The functional response describes the effect on the prey population in terms of the portion of the prey population that is encountered, detected, decided upon, pursued, and subdued. The numerical response describes the effect on the predator population in terms of growth and reproduction that occurs as a result of the interaction. Figure reproduced from **Paper I**.

toxic monarch butterfly caterpillar (see Fig. 7). Such exceptions generally rely on the predator learning - and then deciding - not to consume the prey, and are often accompanied by aposematic coloration to remind the predator to decide not to attack (Skelhorn, Halpin, & Rowe, 2016). By determining which steps are most important for a given interaction or community, it is easier to determine which traits have the strongest impact on that step and therefore the interaction as a whole.

Once the most important steps have been decided upon, they can then be represented by terms in a dynamic model (Fig. 11). These terms can be understood as the probability that the step will occur successfully (from the predator's perspective) based on the traits of predator and prey. Less important steps can be omitted from the model. Note that this model will necessarily be a simplification; all steps could be argued to be important, but to progress it will likely be necessary to focus on the few most important steps for the system of interest. Traits parameterize each term, with the formulation of the term depending on the nature of the relationship between traits and that step, our level of understanding, and available information. This term can be as simple or as complex as needed. For example, when studying a given community, a researcher may decide based on the available knowledge of that community that detection and pursuit are the most important steps and therefore the only terms to be included in the model. If she knows that detection is a complex function of prey behaviour and experience and predator size, and has or can gather information on those traits, she can include this complex formulation as the term for detection. If she does not know exactly how pursuit is related to traits, but knows only that it is an active pursuit, she may note that the ATN model (Berlow et al., 2009; Schneider et al., 2012) has a general formulation for pursuit success based on predator and prey body size, and so decide to use their formula. If later, due to further research or information becoming available, a more accurate formulation for pursuit in that system becomes available and she has access to data on the relevant traits, she can replace the previous term for the newer, more accurate term, while leaving the rest of the model as it was. By making each step explicit, this framework is flexible and generalizable to any system. It is able to use as much or as little information as is available and is easily modified when new information becomes available.

Within **Paper I**, I stepped through an explicit example of how to apply this framework, using four real beetle species and the empirically measured traits of body size and temperature optima to predict interaction strength with prey at different temperatures. In this example, I showed that fluctuations in temperature can have dramatic effects on trophic interaction strengths. Given that, globally, temperatures are on the rise and likely to increase by several degrees (IPCC, 2014), this may lead to substantial alterations in food-web structure and dynamics (Cirtwill, 2020). While the impact of temperature on trophic interactions is not novel (e.g. Dell, Pawar, & Savage, 2014; Gilbert et al., 2014; O'Connor, Gilbert, & Brown, 2011; Rall et al., 2010), by applying it within this framework, it is possible to make explicit and testable predictions of how temperature may interact with other traits to affect food-web dynamics.

The framework developed in **Paper I** facilitates (i) comparison between ecosystems or trophic interactions of different types and (ii) the flexibility to include whichever trait(s) are deemed most important for a particular community, where (iii) the proposed mechanism whereby the trait affects the trophic interaction can be as simple or complex as required and developed as more information becomes available. Finally, by explicitly linking traits to one or more steps of an interaction, the proposed mechanism of the trait on that step can be empirically tested in a focused experiment. For example, if the brightly-advertised, stinging spines on slug moth caterpillars are hypothesized to be important for dissuading paper wasp attacks by making the caterpillar look imposing such that the paper wasp decides (step 3) not to attack, one could test this and determine the strength of the relationship simply by comparing how frequently paper wasps initiate an attack on larvae with and without the bright, stinging spines (e.g. Murphy et al., 2010). While in another ecosystem, the prey might not have stinging spines, a different trait may play the same role. For example, when faced with a predator, the puffer fish fills its stomach with water, "puffing" itself to a much larger size (Brainerd, 1994). The predator, faced with a large, spiny, toxic ball of fish, might just decide not to attack. This behaviour, therefore, plays the same role as the slug moth caterpillar's brightly-colored, stinging spines. Using this framework, we can begin to build comparisons between different traits, ecosystems, and interaction types to start developing a wider understanding of what types of traits are important where.

## 5.2 Can we apply a dynamic model parameterized by traits to experimental data?

I employed the framework developed in **Paper I** when choosing traits and developing the model in **Paper II** and **Paper III**. Following a study on a similar community (Jonsson et al., 2018), which found that body size was effective in predicting interaction strengths, but that the preferred habitat of the predators moderated their interaction strength, I modified the allometric trophic network (ATN) model to include microhabitat use. I hypothesized that predators and prey spending more time in the same microhabitat should encounter each other more and thereby have stronger interaction strengths than those utilizing different microhabitats. As trophic complexity increases, the performance of models such as ATN decreases (Jonsson et al., 2018). This is likely due to non-consumptive effects of predators on each other, which is not captured by the model. I therefore additionally added a term for non-consumptive predator-predator effects. I hypothesized that the more likely a predator is to become intraguild prey to another predator (based on their body sizes and habitat overlap), the more time the predator will spend avoiding their potential intraguild predator instead of consuming their own prey.

