ENVIRONMENTAL AND ECOLOGICAL DRIVERS OF FOOD WEB STRUCTURE AND DYNAMICS

by

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ABSTRACT

Natural communities are undergoing accelerated changes due to human pressures such as habitat fragmentation, over-harvesting, and species invasions. Here, I use bioinformatics and mathematical models to examine the environmental and ecological drivers of food-web structure and dynamics. First, I use a spatially expansive food web to examine drivers of spatial turnover in food web interactions across an environmental gradient. I observe that there is a large amount of spatial turnover in food web interactions, however, the fundamental structure of these food webs stays constant. Further, I demonstrate that predicting local realizations of community structure is very difficult, but critical since environmental perturbations occur at the local scale. Then, I integrate empirical data and mathematical models to explore the consequences of omnivory on food-web stability and persistence. I demonstrate that the importance of omnivory depends on both the type of omnivory and the food web within which it appears. Moreover, scale matters - conclusions about the stabilizing effect of omnivory depend on the scale of the mathematical model (i.e. module vs whole food web model). Omnivory is just one repeated structure within food webs. Using a dynamic food web model, I examine the relationship between different network metrics and community, species, and interaction persistence in food webs. I demonstrate that network metrics are successful at predicting community and interaction persistence. They are not, however, the same metrics, and the relationship is dependent on the scale of persistence being examined (i.e community vs species vs interaction). Finally, I derive a novel multi-trophic metacommunity model which demonstrates how movement is a product of both a species' ability to move and the landscape across which it moves. Treating patch connectivity as a species' specific

property can change our conclusions about multi-patch stability. Overall, my thesis integrates data and theory to test the impacts of environmental gradients and change on food webs and provide testable predictions to guide future research in spatial food web ecology.

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CHAPTER 1

Introduction and overview

Determining the drivers of species interactions has long been a goal of ecologists as it is critical for understanding community structure and dynamics. Perhaps most fundamental of these interactions is predation, and the description of communities as food webs, or compiled data of who eats whom. At their most basic, these food webs determine energy fluxes through ecosystems (Brose *et al.* 2008), however, they also aid in understanding nutrient cycling (Carpenter & Kitchell 1988; Lawton 1989), ecosystem stability (May 2001; Loreau & de Mazancourt 2013), and resilience to invaders (Pimm *et al.* 1991; Stouffer & Bascompte 2011). More recently, ecologists have highlighted the importance of examining trophic interactions at wide spatial and temporal scales (Gravel *et al.* 2013; Alofs & Jackson 2015; Kissling & Schleuning 2015; Morales-Castilla *et al.* 2015; Poisot *et al.* 2015), for understanding the drivers of species interactions is paramount in predicting community response to anthropogenic pressures (Araújo & Luoto 2007; Heikkinen *et al.* 2007; Schweiger *et al.* 2008).

Food webs were historically constructed through direct observation of feeding interactions, gut content analysis, immunological techniques, and fecal analysis (Paine 1988). However, these webs were subsequently criticized for bias in taxonomic resolution (Paine 1988; Hall & Raffaelli 1991; Cohen *et al.* 1993; Schmid-Araya *et al.* 2002), underrepresentation of highly mobile species (Paine 1988), and misrepresentation of major variations in spatial and temporal scales of the data presented (Lawton 1989). These critiques led to a renaissance in food web collection and current descriptions of food webs are typically based on a compilation of evidence of antagonistic interactions from the literature, expert knowledge, gut contents, feeding experiments, direct observation, and theoretical predictions (Martinez 1991; Woodward *et al.* 2005; Dunne *et al.* 2008; Woodward 2009; Layer *et al.* 2010). While these new networks have demonstrated that food webs are far more complex than previously thought (Goldwasser & Roughgarden 1993; Woodward *et al.* 2005), they are based on a common assumption that consumer diet preference is preserved. Or, if species A eats species B in one food web then species A will always eat species B whenever these species co-occur, albeit perhaps in different proportions (see Blanchet *et al.* 2020).

The preservation of consumer diet is an important assumption, and one which is neither supported by theory or experimental data. For example, optimal foraging theory predicts that species prefer specific prey, and when it is present at high enough abundances prey switching should occur (Petchey *et al.* 2008). One outcome of prey switching is simply altering the importance of different diet items, however, novel prey items can also be incorporated (e.g. Bartley *et al.* 2019). Additionally, it has been observed that at high predator abundances intraspecific competition leads to an increased diversity in predator diet (Araújo & Luoto 2007). These alterations in diet based on biotic and abiotic cues should be expected. Hutchinson's concept of the fundamental niche suggests that species are able to consume a much wider diversity of prey than their realized niche measures (Hutchinson 1957). And, it is the width of this fundamental niche which allows flexibility in prey selection under variable biotic and abiotic conditions. For example, zooplankton have been shown to alter their prey selection in response to changing abundance and prey diversity (Gentleman *et al.* 2003). Unfortunately, limitations in the collection of high quality food web data based solely on direct observation of trophic interactions makes it difficult to incorporate this body of ecological literature into food web studies. This is not trivial, especially with the recent call to examine spatial differences in trophic interactions to assist in forecasting community response to perturbation (e.g. Alofs & Jackson 2015). The assumption of preservation of consumer diet preferences makes understanding these spatial differences in trophic interactions inherently difficult to examine.

One way of exploring community response to cascading effects of environmental perturbations is through collecting community data along temporal and/or spatial gradients (Tylianakis & Morris 2017). We often lack the prescience, however, to capture these events within the natural world. Thus, another way of exploring community responses to change is through dynamic food web models which allow scientists to explore the role of repeating structures, species' deletions, and press perturbations in a theoretical realm (e.g. Borrvall & Ebenman 2006; Brose *et al.* 2006; Gilljam *et al.* 2015). The evidence for the importance of these structures is typically from studies conducted at two extremes – either within dynamic models of smaller three to four species subwebs, referred to here as modular theory (e.g. McCann *et al.* 1998, 2005; Namba *et al.* 2008 but see Kondoh 2008; Stouffer & Bascompte 2010), or by using classic empirical webs to examine the over- or under-expression of these architectures within natural communities (e.g. Bascompte & Melián 2005). Indeed, both i) whether these module-level conclusions scale to larger dynamic networks and ii) whether the over/under expression of these structures indicates stabilizing features or are anachronisms of assembly remains to be seen. In addition, these studies overlook the spatial arena of which these dynamics are an inherent part. Thus, comprehensive studies merging empirical evidence and theory are necessary to tease out structures promoting food web stability and persistence across spatial and temporal gradients.