To compare the importance of both of these terms, I compared four alternative models with/without each term. I compared the models by fitting them to time-series abundance data of two aphid species and their four predators in a mesocosm experiment. I found that each model was able to fit the data equally well, but did so by having substantially different values for key parameters. What this means is that each model was essentially emphasizing different steps from **Paper I**'s framework. In models with a term for habitat use, differences in habitat use decreased how frequently predator and prey encountered each other. These models had a high attack rate scaling parameter, indicating that if predator and prey encountered each other and an attack was initiated, it was likely to be successful; thus the limiting step was how frequently they encountered each other as a result of their habitat use. Models without this term had a lower attack rate scaling parameter, indicating that a successful attack was less likely to follow an encounter and that pursuit or subjugation were the limiting steps.

While these models all fit well to the data, when applied outside the data range they performed poorly, due to the different mechanisms emphasized in each model. I applied each model to predict the dynamics of a hypothetical new prey species of a different size and habitat niche than those in the experiment. I found that each model predicted vastly different effects of the four predators on the hypothetical prey. To differentiate between the different models and determine which mechanisms were in fact occurring, requires more targeted experiments focused on specific steps of the interaction to ascertain their importance and narrow down the realistic ranges of different parameter values. As **Paper III** was specifically intended to carry out the experiment designed in **Paper II**, however, I did not carry out those experiments here.

The value of developing dynamic models parameterized by species traits is (at least) twofold; we increase our understanding of the mechanisms behind trophic interactions and food-web dynamics, and we are able to use the models to extrapolate to new scenarios. The realities of doing so, however, are not necessarily trivial. In **Paper III**, I applied the framework from **Paper I** and developed four alternative dynamic models with and without microhabitat overlap and non-trophic predator-predator effects and parameterize them with experimental data. Using the four different models and their parameter values, I extrapolated to a hypothetical prey species to demonstrate that if the model we are using is wrong, it can make disastrously erroneous predictions. While such consequences for prediction may be self-evident, the point is that we may have a hard time to evaluate whether a model is wrong or right - since fitting well to the data it was trained on is no guarantee that it is correct. On a more positive note, I demonstrate the potential applications of a (reliable) dynamic food-web model parameterized by species traits (body size for predator-prey interactions and root volume for plant-nutrient interactions) in **Paper V**.

## 5.3 What can species traits tell us about food-web structure?

I primarily studied food-web structure in **Paper IV**, using a tritrophic *Salix*-galler-parasitoid network (Kopelke et al., 2017). This was a particularly interesting data set as I was able to study food-web structure in both a plant-herbivore network and a host-parasitoid network, where the herbivores and hosts were one and the same species. I used a range of statistical approaches to understand how both network components were structured and how this structure was driven by species traits. In concert, these methods provided a more nuanced and fuller understanding of the structures and interactions. Together with my coauthors, I also provided new software and methods for evaluating this, to the benefit of the wider field.

I first explored the intrinsic structure of the network, i.e. with methods using latent traits (Rohr et al., 2016, 2010) or the structure of the network (Desjardins-Proulx et al., 2017) rather than real traits. This was to give a baseline for how much structure there was in the data that could be explained by traits. I also compared linear and non-linear methods to determine whether the trait-matching relationship was simple or complex.

I found that the plant-herbivore network was much more modular than the host-parasitoid network, and most herbivores interacted with very few plant species (at most four, and in the majority of cases only one). The host-parasitoid network, in contrast, was more nested. Both networks contained groups of species that tended to share similar interactions; i.e. a species was likely to interact with the same species as its ‘neighbours’. ‘Neighbours’ could be determined based simply on sharing similar interactions, or based on traits or phylogeny. I first used similarity in shared interactions to ascertain how much the networks were in fact structured based on neighbours sharing interactions, providing the upper bound on how much traits or phylogeny could predict. I found that traits or phylogeny could explain approximately half of the intrinsic structure in the host-parasitoid network, but neither traits nor phylogeny could explain this structure in the plant-herbivore network. This suggests that either traits are more important for this aspect of network structure in the galler-parasitoid network than in the *Salix*-galler network, or that the traits we used are not the traits structuring the *Salix*-galler network.

I also found that the match between consumer and resource traits was an important factor in how these networks were structured. This ‘trait-matching’ is an important theory underlying a number of food-web models (e.g. Laigle et al., 2018; Rohr et al., 2016; Williams & Martinez, 2000) and supported by multiple empirical studies (e.g Brousseau et al., 2018b; Dehling et al., 2014; Deraison et al., 2015). I first explored the potential for trait-matching using latent traits. Latent traits are not real traits, but are derived to explain the most structure in the data (Rohr et al., 2010). Latent traits allow us to explore the structure of a network even if we do not necessarily have the correct empirical traits, and may help guide the determination of which traits are relevant. Latent traits may correspond to real traits. It is uncommon, however, that any one real trait is able to explain as much network structure as a latent trait (Eklöf et al., 2013; Rohr et al., 2016). Latent traits therefore provide the upper limit on how much real traits could explain based on the structure of the data. Using latent traits, I found the potential for trait-matching in both the *Salix*-galler and galler-parasitoid networks. When comparing to equivalent methods using real traits, I found that the traits I had collected for the plant-herbivore network were poor predictors of that structure, while the traits for the host-parasitoid network were much more successful. This mirrors what I found when using neighbours to predict interactions.

Generally the relationship between traits and interactions is conceived and studied as being relatively linear, with a focus on regression models to analyse the relationship (e.g. Brousseau et al., 2018b; Gravel et al., 2013; Pearse & Altermatt, 2013; Pomeranz et al., 2019). There is some question, however, as to whether these linear methods are appropriate or whether the trait-matching relationship is more complex and whether more flexible algorithms would be better suited to elucidating the relationship (Pichler et al., 2020). I compared linear regression methods to more flexible methods (Random Forest and K-nearest neighbour). The plant-herbivore component of the network appeared to be well characterized by linear methods, even though the traits we measured did not explain the structure captured by latent traits. The herbivores in this network produce galls on the plants, which provide both nutrition and defense to the herbivore larvae (Giron et al., 2016; Stone & Schönrogge, 2003). Inducing these galls requires a sophisticated match between herbivore and plant for the herbivore to manipulate the plant into producing the gall. Additionally, willow species - the plants in this network - have a range of highly specialized chemical defenses that they use to protect against herbivory (Julkunen-Tiitto, 1989; Tahvanainen, Julkunen-Tiitto, & Kettunen, 1985; Volf et al., 2015). The herbivores in the network were specialists in their interactions with willows, which is likely to be a response to both the sophisticated suite of traits required to manipulate the plant into producing a gall (Giron et al., 2016; Stone & Schönrogge, 2003) and to over-coming the plants' specialist protective compounds (Denno, Larsson, & Olmstead, 1990; Roslin & Salminen, 2008; Treutter, 2006). Although I included chemical defenses as a trait, I used a very coarse measure, and I included few traits specific to the formation of galls. It is highly likely that the suite of traits required for a herbivore to successfully produce a gall and survive on their willow host in this network is highly complex, but because the match is so specialized, I found in my analysis that the relationship could be explained by linear latent traits. In the host-parasitoid component of the network, however the non-linear methods performed significantly better than the linear methods. This indicated that there was not a simple linear relationship - such as parasitoids with longer ovipositors parasitizing galls with thicker walls - underlying the trait-network structure relationship, but there were complexities or interactions between traits - for example, maybe ovipositor length was important to access certain gall types but not others, and only if the parasitoid accessed the gall by oviposition rather than by chewing through the gall. The performance of Random Forest (one of the non-linear methods), however, largely depended on which traits were used as explanatory variables. When using categorical traits with relatively few unique values, Random Forest was severely constrained and actually performed worse than the linear methods. While there may still be non-linearity in the trait-network structure relationship with these traits, there was insufficient resolution to capture it and a linear method was more appropriate. In other words, the best method for explaining or predicting interactions depends not only on the true nature of the relationship between traits and interactions, but also the structure of the network as a whole and the data available.

Different kinds of networks are structured in different ways. The results we find here likely cannot be extrapolated closely to other plant-herbivore or host-parasitoid networks. But with more comparative studies such as this, we will begin to draw generalizations and to recognize patterns; perhaps highly specialist relationships require detailed understanding of the particular defenses or mechanisms driving interactions, versus more weakly structured interactions where broader traits are sufficient to capture interactions.

## 5.4 Which species traits have the biggest influence on interactions, food-web structure and food-web dynamics?

Following the successes of body-sized based methods for predicting food-web structure and dynamics, there have been calls to integrate other traits into these models to address their shortcomings (Bartomeus et al., 2016; Boukal, 2014; Morales-Castilla et al., 2015). One of the major difficulties in understanding the relationship between traits and interactions is that organisms display a dizzying array of traits and the role played by even the same trait differs from network to network (Brousseau et al., 2018a; Eklöf et al., 2013; Zakharova et al., 2019). My results do not solve this problem. What they do provide, is a way to classify and compare diverse traits according to which parts of a trophic interaction they influence (**Paper I**) and some small beginnings as to which traits were important in the ecosystems I studied.

In **Paper III**, I developed a metric for quantifying microhabitat overlap and incorporating it into dynamic food-web models. While my results were inconclusive as to the importance of microhabitat overlap for driving interactions, they provide a road map for refining our understanding of the mechanisms at play and for determining narrower bands for parameter values so that we can be more certain of the role that traits such as microhabitat use play. In **Paper IV**, I explored a wide range of traits in a *Salix*-galler and galler-parasitoid network. Gall type was overwhelmingly the most important trait in both networks, but it seems that I was missing important information on traits structuring the *Salix*-galler component of the network, and that the missing traits would be more important than gall type. In terms of using traits to predict interactions, ideal traits will be easily measurable at the individual level (Lavorel et al., 2007; Violle et al., 2007; Zakharova et al., 2019), and explain elements of food-web structure and dynamics not already captured by other traits, e.g. body size. Gall type is perfect in this regard; it is clearly visible and obvious and is the first piece of information recorded about a gall-inducing species (e.g. Liston et al., 2017). In **Paper IV**, gall type actually came out as being substantially more informative than body size. Intriguingly, for the galler-parastoid part of the network, the trait "oviposition strategy" was nearly as effective as gall type for explaining interactions, but this was not so in the *Salix*-galler part of the network. Oviposition strategy is essentially a coarser grouping of gall type, grouping gallers into those that oviposit on the leaf blade (leaf folders and rollers), those that oviposit through the midrib (leaf blade sausage gallers, and leaf midrib pea and bean gallers) and those that oviposit elsewhere (bud and stem gallers). It seems that parasitoids, which tend to be much more generalist than gallers in terms of the number of species they interact with, are more restricted by how easy it is to access the gall (bud and stem galls have very tough walls, while leaf folders and rollers are only protected by the leaf itself, and other galls fall somewhere in between), while the relationship between the type of gall formed and the *Salix* species it is formed on seems to be more restrictive.