1.1 Empirical evidence for preservation of network structure

Much of the empirical work describing generalities in network structures has been done at a global scale, comparing high resolution food webs compiled from both direct and indirect evidence of species interactions across ecosystems (e.g. Cohen & Newman 1985; Havens 1992; Banašek-Richter *et al.* 2004). There have been few studies, however, examining preservation of local network structures along gradients. In particular, because of the way these networks are constructed based on the assumption that co-occurrence of species that have been observed to interact is sufficient to ensure local interaction of those species. When this assumption is used in the compilation of food webs, researchers risk confounding changes in species assemblages across these gradients with changes in interaction networks (e.g. Araújo *et al.* 2011). For example, the addition of a single species across a gradient will increase the number of trophic links between species in the network. The implicit assumption of this compiled food web approach is that these additional links will occur predictably, adding interactions, but not altering the distribution of links within the species which co-occur across the entire gradient. Indeed, this assumption that co-occurrence implies interaction makes it impossible to determine environmental or ecological driven differences in species interactions between networks since it ignores the influence of both intra and inter-specific competition (e.g. (Araújo *et al.* 2008; Petchey *et al.* 2008; Kefi *et al.* 2015), environmental changes, and regime shifts (e.g. Memmott *et al.* 2004; Tylianakis *et al.* 2008; Albrecht *et al.* 2010; Layer *et al.* 2010; Valiente-Banuet *et al.* 2015). While these highly resolved food webs based on both direct and indirect evidence of interaction have been instrumental in demonstrating key food web properties, there is merit in considering food webs compiled on direct evidence alone when examining changes in local network structures along gradients.

Despite the inherent difficulties associated with collecting these highly resolved networks, there is evidence of spatial and temporal changes in species interactions along gradients. For example, while some of these changes may just be due to sampling effort, there are numerous other reasons why an interaction may be present in one location and not another, including low abundances or morphological uncoupling whereby trait mismatching precludes two species from interacting, often termed forbidden links (e.g. Olesen *et al.* 2011; González-Varo & Traveset 2016)). For example, morphological mismatch has been observed in frugivory networks (e.g. González-Varo & Traveset 2016) where spatiotemporal fluctuation in fruit sizes results in areas where fruit is too large for a frugivores' gape, and in consumer-resource interactions more broadly as a consequence of changing climate (e.g. Kerby & Post 2013). Phenological mismatch, or temporal uncoupling, has also been observed in pollination networks with anthropogenic climate change driving earlier flowering times. For example, Olesen *et al.* (2011) found that 28% of all links in an Arctic pollination network were unobserved due to phenological mismatch. Similar to the frugivory networks presented above, food web interactions within aquatic systems are also size structured (Jennings *et al.* 2007; Woodward 2009; Gravel *et al.* 2013), and famously we are altering the size distributions of these systems through anthropogenic pressures (e.g. Pauly *et al.* 1998). Thus, they present the same potential for species-specific traits and their environment to interact leading to morphological and phenological mismatch causing the realization of specific species interactions in some locations but not others.

Freshwater fish are predominantly gape limited, however, they consume prey within an optimal body size in relation to their size to obtain the most energy for the lowest energetic cost (e.g., Werner 1974; Kislalioglu & Gibson 1976; Wankowski 1979; Scott 1987; Prejs *et al.* 1990; Woodward *et al.* 2005). In this way, there is the potential for morphological mismatch on either side of the prey size spectrum. Moreover, differences in thermal tolerance can lead to habitat shifts for predators as they grow, leading to spatial mismatch. For example, thermal stratification in larger lakes drives cool and cold water fish to benthic resources instead of foraging in the more energetically costly pelagia (Roy *et al.* 2004). However, the consequences of these mismatches in aquatic food webs remains poorly understood. This is not a trivial question. In my thesis I examine variation in freshwater food web structure across a broad environmental gradient and determine how environmental and ecological drivers influence food web structure. Moreover, I take the examination of variation in food web structure a step further by determining what effect these changes in species' interactions have on the fundamental structure of food webs.

1.2 Theoretical evidence for the preservation of food web structure

Observing the repetition of food web structure across spatial gradients is compelling evidence that these structures may be integral to the persistence and stability of these networks. Indeed, one of the central paradoxes in ecology is the observation of complex, diverse natural communities which theory predicts should be inherently unstable (see May 1972). One way of reconciling these theoretical predictions with empirical evidence to the contrary is through the presence of stabilizing structures and/or interactions. To derive meaning from these complex tangles of interactions, food web theory is often based on 3 to 4 species sub-models, termed modules here (e.g. Holt 1997; Stouffer & Bascompte 2010). Results of both theoretical and empirical explorations of these modules have yielded many important insights into the influence of factors such as environmental perturbations (see Ruokolainen & McCann (2013) for a theoretical and Sentis *et al.* (2014) for an empirical example), or interaction strength (see McCann *et al.* (1998) for a theoretical and Bascompte *et al.* (2005) for an empirical example) on food web stability and persistence.

One food web module shown to be frequently observed in natural food webs is omnivory (e.g. Menge & Sutherland 1987; Polis 1991; Arim & Marquet 2004; Bascompte & Melián 2005). It has received a lot of attention in theoretical models (e.g. McCann *et al.* 1998; Holt & Huxel 2007; Namba *et al.* 2008; Hall 2011) whereby an omnivore and a consumer (which the omnivore also consumes) compete for a shared resource, but its prevalence in nature is difficult to reconcile with theory. Theoretical predictions only find the persistence of omnivory modules in a constrained parameter space. For instance, persistence of the species involved in an omnivory module can only occur at intermediate levels of resource productivity when the intermediate consumer is a better competitor for the resource (Holt & Polis 1997; Diehl & Feissel 2001; Křivan & Diehl 2005). At low resource densities the intermediate consumer drives the top consumer to extinction, while at high resource densities the top consumer drives the intermediate consumer to extinction (Amarasekare 2000; Diehl & Feissel 2001; Křivan &

Diehl 2005). Empirical evidence, however, demonstrates the persistence of omnivory, even in resource rich environments (Diehl & Feissel 2001; Mylius *et al.* 2001; Amarasekare 2003, 2007). There are two potential explanations for this. First, there are a diversity of definitions of omnivory with different studies exploring the prevalence of different types, while theory explores yet another. Second, omnivory modules do not exist in isolation. Instead, incorporating community effects such as species immigration, alternative resources, and top predator pressures into omnivory models demonstrates how these mechanisms can enhance species coexistence. Thus, we need module theory to suggest stabilizing structures, however, we also need whole food web theory to scale these predictions to reflect the complexity of natural systems.