With the exception of body size, few traits have been compared across more than one or a few species or communities (Brousseau et al., 2018a). Here, I explored the importance of microhabitat in a six-species community, and the importance of gall type and other traits across two entire communities. Crucially, though, I provided the framework to allow these and future findings to be compared with each other, hopefully leading to a more general understanding of which traits matter where.

## 5.5 How do coupled food webs affect each other?

One cannot study a species in isolation and expect to truly understand its dynamics; neither can one study food webs in isolation and expect to fully understand their dynamics. For simplicity, we tend to draw boundaries around a community or ecosystem and study those species and interactions within the boundaries, while ignoring what happens outside. In reality, however, ecological communities are not isolated systems and frequently exchange large or small quantities of individuals, matter, or nutrients which can have dramatic effects for one or both systems (e.g. Loreau, Mouquet, & Gonzalez, 2003; McCann et al., 2020; Polis et al., 1997). Cross-ecosystem subsidies, such as plant detritus falling in a stream or bears fishing salmon from a river, can support ecological communities that cannot otherwise exist (Nakano & Murakami, 2001; Sabo & Power, 2002). Similar to these one-way subsidies, mobile species are able to couple diverse ecosystems by feeding in both (Rooney & McCann, 2012).

To explore how coupled food webs affect each other, I simulated similar food webs that differed in basal species diversity and/or fertility and were coupled by the foraging movement of mobile herbivores and predators (**Paper V**). The advantage of using dynamic models such as those developed in **Paper I**, **Paper II** and **Paper III** is that we can relatively simply create a wide range of replicates to explore a wide range of scenarios. In **Paper V**, I explored 45 different scenarios varying in basal diversity and fertility of two coupled habitats, as well as the amount of consumer foraging movement between habitats, and replicated each scenario 100 times. By using parameter values that are as realistic as possible and models incorporating realistic mechanisms, we can hopefully generate realistic predictions. As our understanding of parameter values and mechanisms increase through frameworks and experiments such as those in **Paper I**, **Paper II**, and **Paper III** we can improve and refine our models parameter values, and predictions.

I found that coupled food webs differing in basal diversity and/or fertility can indeed affect each other. I observed the strongest effects in low fertility habitats when they were connected to high fertility habitats. The spill-over of mobile consumers from the high fertility habitat was able to support biomasses and even trophic levels in the low fertility habitat that were unsustainable without this subsidy. All elements of the food web and nutrient cycle were affected.

Crucially, I also observed that it is not only stocks, i.e. levels of biomass and nutrients, but also flows, such as productivity and decomposition, that we must consider when exploring these impacts. For example, I found that the *size* of the regional nutrient pool (a stock) was not affected by consumer movement. The *uptake* of nutrients from the environment to the regional nutrient pool (a flux), however, was affected by consumer movement. At the extreme end, in low fertility habitats connected to high fertility habitats, the influx of consumers supplemented the detritus pool (and therefore the supply of nutrients from decomposition) to such an extent that the uptake of nutrients from the environment to the regional nutrient pool decreased to zero. In a real-life situation, this could have serious implications for nutrient run-off or the efficacy of fertilizers. If only considering the change in stocks, i.e. regional nutrient pool concentration, this effect would never be observed.

My results come with crucial implications for understanding food webs in the real world. With increasing use of land for agriculture and other human uses, we are dramatically altering the composition of the landscape (Fahrig et al., 2011; Millenium Ecosystem Assessment, 2005; Ramankutty et al., 2018). To predict the future dynamics of ecosystems, we may need to look beyond the changes happening within the ecosystem to include changes happening outside its borders. While such impacts have been studied for dispersal, i.e. species migrating from one habitat to another, the effect of consumers coupling similar but different neighbouring habitats through foraging has received less attention (Gounand et al., 2018; Rand & Louda, 2006). I found that this too can have substantial effects on all aspects of ecosystem functioning.

# 6 Toward prediction

With a rapidly changing world due to climate change, habitat loss, and other anthropogenic drivers, ecology is increasingly being called upon to make predictions of how ecological communities will respond and change (Clark et al., 2001; Purves et al., 2013). Extrapolating from current states to uncertain future scenarios is a difficult task (Petchey et al., 2015). Predicting whom a novel species will interact with and the effect it will have if it has never encountered the focal community before, or what the impact of a change in temperature, seasonality, habitat structure, or many other aspects will be, requires an understanding not only of the status quo, but also how individual species and interactions will be impacted by the changes. An understanding of how traits structure food webs (**Paper IV**), the mechanisms underlying trophic interactions and how they may be used to develop dynamic models (**Paper I**, **Paper II**, **Paper III**), as well as an understanding of the potential impact of adjacent habitats (**Paper V**) can help us make better predictions, and provide a framework for improving predictions as more information becomes available. Here I have made predictions of how temperature may affect trophic interactions among ground beetles and their prey (**Paper I**), predictions of which interactions may have been missed from a network (**Paper IV**), predictions of trophic dynamics of four invertebrate predators with a hypothetical new prey species based on different models (**Paper III**) and predictions of how coupled food webs differing in fertility and basal species diversity affect each other (**Paper V**). Crucially, in all of these predictions, I showed how a difference in model formulation (**Paper I**, **Paper III**, and **Paper IV**) or in what information was included in the model (**Paper I** and **Paper V**) can lead to vastly different predictions.

Understanding the natural world in terms of species traits and trophic networks is not an easy task, and any model we use to do so will necessarily be an imperfect simplification of the real world. There is promise, however, that sufficient understanding can be reached with few traits (Eklöf et al., 2013) and there is a burgeoning array of methods by which to do so (e.g. Gravel et al., 2013; Laigle et al., 2018; Pichler et al., 2020; Portalier et al., 2019). With a way to focus and guide the selection and application of traits for trait-based models across systems (**Paper I**), a selection of complementary methods to provide a more nuanced view on trait-network relationships (**Paper IV**), and empirical experiments grounded in theory (**Paper II**) to test and parameterize proposed models and relationships (**Paper III**), we can broaden our understanding of the forces that structure networks and their dynamics and explore a wider range of scenarios through simulations to predict how communities will respond to different conditions (**Paper V**).

# 7 Conclusions

In my thesis, I developed a framework for incorporating traits into dynamic models (**Paper I**), which should also help guide comparison among interaction and ecosystem types and the development of mechanism-focused research. In **Paper II** and **Paper III**, I applied this framework to incorporate specific traits into a dynamic food-web model and run mesocosm experiments to parameterize the models. I also demonstrated how difficult it can be to distinguish among models (and therefore relevant traits), and gave examples of groundwork experiments to address this.

In **Paper IV**, I demonstrated how a suite of statistical analyses can be combined to quantify the extent to which different traits structure interactions in trophic networks of different types, and how we might use this to find interactions missed from the observed network. I identified certain traits, such as gall type and potentially microhabitat use, that structure trophic networks, but also showed that the most important traits vary across ecosystems and interaction types. I have shown that distinguishing among traits based only on dynamic data may not always be possible (**Paper III**), and that we may need more ground work to understand the mechanisms and limits underlying interaction dynamics.

I applied trait-based models to explore diverse scenarios in **Paper V**, examining the effect of coupling habitats differing in fertility and basal diversity by consumer foraging movement. There I showed that such factors affect not only the system they are applied in, but can spill over to affect adjacent habitats through consumer movement. Additionally, I showed that the effects can only be fully understood by examining both stocks and fluxes, and that this may have practical and theoretical implications.

Overall, I have shown that a trait-based approach to food webs has great promise for our understanding of ecological communities and our ability to make accurate predictions, but that there are still a number of challenges to address. I laid out a framework and ground-work experiments for addressing some of these challenges, and showed how the iteration between theory, empirical experiments, and analysis is ultimately required to reach the promise that trait-based approaches hold.

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# Popular science summary

Why do lady beetles (aka ladybirds or ladybugs) eat aphids and not spiders? Do spiders also eat aphids? How much of my crop would get eaten by aphids in a field with lots of lady beetles compared to lots of spiders? What about if the field next door has lots of lady beetles; will that affect my own field?

These are the kinds of questions we can answer by studying food webs. Food webs describe the network of who-eats-whom in an ecological community. Food-web *structure* tells us who-eats-whom (i.e. lady beetles and spiders both eat, but are not eaten by, aphids) while food-web *dynamics* describes how the population sizes of the species fluctuate as a result of the interactions (i.e. a field with lots of lady beetles will have fewer aphids and therefore healthier plants than one with spiders but no lady beetles). In my thesis I have been asking questions about why certain species interact but not others (i.e. why lady beetles eat aphids but don't eat spiders) and whether we can use that information to make predictions about food-web structure and dynamics.

Species are different. Some are large, some are small. Some are fast, some fly, some taste bad, others have eight legs. These traits, in addition to providing naturalists with lifetimes of enjoyment studying them, limit which species can and can not eat each other. Lady beetles happen to have all the traits to be highly efficient aphid-eating machines, but spiders are much larger and faster than aphids and don't have much to fear from lady beetles. The aphids' traits make them vulnerable to lady beetles, while the spiders' traits don't. The idea is that by figuring out specifically which traits are most important, and why, that we can use them to predict food-web structure and dynamics.

The first step is having some kind of framework where we can decide which traits are important and how we can use them to build a mathematical model capable of predicting food-web dynamics. I do this in my thesis by breaking a feeding interaction into steps; a predator first has to encounter and detect its prey, then decide to attack it, successfully pursue and subdue it, and finally ingest, digest and allocate the nutrients to growth or reproduction. For a given interaction, although all of these steps occur, many of them are not very important and we can simplify things by only considering those that are important. For example, for a lady beetle or spider eating aphids, the most important steps are probably encounter - since the lady beetle or spider needs to be in the same place as the aphids to find and eat them - and ingestion - since it takes time to eat an aphid, limiting the number that an individual lady beetle or spider can eat in a given period of time. Other steps may play a role, but these are probably the most important ones to start with since aphids are generally rather stationary and not too difficult to detect.