Omnivory is not the only module that has been shown to be consistently over-expressed within empirical webs, rather it is just one of the more well-studied ones. Actually, omnivory is one of thirteen possible unique three species subgraphs, termed motifs, all of which demonstrate consistent patterns of expression (e.g. Stouffer *et al.* 2007). Despite their predictability, whether these motifs are simply artefacts of community assembly, anachronisms of previous perturbations, or truly contribute to food web persistence is unclear. Frequency of a three species motif can be a network level property, however, they can also be used to quantify node and interaction-level metrics (e.g., Baker *et al.* 2015; Cirtwill & Stouffer 2015). For example, within a three species motif a species can be characterized by its frequency at each node. This is termed a species ‘role’ in the motif (e.g. Baker *et al.* 2015). Whether these node and interaction-level network metrics can be used to predict species and interaction persistence is an open question.

1.3 The effect of space

One aspect that both the classic empirical webs and the described food web models overlook, however, is that these communities are not closed communities of homogeneous mixtures of species. Organisms within and across communities experience their environments at vastly different scales (Holt 1993). Moreover, while studies of food webs typically describe networks as discrete entities within borders defined by landscape attributes, species interactions do not necessarily recognize these borders. For example, in a study of parasitism on California red scale insects, Snyder *et al.* (2005) demonstrated that it is only by recognizing different habitat boundaries that the coexistence of a parasitoid and an invasive pest is possible. In fact, while both species live on the same citrus trees, it is their difference in preferred microhabitats (stem vs leaf) which enables coexistence. This contrast becomes especially stark when we add an avian top predator to this system which may view the entire citrus grove as its preferred microhabitat.

The importance of space is well recognized. Patch occupancy meta-community models are one of the simplest spatial models for species, developed from Levin's meta-population model looking at the change in the number of patches occupied by a species based on colonization and extinction rates (Levins 1969). This simple model was expanded upon to incorporate a finite number of competing species and a trade-off between competition and colonization (Nee & May 1992; Tilman 1994). These meta-population models of competition were then extended to specialist predator-prey models, assuming that predators required unique prey to survive and thus, could only colonize patches with prey present (May 1994; Bascompte & Solé 1998). Somewhat predictably, these models demonstrated that specialist predators are driven to extinction by habitat loss before their prey. To consider generalist predators, an additional parameter accounting for the cost required for predators to colonize patches without the preferred prey was incorporated (see Swihart *et al.* 2001). Subsequently, the models have been expanded to include top predators (Melián & Bascompte 2002), and more recently, synthetic food webs (Gravel *et al.* 2016).

Indeed, the incorporation of a spatial dimension into classic questions such as competitor coexistence (Hanski 1981), species richness patterns (Cornell & Lawton 1992), and predator prey population cycles (see Briggs & Hoopes (2004) for a review) has resolved many discrepancies between theory and observation. Moreover, patch dynamics can be observed whereby the connector species provide recolonization-rescue effects for the linked populations (e.g. Holyoak *et al.* 2005). While studies examining the impacts of these spatial couplers are typically restricted to highly mobile top predators or species with complex life history (e.g. Woodward & Hildrew 2002; McCann *et al.* 2005; Rooney *et al.* 2008; McCoy *et al.* 2009), there is growing evidence that dispersal of lower-trophic level organisms may be just as important spatial couplers as these larger, higher trophic level species (see Pedersen *et al.* (2016) for a discussion of non-hierarchical dispersal). Perhaps more importantly though, these models all treat connectivity of patches as a global property, assuming that species ability to access a patch is conditional on its movement ability – for example, patches which are further away are less accessible for a species with poor dispersal ability. Connectivity of patches, however, is the interplay between species' specific properties like dispersal ability (e.g. Gounand *et al.* 2018; Guzman *et al.* 2019), but also how those species interact with their landscape (e.g. Baguette *et al.* 2013). For example, lake systems are only accessible for a highly mobile fish species if they are connected by rivers or streams, while a highly mobile bird species may be able to fly between them all. Overlooking the landscape, or abiotic controls, on species movement is neglecting an important piece of community dynamics.

1.4 Thesis Overview

My thesis combines bioinformatics and mathematical models to examine the environmental and ecological drivers of food web structure and dynamics. Overall, my thesis is one of the few examples of a project which merges empirical observations, module-scale theory, and dynamic whole food web models to examine food web persistence and stability across multiple scales.

In Chapter 2, I use a spatially expansive food web to examine drivers of spatial turnover in food web interactions across a large environmental gradient (1000s of kms). Here, I use beta-diversity metrics to determine the degree of spatial turnover in interactions and how this relates to underlying environmental gradients. I then use trait-based food web models to determine if species-specific traits can be used to predict these changes in interactions. Finally, I use a motif analysis to determine whether species roles are preserved across this spatial gradient. I demonstrate that predicting local realizations of community structure is very difficult, but suggest it is of paramount importance since environmental perturbations often occur at the local scale. Further, I demonstrate that despite the high spatial turnover in interactions, species' roles were highly conserved suggesting that while the players may be changing, the overall network structure is invariant.

In Chapter 3, I integrate empirical data and mathematical models to explore the consequences of both omnivory module type (including classic, multi-resource, trophic, mutual predation, and cannibalism) and omnivore-resource interaction type on food web persistence. I use six classic empirical food webs to contrast expression of these omnivory modules with stability of these different kinds of omnivory within a multi-species consumer-resource model module context. Finally, I determine if these predictions scale to whole food web results using a 50 species food web model. I demonstrate that the importance of omnivory depends on both the type of omnivory and the food-web within which it appears. And, crucially, I highlight the discrepancies between food web module predictions and whole food web predictions demonstrating that future work should thus integrate both module and whole food-web theory.

In Chapter 4, I use the same 50 species consumer-resource food web model to determine the importance of food-web structure on predicting whole network persistence. In particular, I determine if there are food web metrics related to whole food web persistence, and whether those properties translate to predictions of both species-level and interaction-level persistence. Despite the multitude of studies using these network metrics to distill food-webs into simpler statistics, it is not obvious whether these metrics actually impact food-web persistence. I highlight the incongruent relationships between network metrics and the persistence of different network components (i.e. whole community, individual species, and specific interaction). In particular, network metrics are sufficient predictors of community and interaction persistence, but poor predictors of species' persistence. Moreover, those metrics which are successful predictors of community persistence are not necessarily the best predictors of interaction and species persistence.

These previous two chapters have treated food webs as closed communities. Local systems are influenced by the movement of energy, materials, and species between local systems. In Chapter 5, I develop a mathematical framework to explore how abiotic features can influence metacommunity dynamics. Specifically, I demonstrate how movement is a product of both a species' ability to move and the landscape across which it moves. Treating patch connectivity as a species' specific property can drastically change our conclusions about multi-patch community stability.