Having decided on steps, we need to think about what traits affect each step and how so that we know how to put traits and steps together in the model. I tried this out. I decided that habitat use was probably the most important trait affecting encounter - lady beetles spend more time in the foliage of the plant where the aphids are, while spiders spend most of their time on the ground. I reasoned that the more time predator and prey were in the same place, the more often they would encounter each other and the stronger their interaction would be. I also included body size; the bigger the difference between predator and prey, the easier it should be for the predator to handle and ingest the prey. I put together a model using these traits, and then designed an experiment to test it. I planted some beans and barley for aphids to eat in some crates, put a cage over the top — about 60cm high by 60cm wide and 40cm deep — and then added aphids and lady beetles, spiders, and some other predators. Every 1-2 days for a week I counted how many aphids were in each cage. Then I teamed up with some mathematicians to help fit the model to the data. We tried a model with habitat versus one without habitat, and the idea was that one of them would fit better than the other, and that would tell us whether habitat use was important or not. As it turns out, they both fit almost exactly the same. While that didn't help us find out whether habitat use was important, it didn't mean the models were equivalent; when I tried to predict how a hypothetical new species would fit in, each model predicted different things. To really find out what is going on, we need to do some more focused experiments first to understand what is happening at each one of those steps.

So maybe habitat use is important on that small scale, and maybe it isn't. We need to do a few more experiments to find out. But what then happens on a bigger scale? Predators like spiders and lady beetles, and also herbivores like aphids, can move between habitats. What happens if there are two habitats next to each other that are different? Perhaps one is a crop — only one plant species, and lots of fertilizer so the plants have plenty of nutrients to grow — while the other is a meadow, lower in nutrients but with more plant species. Do predators or herbivores moving from one to the other to feed have an effect on either or both habitat that they wouldn't have if they didn't move? This is a much bigger question to tackle, so I moved away from the greenhouse and to the computer. Using a mathematical model similar to the one I was trying out with the cage experiments, I used computer simulations to pair up habitats with different nutrient levels and numbers of plant species and allowed some of the herbivore and predator species to feed in both habitats. I found that the movement of herbivores and predators does affect the habitats — I saw the strongest effects in habitats with low nutrients when they were next to habitats with high nutrients because there was an over-abundance of herbivores and predators in the high nutrient habitat and they spilled over to feed in the low nutrient habitat. If there was a difference in plant diversity then the effect was even stronger. I saw that this affected the plants, herbivores, predators, and soil nutrient cycle, both in terms of how much biomass or nutrients there were in each level, but also how much was moving between each level, i.e. how much herbivory or decomposition was occurring. I was looking at this in a computer simulation and there were many aspects I didn't consider, so I can't say that this is exactly what will happen in the real world. But it does show that these effects are possible and that we might need to look not only at what is there at any given moment (i.e. how many plants, herbivores, predators, or detritus) but also at the processes (i.e. herbivory or decomposition) to understand what is happening and the effects it might have.

I next deviated from aphids to explore how traits affected food-web structure on a larger scale than the cage experiment and in a more realistic setting than the computer simulations. I needed a food web with more species, so I used the network of willow species, sawflies that produce galls on willows, and the insects that parasitize the sawfly larvae. This network had 35 willow species, 88 sawfly species, and 51 parasitoid species, and was collected from sites across Europe over 30 years. It seemed big enough. I collected as much trait information as I could; I scoured books and scientific literature, quizzed the experts, measured (actually Andrew Liston measured) previously-collected adult sawflies and parasitoids, and spent three weeks (and Laura Riggi spent another two months) measuring leaves and trees and galls in the field. Once I had the trait data and the food web data, I used five different statistical methods to analyze how the traits affected the food-web structure. Five methods seems like overkill? Each method could tell us something that the others could not. Some methods showed how much of the food-web structure *could* be explained by traits, assuming we had the right traits. Other methods showed that, in the sawfly-parasitoid part of the network, the traits we actually used could explain two-thirds of what was possible, but in the willow-sawfly part the traits we used explained very little of what was possible. Still other methods showed that the type of gall that the sawfly causes the willow to produce was the most important trait for both willow-sawfly and sawfly-parasitoid parts of the food web. By combining and comparing the results of the different methods I could get a much fuller and more nuanced picture of how species' traits affected food-web structure than any of the methods alone could tell.

Altogether I found that species traits *can* tell us something about food-web structure and dynamics, but that there are a number of challenges to be addressed before we can pick up a species, measure a few things, and say exactly whom it will interact with in a community. The work I present in my thesis should provide direction and a framework for how to proceed with this line of research, as well as providing an insight into the kinds of understanding we can gain and predictions we can make as we do. Ultimately, if we are to make accurate predictions in ecology, we need to both understand the mechanisms underlying food-web structure and dynamics and have a way to relatively easily and effectively apply that understanding to new scenarios. Species traits offers the best avenue for both.

# Populärvetenskaplig sammanfattning

Varför äter nyckelpigor bladlöss och inte spindlar? Äter spindlar också bladlöss? Hur stor del av mina grödor kommer bli uppätna av bladlöss om det finns nyckelpigor på åkern jämfort med om det finns spindlar där? Om det finns massor med nyckelpgor i grannens åker kommer det att påverka min skörd?