Taken together my thesis makes a major contribution to spatial food-web theory and should help us predict changes to community structure as we progress into the Anthropocene. In particular, my thesis highlights the importance of scale. First, I demonstrate the inability of trait-based models to predict local community structure despite evidence to the contrary at the regional scale. And second, I demonstrate issues in developing unifying theory about the importance of structural features as we increase the scale of our theoretical explorations. In fact, food webs are collections of ephemeral interactions linked through space and time and, by ignoring this spatial context, I demonstrate that we risk mischaracterizing critical stabilizing features.

The associated data and R codes used in this thesis can be found in each chapter's data accessibility section.

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1.6 Co-authorship Statement

This thesis is the result of my independent research. The breakdown of contributions by each author is as follows:

Chapter 2: Effects of species traits, motif profiles, and environment on spatial variation in multi-trophic antagonistic networks

S. Leroux and I designed the project, Cindy Chu contributed the data, I conducted the analysis and S. Leroux and I wrote the manuscript. All of the authors provided feedback on analyses, interpretation of results, and edited the manuscript.

Chapter 3: The multiple meanings of omnivory influence empirical, modular theory, and whole food web stability relationships

S. Leroux and I designed the project, interpreted results, and wrote and revised the manuscript. I conducted the analyses.

Chapter 4: Multiscale analysis reveals incongruent relationships between network metrics and community, species, and interaction persistence in food webs

S. Leroux and I designed the project, I conducted the analyses. S. Leroux and I interpreted the results and wrote and revised the manuscript.

Chapter 5: Incorporating abiotic controls on animal movements in metacommunities

S. Leroux and I conceived of the project and analyses, interpreted results, and wrote and revised the manuscript. I conducted the analyses.

CHAPTER 2

Effects of species traits, motif profiles, and environment on spatial variation in multi-trophic antagonistic networks

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2.1 Introduction

Ecological networks can be very complex, characterized by closely-connected species and dense patterns of interactions (Montoya *et al.* 2006). Understanding the drivers of these interactions at multiple temporal and spatial scales is critical for predicting community structure and dynamics (e.g., Araújo and Luoto 2007, Morales-Castilla et al. 2015). One way of determining drivers of network variability is through measurements of network dissimilarity (e.g., Petanidou et al. 2008, Novotny 2009, Poisot et al. 2012). These analyses extend the use of β–diversity metrics (see review in Anderson et al. 2011) to investigate site-to-site variation in species' interactions (e.g., Novotny 2009, Poisot et al. 2012, CaraDonna et al. 2017). While studies of temporal turnover in interactions across seasons and years demonstrate that species interactions are ephemeral (Petanidou *et al.* 2008; MacLeod *et al.* 2016; CaraDonna *et al.* 2017), similar studies of spatial interaction turnover have been lacking (but see Trøjelsgaard et al. 2015, Poisot et al. 2017). Moreover, the spatial studies are focused primarily on bipartite networks involving plant-pollinator (Carstensen *et al.* 2014; Simanonok & Burkle 2014; Trøjelsgaard *et al.* 2015; Emer *et al.* 2018; Timóteo *et al.* 2018), host-parasitoid (Poisot *et al.* 2012; Baker *et al.* 2015), or consumer-resource (Novotny 2009; Lu *et al.* 2016; Kemp *et al.* 2017; Saavedra *et al.* 2017) systems leaving a gap, to our knowledge, in the study of spatial interaction turnover in multi-trophic, antagonistic (i.e. unipartite) networks.

The drivers of interaction turnover may not be that different from the drivers of β–diversity across large spatial or temporal gradients (e.g., Trøjelsgaard et al. 2015, CaraDonna et al. 2017) since one way interaction turnover can occur is through a change in species composition between sites resulting in novel interactions. But the patterns may be more complex, as interaction turnover (β_{INT}) is the additive result of two distinct processes; differential interactions due to changes in species composition between sites (β_{ST}), and site to site differences in realized interactions between species co-occurring at sites reflecting a rewiring of interactions between sites (β_{RW}; Petanidou et al. 2008, Novotny 2009, Poisot et al. 2012; see Bartley et al. (2019) for further discussion). Moreover, the two sub-components of interaction turnover (i.e., β_{ST} and β_{RW}) can combine to alter interactions between shared species in surprising ways. For example, in a comparison of lakes with and without invasive *Micropterus dolomieu* (smallmouth bass), Vander Zanden et al. (1999) found that the presence of smallmouth bass caused *Salvelinus namaycush* (lake trout) to shift their diet from 60% forage fish and 40% pelagic zooplankton to 20% forage fish and 80% pelagic zooplankton. Thus, a species invasion introduced new interactions between the invader and native species, but also caused native predators to shift prey resources (Vander Zanden *et al.* 1999). Both of these outcomes increase interaction turnover but arise from different mechanisms with different implications for forecasting the re-assembly of ecological networks under global change.

Community network structure arises through a combination of ecological drivers including random assortments of interactions proportional to species' abundances (Vázquez *et al.* 2009; Olito & Fox 2015; CaraDonna *et al.* 2017), species' trait mismatch (i.e., forbidden links; Olesen et al. 2011, Eklöf et al. 2013, González-Varo and Traveset 2016), and environmental constraints (Post *et al.* 2000). One of the more tangible consequences of global change is fluctuations in local trait distributions, potentially leading to the uncoupling of traits between species (e.g., Olesen et al. 2011, González-Varo and Traveset 2016) – a de-coupling which could be causing the rewiring of interactions across spatial gradients, potentially altering network structure and function. It has been recently demonstrated, however, that many mechanistic explanations of species' interactions are successful at predicting the summary statistics of networks (e.g., connectance), but fail to predict species-specific interactions (e.g., (Allesina *et al.* 2008; Vázquez *et al.* 2009; Olito & Fox 2015; Simmons *et al.* 2019). Studies testing mechanisms for interaction turnover rarely validate that their proposed mechanisms are correctly predicting observed interactions and thus, the observed similarity between empirical and predictive models of interaction turnover may be arising for the wrong reasons (Olito & Fox 2015). Moreover, the implications of this interaction turnover on local food web structure and function is rarely investigated.

Quantifying the importance of individual species to community structure and function is an essential aspect of ecology, especially when predicting community response to species extinctions (e.g., Lewinsohn and Cagnolo 2012). A promising approach for measuring this preservation of species' roles across networks is based on a species' configuration within three-species subnetworks, termed motifs (e.g., Stouffer et al. 2012). These three-species motifs consist of 13 possible recurring three node sub-graphs observed across a variety of networks from biomolecules to neural cells (see Milo et al. (2002) for more discussion). A recent study by Simmons et al. (2019) used a motif approach and demonstrated that it was significantly more effective at describing network structure than traditional network metrics. Further, when Baker et al. (2015) used this approach to measure the spatial and temporal variation in individual species roles in 22 host-parasitoid communities, they observed that despite a 50% turnover in species and a 70% turnover in interactions between years, species' roles were highly conserved. This demonstrates that, in this system, the fundamental network structure was resilient to turnover in species, reassembling to preserve fundamental roles. A more recent study of spatial plant-pollinator networks in the high arctic, however, demonstrated a substantial community turnover that was related to significant variation in species' roles (Cirtwill *et al.* 2018). Thus, which trend holds true for the turnover in interactions across spatial or temporal gradients in multi-trophic antagonistic networks remains to be tested. Consequently, a frontier in the study of ecological networks under global change is both understanding the discrepancy between the predictive accuracy of network properties (e.g., connectance, spatial turnover in interactions) and species-specific interactions (Vázquez *et al.* 2009; Olito & Fox 2015; Simmons *et al.* 2019) and how individual species roles are altered by interaction turnover Baker et al. (2015). Together they have the potential to improve the predictive capacity of our network models.

Here, we use a novel and spatially expansive freshwater fish-only food web data set (n = 129 lakes, 1094 km from south to north; Fig. 2.1) to quantify the spatial turnover in food web interactions, examine the environmental and ecological drivers for this turnover, and assess the implications on individual species' roles (see Fig. 2.2). Specifically, we examine (1) the relative contributions of interaction rewiring and turnover in top, intermediate, and basal species to overall spatial network turnover, (2) the potential environmental and ecological drivers of this turnover, including the relative and combined effect of abundance, phylogenetic relatedness, competition, thermal tolerance, and morphology on internal network structure, and (3) the implications of these changes by quantifying the fidelity of individual species' roles across networks.

2.2 Methods

2.2.1 Study area and data collection

Data were collected as part of the Broad-scale Monitoring Program run by the Ontario Ministry of Natural Resources and Forestry (Sandstrom *et al.* 2013). For this program, fish abundance and fish stomach content information was collected from 741 lakes across Ontario, Canada, between 2008 and 2012. For each lake environmental parameters including temperature profiles (°C), lake area (ha), mean depth (m), number of degree days above 5 °C, pH, and total phosphorus were measured in conjunction with fish sampling (see Appendix A.1). We used the fish stomach content information to build binary species interaction networks (where a 1 indicates the presence of an interaction and a 0, the absence) at both the individual lake and metaweb (i.e., food web of all fish only interactions observed in stomach content of fish from the 741 lakes) level.

Studies of spatial interaction turnover are robust to sampling effects when measured against the metaweb (Poisot *et al.* 2012), while other studies have shown that interaction turnover between sites may be more susceptible to sampling effort (Novotny 2009). Thus, we used rarefaction techniques to minimize sampling bias (see Appendix A.2). Ultimately, 129 lakes consisting of 30 different species and 1793 interactions met our criteria for inclusion. These criteria required lakes to have more than 5 observed interactions and a sampling effort sufficient to detect a minimum of 75% of the pairwise interactions occurring in each lake (S_{Obs}/S_{Chao1} x 100; see Fig. 1 for locations and Appendix A.2 for details on S_{Obs} and S_{Chao1}). In addition, we re-analyzed our data after removing the rare interactions (i.e., those interactions occurring once in a lake) to assess the influence of rare interactions on species interaction patterns (see Appendix A.3 for results with rare interactions removed).

2.2.2 Spatial interaction turnover

To quantify spatial turnover in food web interactions the relative contributions of interaction rewiring and turnover in top, intermediate, and basal species were calculated between all pairs of lakes (Fig. 2.2). Specifically, following Novotny (2009), we calculated species' interaction turnover between lake pairs using Whittaker's dissimilarity index:

$$\beta_{INT} = \frac{a+b+c}{(2a+b+c)/2} - 1 = \frac{b+c}{2a+b+c} \qquad (1)$$

where a is the number of interactions shared between lakes, and b and c are the number of interactions unique to Lake 1 and Lake 2, respectively. In this way, β_{INT} ranges from 0 (no turnover in interactions) to 1 (complete turnover in interactions). We can further differentiate β_{INT} into its two components, turnover in species involved in the interactions (β_{ST}) or rewiring of interactions between shared individuals (β_{RW}). The contributions of β_{ST} and β_{RW} to β_{INT} can be determined using similar methods laid out in Novotny (2009). In this way, both b and c, or those interactions unique to Lake 1 (b), or Lake 2 (c) can be broken down into their rewiring and species turnover components such that

$$b = b_{RW} + b_{ST} \qquad (2)$$

where b_{RW} represents the interactions unique to Lake 1 that are due to rewiring, and b_{ST} the interactions unique to Lake 1 that are due to species turnover (and similarly for *c,* those interactions unique to Lake 2). Note that this derivation of β_{ST} and β_{RW} differs from Poisot et al. (2012) in one critical way – our denominator (and that presented by Novotny (2009)) is always the total number of interactions observed, while the denominator in Poisot et al. (2012) varies depending on the metric being calculated. In this way we consider β_{ST} as interactions and are able to explicitly estimate the β_{ST} component of interaction turnover instead of inferring from β_{RW} and β_{INT}.

With this in mind, equation (2) can be re-formulated as:

$$\beta_{INT} = \frac{(b_{RW}+c_{RW})}{2a+b+c} + \frac{(b_{ST}+c_{ST})}{2a+b+c} \qquad (3)$$

And thus, interaction turnover (β_{INT}), can be considered the additive result of two distinct processes; (1) turnover in one or both of the species involved in the interaction (β_{ST}), or (2) rewiring of interactions between shared individuals (β_{RW}):

$$\beta_{INT} = \beta_{RW} + \beta_{ST} \qquad (4)$$

By partitioning β_{INT} in this way we are able to differentiate whether turnover in species interactions across lakes is driven by turnover in species composition ($\beta_{ST} > \beta_{RW}$), or due to rewiring of interactions between shared species ($\beta_{ST} < \beta_{RW}$). This allows us to determine if the co-occurrence of species is sufficient to assume an interaction ($\beta_{RW} = 0$), or if other environmental and species-specific factors influence turnover in species interactions between shared species ($\beta_{RW} > 0$).

Turnover due to changes in species composition, β_{ST}, can be further broken-down (see Novotny 2009, Simanonok and Burkle 2014, Trøjelsgaard et al. 2015):

$$\beta_{ST} = \beta_T + \beta_B + \beta_I + \beta_N \qquad (5)$$

Where the first three β_is are turnover due to only one interacting partner being present in one of the sites (novel basal (β_B), intermediate (β_I), or top (β_T) species), and β_N occurs when both interacting partners are found in only one of the sites.