Det här är exempel på frågor som vi kan besvara med hjälp av näringsvävar. En näringsväv beskriver nätverket av "vem som äter vem" i ett ekologiskt samhälle. Näringsvävsstrukturen berättar vem som äter vem (t.ex. både nyckelpigor och spindlar äter, men äts inte av, bladlöss) medan näringsvävsdynamiken beskriver hur populationsstorlekar varierar till följd av interaktionerna mellan arterna (t.ex. ett fält med många nyckelpigor kan komma att ha färre bladlöss och därför friskare växter än ett fält med spindlar men inga nyckelpigor). I min avhandling har jag ställt frågor om varför vissa arter interagerar med varandra och varför andra inte gör det (t.ex. varför nyckelpigor äter bladlöss men inte äter spindlar) och om vi kan använda den kunskapen för att göra förutsägelser om näringsvävars struktur och -dynamik.

Arter är olika. Vissa är stora, andra är små. Vissa är snabba, andra flyger, en del smakar illa, andra har åtta ben. Denna variation i egenskaper, som ger livslång glädje till många av de forskare och naturintresserade som studerar dem, har också en fundamental betydelse genom att begränsa vilka arter som kan och inte kan äta varandra. Nyckelpigor råkar ha många av de egenskaper som krävs för att vara mycket effektiva bladluspredatorer. Spindlar, som är mycket större och snabbare än bladlöss, behöver däremot inte vara rädda för nyckelpigor. Bladlössens egenskaper gör dem sårbara för nyckelpigor, medan spindlarnas egenskaper inte gör det. Den grundläggande idén i denna avhandling är att vi kan använda oss av kunskap om arters egenskaper för att förutsäga näringsvävars struktur och dynamik.

För att lyckas med detta måste vi först ha någon form av ramverk för att bestämma vilka egenskaper som är viktiga i olika situationer och hur dessa egenskaper kan användas matematiska modeller som förutsäger näringsvävarnas dynamik. Detta gör jag i min avhandling genom att dela upp en födointeraktion i faser; ett rovdjur måste först stöta på och uppfatta sitt byte, sedan bestämma sig för att attackera det, därefter framgångsrikt förfölja och nedlägga det, och slutligen inta och smälta det samt fördela näringen mellan tillväxt och reproduktion. Även om alla dessa faser inträffar i en interaktion mellan två arter så är inte alla nödvändigtvis lika viktiga. Därför kan vi förenkla saker genom att bara ta hänsyn till de viktiga faserna. Till exempel: för en nyckelpiga eller spindel som äter bladlöss, är de viktigaste faserna troligen att stöta på bytet - eftersom nyckelpigan eller spindeln måste vara på samma plats som bladlössen för att hitta och äta dem - och att inta det - eftersom det tar tid att äta en bladlus, vilket begränsar antalet byten som en enskild nyckelpiga eller spindel kan äta under en bestämd tid. Andra faser kan förvisso spela roll, men dessa är förmodligen de viktigaste eftersom bladlöss i allmänhet är ganska stationära och inte alltför svåra att upptäcka.

Efter att ha bestämt oss för vilka faser vi bör inkludera, måste vi tänka på vilka egenskaper som påverkar varje fas och hur. På det viset kan vi avgöra hur vi bör inkludera egenskaper och faser i modellen. Det här var en approach som jag prövade på i praktiken. Jag bestämde mig för att hur olika arter använder olika delar av sin livsmiljö förmodligen var den viktigaste egenskapen som påverkar möten. Nyckelpigor tillbringar mer tid i bladverket på växten, och där sitter bladlössen också. Spindlar däremot tillbringar större delen av sin tid på marken. Jag resonerade så att ju mer tid rovdjur och bytesart befinner sig på samma plats, desto oftare kommer de möta varandra och desto starkare blir deras interaktion. Jag inkluderade också kroppsstorlek; ju större skillnaden mellan rovdjur och byte, desto lättare bör det vara för rovdjuret att hantera och äta bytet. Jag satte ihop en matematisk modell med dessa egenskaper och utförde sedan ett experiment för att testa den. Jag planterade bönor och korn i lådor och täckte dessa med en nätbur (cirka 60 cm hög, 60 cm bred och 40 cm djup) och tillsatte sedan bladlöss och nyckelpigor, spindlar och några andra rovdjur. Varje eller varannan dag under en vecka räknade jag hur många bladlöss som fanns i varje bur. Därefter samarbetade jag med matematiker för att anpassa modellen till vårat insamlade data. Vi testade en modellvariant som inkluderade livsmiljö kontra en utan livsmiljö, och tanken var att en av dessa skulle passa bättre än den andra, och att det skulle avslöja om arternas användningen av livsmiljöer var viktig eller inte. Det visade sig dock att båda modellvarianterna kunde beskriva data från experimentet nästan exakt lika bra. Även om det inte hjälpte oss att ta reda på om användningen av livsmiljöer var viktig, betydde det inte att modellerna var likvärdiga. När jag försökte förutsäga hur en hypotetisk ny art skulle passa in i näringsväven, förutspådde de olika modellerna olika saker. Detta illusterar att vi behöver göra mer fokuserade experiment för att förstå vad som händer i vart och ett av predationsfaserna så att olika modellalternativ kan utvärderas på ett bättre sätt.