2.2.3 Environmental drivers of spatial interaction turnover

The change in community composition over environmental gradients has been well studied (see Anderson et al. 2011 for detailed review). Few studies, however, have examined changes in species interactions over large spatial extents (Trøjelsgaard *et al.* 2015; Poisot *et al.* 2017). To determine the influence of environmental factors including latitude, area, mean depth, pH, morphoedaphic index (MEI), total phosphorus (TP), degree days above 5 °C (DD5), and species richness on interaction turnover across lakes (see Fig. 2), we first tested for collinearity (see Appendix A.4; Table A.4.3 for the Pearson correlation coefficients). We then used a permutational multivariate analysis of variance (perMANOVA) using distance matrices to examine the relationships between each β (i.e. β_{INT}, β_{RW}, β_{ST}, β_B, β_I, β_T, and β_N) and the full set of environmental variables (i.e. β ~ Latitude + Surface Area + Depth + pH + MEI + TP + Richness). We conducted these analyses both with and without highly correlated environmental variables (those with a correlation coefficient greater than $|0.35|$). There is no evidence to suggest an interaction between the environmental variables will improve fit (e.g., Dolson et al. 2009) and therefore we did not include interactions among variables in our models. We used the 'adonis' function in R package 'vegan' package in R (version 3.5.1) and 5000 permutations (Oksanen et al. (2018); see Appendix A.4 for parameter specific hypotheses).

2.2.4 Ecological drivers structuring interactions

Studies have shown that food web interactions can be predicted by a few trait dimensions (e.g., Eklöf et al. 2013). Therefore, we hypothesized that turnover in interactions across lakes could be due to ecological drivers including combinations of species abundances and trait-based explanations. We used a trait-based approach to see if lake and species-specific drivers could be used to explain lake-level realizations of the metaweb, and by extension, explain the large amount of interaction turnover across lakes. We tested that the following five ecological drivers structure fish interaction networks and that between-lake variations in these drivers may cause interaction turnover. *Abundance:* Neutral theory suggests that all species are ecologically equivalent and that ecological network patterns result from random interactions of individuals (e.g., Vázquez et al. 2009). Therefore, we predict that more abundant species will have a higher probability of interaction than rare ones.

Phylogenetic relatedness: It has been demonstrated that closely related species share similar traits determining trophic interactions. Further, it has been shown that the more similar species are the higher their likelihood of interaction (Cattin *et al.* 2004; Rezende *et al.* 2009). Therefore, we predict a high likelihood of interaction in closely related species.

Competition: Species with niche overlap will compete for shared prey species, and decrease the probability of interaction betweeen a predator and a shared prey. As such, coexistence of predators with shared prey should have increased competition for prey species. Therefore, we predict that the greater the number of co-existing predators the lower their probabilities of interacting with shared prey.

Thermal tolerance: Lakes are divided into distinct microhabitats distinguished by species-specific traits, such as thermal preference (e.g., Bartomeus et al. 2016). Depending on the temperature profile of the lake, the frequency with which a predator might overlap with different prey species will change (Bartomeus *et al.* 2016). Therefore, we predict that greater overlap in thermal optima between predator and prey species should lead to higher probabilities of interaction.

We developed a metaweb of species interactions using all observations of interactions across the 741 lakes in Ontario for which we had stomach content data. We used data from all 741 lakes to provide the most complete representation of the possible interactions observed from the empirical data.

We then constructed lake-specific interaction probability matrices or estimates of the probability of choosing a given interaction out of all possible species interactions within a lake. First, we subset the metaweb to include only lake-specific species to identify all potential feeding interactions within a lake, and then used the ecological drivers, and all possible combinations of these, to assign probabilities of observing each of these potential interactions (n = 32 combinations; Appendix A.5 for more details). Probabilities for all combinations of the five base ecological matrices were calculated by multiplying the respective base model species pair probabilities together. In this way, two species with high (low) probabilities of interacting in the respective base models will have a high (low) probability of interacting in the combination of these models (see Appendix A.5: Fig. A.5.5). This allowed us to determine the relative and combined role of each driver for describing the observed species interactions within lakes. Following Vázquez et al. (2009) and CaraDonna et al. (2017), we normalized the lake-specific probability matrices so that each matrix summed to one. This normalizing step was performed for all five base ecological models (e.g., abundance (A) or phylogenetic relatedness (P)) and all combinations of these base models (e.g., AxP, AxM, AxT; see Appendix A.5: Fig.

A.5.5). We also created a lake-specific null model based on the metaweb where equal interaction probabilities were assigned for all species found in the lake that interact in the metaweb.

We used these lake-specific probability matrices to generate 5000 predicted interaction matrices for each lake (1 indicates the presence of an interaction, 0 the absence and the likelihood of an interaction is directly related to its probability in the lake-specific probability matrix). To do this, we fixed the number of interactions occurring at each lake to the number of interactions observed, and fixed the species present at each lake to those sampled in the lake, and then sampled interactions without replacement. From these lake-specific predicted interaction matrices we calculated the specific True Skill Statistic (TSS; ranging from 1, perfect fit, to -1, inverted fit) and sensitivity value (proportions ranging from 0, poor fit, to 1, perfect fit). While we present results only for well-sampled lakes, we recognize that the absence of an interaction does not necessarily imply a true absence of that interaction in nature (see Bartomeus et al. 2016). The sensitivity values, however, allow us to avoid the problem of false absences when assessing model fit. We measure TSS and Sensitivity as:

$$TSS = \frac{(ux - vw)}{(u+w)(v+x)} \qquad (6)$$

$$Sensitivity = \frac{u}{u+w} \qquad (7)$$

where *u* are the interactions that were both predicted and observed to occur, *v* are the interactions which were predicted to occur, but observed absent, *w* are the interactions which were predicted to be absent, but observed to occur, and *x* are the interactions which were both predicted and observed to be absent. Because we are using stomach content data as evidence of interactions we only predict interactions for those species for which we have stomach content data (i.e., piscivorous species). This consideration makes the model simulations directly comparable to the observed data for each lake. Finally, by the nature of their construction, the interaction probability matrices over-estimate the prevalence of cannibalism (e.g. a species will completely overlap with its own thermal optima), thus we removed the possibility of cannibalism in our interaction probability matrices. There were 0.13 ± 0.34 cannibal interactions per lake (mean ± standard deviation), and thus not a major contribution to network structure.

2.2.5 Fidelity of species roles

Finally, we determined how interaction turnover influenced species' roles (Fig. 2.2). Following Kashtan et al. (2004) and Stouffer et al. (2012), we used the frequency with which each species in each lake was found at each position within three-species motifs to quantify species' roles in their networks (see Baker et al. (2015) for more discussion in a bipartite network). There are 13 possible unique motifs and 30 possible unique positions within these three-species motifs (Stouffer *et al.* 2012). We quantified species' roles by calculating the frequency, f_{ij}, that an individual species *i*, appears in each position *j*, within a lake normalized by that species' degree within that lake since species with a higher degree will have a larger value of f_{ij}. In this way, each species within a network is then represented by a vector $\overrightarrow{f_i} = \{f_{i1}, \ldots, f_{i30}\}$, which is henceforth referred to as the species' role.

We followed the methods outlined in Baker et al. (2015) and determined species' role conservation across lakes by performing a perMANOVA. Here, total dissimilarity D across all species and networks was calculated with:

$$D = \frac{1}{N} \sum_{i=1}^{N-1} \sum_{j=i+1}^{N} {e_{ij}}^2 \qquad (8)$$

where N is the total number of species' roles (across all species and lakes) and e_{ij} is the distance between role i and role j. The distance metric, e_{ij}, was calculated using the Bray-Curtis dissimilarity metric:

$$e_{ij} = 1 - F_{ij} \tag{9}$$

where F_{ij} is the sum of the lesser frequencies for only those motif positions shared between species' i and species' j.

Comparisons of species' roles across networks are determined by grouping species' roles by species identity and comparing across lakes. Thus, the within species' dissimilarity for any species k is determined by:

$$d_k = \frac{1}{g_k} \sum_{i=1}^{N-1} \sum_{j=i+1}^{N} {e_{ij}}^2 \, \delta_{ij|k} \tag{10}$$

where g_k is the total number of species' roles across all lakes, and $\delta_{ij|k}$ is Kronecker's delta (where $\delta_{ij|k} = 1$ if motif position k is shared between species' i and j and $\delta_{ij|k} = 0$ otherwise).

To test for significance, we conducted two randomizations to serve as null models. The first was a true randomization where species' identity within the lakes in which they occurred were randomly shuffled. This first randomization procedure can determine whether species' roles are more conserved than random but lend little more insight into why. The second randomization assumes that species with similar generality have similar species' roles. To this end, the second randomization kept species' generality constant and shuffled species' identities within lakes with those species with the same lake-specific generality. To determine overall significance of species' roles we compared observed D to the randomized D (D_{RAND} and D_{GEN}). We repeated each randomization 5000 times. Further, we compared the reshuffled d_k's (eq. 10) to the observed d_k's to determine which species contributed more, or less, to the observed variation in species' roles. Here, we directly compared the proportion of randomized d_k's that are of equal or greater similarity than observed empirically. All analyses were performed in R 3.5.1 (R Core Team 2017) and the data and code are provided (https://figshare.com/s/63db9179b0ec429e6b00).

2.3 Results

2.3.1 Spatial interaction turnover

Overall turnover in interactions across lakes (β_{INT}) ranged from 0 to 1 with a mean of 0.76 (Fig. 3). We further observed that turnover in species composition (β_{ST}, mean = 0.45) contributes more to β_{INT} than interaction rewiring (β_{RW}; mean = 0.31; Fig. 2.3), however, there was a lot of overlap between β_{ST} and β_{RW} demonstrating that for some lake pairs β_{RW} was a more important component of β_{INT} than β_{ST}. Further breakdown of β_{ST} into turnover of top, intermediate, basal, and novel components (β_T, β_I, β_B, and β_N) indicated that turnover in basal species (mean = 0.17) is the main component of β_{ST} followed by turnover in top species (mean = 0.14; Fig. 2.3).

2.3.2 Environmental and ecological drivers

Environmental variables explained less than 40 % of the variation in overall interaction turnover (β_{INT}), and the variables which explained the most variation were species richness, mean depth, and latitude (R^2 = 0.12, 0.12, and 0.06, respectively; see Table 1 and Appendix A.4: Fig. A.4.3). This was primarily due to the influence of environmental drivers on β_{ST} which explained almost 50% of the variation in interaction turnover due to changes in species composition. Again, this was driven primarily by depth, species richness, and latitude (R^2 = 0.17, 0.12, and 0.10, respectively; see Table

2.1). Rewiring (β_{RW}), however, was relatively unrelated to environmental drivers as they explained less than 10% of the variation, with only pH a significant predictor, ($R^2 = 0.03$ Table 1). The correlation analysis demonstrated that MEI and degree days greater than 5 °C were correlated with many other parameters (correlation coefficient > 0.35), while depth and total phosphorus were correlated (see Appendix A.4: Table A.4.3). Even after removing MEI, degree days, and total phosphorus from the model the above patterns held (see Appendix A.4: Table A.4.4).

While environmental variables do predict some of the variation in interaction turnover across lakes, there is still unexplained variation. Hence, we hypothesize that the sizeable turnover in interactions across lakes (Fig. 2.3) could be due to ecological drivers including combinations of species abundances and trait-based explanations. To that end we used a trait-based approach to see if lake and species-specific drivers could be used to explain lake-level realizations of the metaweb, and by extension, explain the large amount of interaction turnover across lakes. The five ecological drivers, abundance (A), phylogenetic relatedness (P), competition (C), thermal tolerance (T), and morphology (M), and any combination of these drivers, were poor predictors of species-specific interactions per lake (TSS < 0.23, Sensitivity < 0.39; Table 2.2). However, almost all ecological drivers performed better than the null model which had a TSS of 0.096 and a Sensitivity of 0.283. The exceptions were the competition model, both alone and in combination with phylogeny and morphology. Abundance, phylogeny, morphology and thermal tolerance combined was the best model (TSS of 0.220 and Sensitivity of 0.388), however, the addition of phylogeny, morphology, and thermal tolerance only had marginal contributions to the model which incorporated only abundance (TSS of 0.196 and Sensitivity of 0.365; Table 2.2).

2.3.3 Fidelity of species roles

The species-level perMANOVA analysis for both the random null model and the generality null mode demonstrated that species' roles explained a high amount of role variability across lakes compared to the null model (observed $D_W << D_{RAND}$ & observed $D_W << D_{GEN}$). These results are summarized in Figure 4, where the observed species' dissimilarity index is shown by a horizontal line, while the violin density plots are the null model results. Those species' which are significantly different from the null model results have a horizontal line significantly lower than the violin plots and are denoted by an asterisk. When examining how individual species contribute to overall species fidelity, we observed high role fidelity across all species with the exception of *Luxilus cornutus* (common shiner), *Ambloplites rupestris* (rock bass), *Lota lota* (burbot), and *Sander canadensis* (sauger*;* Fig. 2.4 a and c) compared to the random null model. These results differed for the generality null model where only seven species had observed species' roles significantly different from the null model (Fig. 2.4 b and d). Overall, these analyses suggest that species' roles in freshwater fish are highly conserved across the different lakes, but that these species' roles can be predicted, for some species, by their generality.