Kanske är det så att hur olika arter använder olika delar av sin livsmiljö är viktigt i ett litet rumsligt sammanhang, och kanske är det inte det. Vi behöver göra fler experiment för att ta reda på den saken. Men vad händer då i ett större rumsligt perspektiv? Rovdjur som spindlar och nyckelpigor, och även växtätare som bladlöss, kan ju röra sig mellan olika livsmiljöer. Vad händer då om två grannmiljöer är sinsemellan olika? Den ena kanske är en åker med bara en gröda och mycket gödning, så att växterna har gott om näringsämnen. Den andra kanske är en äng, fattigare på näringsämnen men med fler växtarter. Kan rovdjur eller växtätare som rör sig från den ena till den andra livsmiljön för att äta då påverka den ena eller båda livsmiljöerna? För att svara på den fråga övergav jag växthuset till förmån för min dator. Jag tog fram en matematisk modell lik den som jag testade med burexperimenten. Därefter använde jag datorsimuleringar för att para samman ekosystem med olika näringsnivåer och antal växtarter. Av växtätar- och rovdjursarterna tillät jag vissa att äta i båda ekosystemen. Jag fann att rörelsen av växtätare och rovdjur påverkade ekosystemen; de starkaste effekterna såg jag i ekosystem med låga näringsnivåer som gränsade till system med höga näringsnivåer. Det uppstod ett överflöd av växtätare och rovdjur i det näringsrika ekosystemet, som spillde över till det näringsfattiga systemet. Om det också fanns en skillnad i ekosystemens växtdiversitet var effekten ännu starkare. Jag såg att detta påverkade växter, växtätare, rovdjur och markens näringscykel. Det påverkade både hur mycket biomassa eller näringsämnen som fanns i varje nivå, t.ex. mängden växtbiomassa eller mängden näringsämnen i marken, men också hur mycket som rörde sig mellan varje nivå, t.ex. hur mycket växtätning eller nedbrytning som inträffade. De här effekterna studerade jag i en datorsimulering - och eftersom det fanns många aspekter som jag inte beaktade, så jag kan inte säga att det är exakt vad som kommer att hända i den verkliga världen — men det visar att dessa effekter är möjliga. För att vi ska kunna förstå vilka effekter det kan ha när djur rör sig mellan olika livsmiljöer kan vi därför behöva titta inte bara på hur mycket växter, djur, och näringsämnen som finns i ett ekosytem utan också på hastigheten hos de processer som de är inblandade i (t.ex. växtätning och nedbrytning) .

Härnäst övergav jag bladlössen för att utforska hur artegenskaper påverkade näringsvävar i större skala än bur-experimentet och i en mer realistisk miljö än datorsimuleringarna. För att kunna göra det så behövde jag en näringsväv med fler arter. Därför, använde jag ett nätverk som bestod av olika arter av vide, sågsteklar som producerar gallbildningar på vide, och insekter (parasitoider) som parasiterar sågstekellarver. Jag samlade in så mycket artegenskaper som jag kundeoch sen använde jag fem olika statistiska metoder för att analysera hur egenskaperna påverkade näringsvävens struktur. Men är inte fem olika metoder lite att ta i? Faktiskt inte, varje metod kunde säga något som den andra inte kunde. Vissa metoder visade att det fanns struktur i datat som egenskaperna kunde fånga. Andra metoder visade att de egenskaper som vi hade uppmätt kunde förklara två tredjedelar av denna struktur i sågstekel-parasitoid-delen av näringsväven, men väldigt lite i vide-sågstekel-delen. De visade också att den typ av gallbildning som sågsteklar får videt att producera var den viktigaste egenskapen för både vide-sågstekel- och sågstekel-parasitoid-delarna av näringsväven. Genom att kombinera och jämföra resultaten från de olika metoderna kunde jag få en mer fullständig och nyanserad bild av hur arternas egenskaper påverkade näringsvävens struktur än någon av metoderna kunde ge på egen hand.

Sammanfattningsvis fann jag att artegenskaper *kan* berätta en hel del om näringsvävars struktur och dynamik, men att det finns ett antal utmaningar som vi måste ta itu med innan vi kan plocka upp en art, mäta några väl valda egenskaper och säga exakt vem den arten kommer att interagera med i ett växt- och djursamhälle. Det arbete jag presenterar i min avhandling ger vägledning och ramar för hur vi kan gå vidare med denna forskning, och ger också en inblick i vilka insikter vi kan uppnå och vilka förutsägelser vi kan hoppas kunna göra. I slutändan, om vi ska kunna göra mer tillförlitliga förutsägelser inom ekologi så måste vi dels förstå de mekanismer som ligger bakom näringsvävars struktur och dynamik, och dels ha ett sätt att relativt enkelt och effektivt tillämpa denna kunskap under nya scenarier. Att utgå från arternas egenskaper är (för närvarande) den bästa utgångspunkten för båda ändamålen.

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Food webs describe who-eats-whom in an ecological community. This thesis examines the role of species' traits in structuring food webs and their dynamics, and how species' use of space on both small and large scales can alter food-web dynamics and ecosystem functioning. Synthesizing theoretical and empirical approaches across a range of ecosystems demonstrates the potential of a trait-based understanding of food webs for predicting how ecosystems may respond to an increasingly changeable world.

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