All results were qualitatively the same when rare interactions were removed (Appendix A.3: Table A.3.1, A.3.2, and Fig. A.3.1, A.3.2).

2.4 Discussion

We provide one of the first broad-scale assessments of spatial interaction turnover in multi-trophic antagonistic networks. We examine the relative and combined contributions of multiple ecological drivers and the environment to this turnover in a novel lake data set which spans over 1000 kms and includes over twice as many sites as the next largest spatial interaction turnover study (e.g., n = 51 in Poisot et al. (2017), n = 22 in Baker et al. (2015), and n < 20 in Carstensen et al. (2014)). Here, we find substantial interaction turnover across lakes with a larger contribution of interaction rewiring than previous bipartite food web studies (Novotny 2009; Kemp *et al.* 2017), but with the contribution of species turnover still as the primary driver. In addition, we find that most environmental variables were poor predictors of spatial interaction turnover and that the ecological drivers we considered were inadequate predictors of species-specific interactions per lake. Despite the substantial turnover in interactions observed across lakes we found that species maintain high fidelity to their fundamental roles. This preservation of species' roles, especially given the large spatial extent of our study, demonstrates that despite prey switching by predators specific network structures are maintained. In many cases, species' roles are constrained by species' generality illustrating the potential power of combining functional guilds with network models to predict local community structure.

Quantifying spatial turnover in species interactions enables us to better understand the dynamic nature of food webs across space, especially since historically, feeding interactions have been considered invariant, particularly within the same habitat type and geographic region (e.g., Morris et al. 2014). We observed a high degree of interaction turnover across lakes. The spatial interaction turnover we report ($\beta_{INT} = 0.76$) is, on average, lower than recent studies of spatial turnover in bipartite mutualistic networks (e.g., mean β_{INT} ~0.9 in Trøjelsgaard et al. (2015), mean ~ 0.95 in Simanonok and Burkle

(2014) and other studies of spatial turnover in bipartite antagonistic networks (e.g., mean β_{INT} ~ 0.85 in Novotny (2009) and mean β_{INT} ~ 0.97 in Kemp et al. (2017). Consequently, current evidence suggests that overall interaction turnover may be lower in multi-trophic networks than bipartite networks, but is far from invariant as previously suggested (Morris *et al.* 2014). When β_{INT} was deconstructed into β_{ST} and β_{RW}, β_{ST} contributed more to β_{INT} than β_{RW} (mean 0.45 and 0.31, respectively; Fig. 3) as has been shown in other studies of bipartite food webs. However, in the bipartite food webs studied by both Novotny (2009) and Kemp et al. (2017), the contributions of β_{RW} were much lower (0.08 for both) than what we observed. This suggests that consumers in our study system demonstrate greater flexibility in prey choice than those in bipartite webs where herbivores demonstrate high resource fidelity (Kemp *et al.* 2017). Species turnover in plant-herbivore networks also fluctuate according to strong environmental signals (e.g. Renner and Zohner 2018). The three-dimensional nature of aquatic systems, especially large bodies of water like lakes, buffers against these effects to some extent and gives species time to access suitable habitats seasonally while remaining part of the broader community. The seasonal shifts that fish may experience due to these environmental changes (e.g., changes in depth preference due to changes in thermal profile) may be at a finer scale than our sampling methods could detect. Thus, while some of the interaction turnover is interpreted as rewiring, it may be due to species turnover at a micro-scale.

One potential explanation for the observed turnover in interactions is the underlying environmental gradients. Interaction turnover across lakes was significantly correlated with some environmental gradients, and for most of the environmental gradients we considered there was a significant relationship with at least one component of turnover except for surface area which was never a significant predictor. Depth was a significant predictor for both β_{INT} and β_{ST} ($R^2 = 0.12$ and 0.17, respectively; see Table 2.1 and Appendix A4: Fig. A.4.3), but a poor predictor for β_{RW}. This contrasting influence of environmental drivers on different components of interaction turnover highlights the need for caution when predicting the impact of environmental change on species interactions. For example, pH has been shown to correlate positively with many structural aspects of food webs including food web size, linkage density, and complexity (Layer *et al.* 2010). Here, we see that while pH is a significant predictor for turnover in interactions, it is positively correlated with turnover in interactions due to species turnover, but negatively with rewiring (see Appendix A4: Fig A.4.3) suggesting that the positive correlation between pH and food web complexity is due primarily to new species entering the food web. For example, Kortsch et al. (2015) demonstrated that the poleward movement of generalist predators in response to a changing climate within the Barents Sea has led to significant topological changes within both the pelagic and benthic food webs. Thus, uncovering the implications of rewiring due to novel species on the stability of communities is ripe for empirical investigation – particularly as the effect of global change increases.

Beyond the influence of environmental gradients, the propensity of species to interact given trait overlap is widely recognized to be an important driver of ecological network structure (e.g., Olesen et al. 2011, Eklöf et al. 2013, Morales-Castilla et al. 2015). For example, freshwater fish are predominantly gape limited, consuming prey within an optimal body size in relation to their size to obtain the most energy for the lowest cost (e.g., Woodward et al. 2005). And, evidence suggests that a single trait can sufficiently reproduce ecological network structure (e.g., Petchey et al. 2008) and that only a few traits are needed to successfully predict specific species' interactions (Eklöf *et al.* 2013). Encouragingly, our comparisons between ecological traits and the null model did demonstrate that the ecological drivers improved predictions relative to a null model due to the importance of species abundance on trophic interactions. However, despite evidence suggesting the importance of the traits we modeled in determining food web interactions (i.e. phylogenetic relatedness (e.g., Rezende et al. 2009, Stouffer et al. 2012), competition (e.g., Violle et al., 2011), overlap in thermal tolerance (Bartomeus *et al.* 2016) and morphological matching (e.g., Woodward et al. 2005)), our best model (AxMxPxT, TSS of 0.22) had lower success in predicting observed and unobserved interactions (i.e. lower TSS) than those reported elsewhere in the literature. For example, a study of the influence of predator-prey body size relationships on food web structure Gravel et al. (2013) report TSS values ranging from 0.13-0.76, depending on the food web data set used. Likewise, a study of the influence of traits on food web interactions in ground beetles, Brousseau et al. (2018) reported TSS values ranging from 0.1 – 0.65, depending on the model used. Studies attempting to reproduce ecological network structure from traits, however, typically use highly resolved networks encompassing large regional networks (e.g., Allesina et al. 2008, Eklöf et al. 2013). In our case, that would mean predicting the highly resolved metaweb of interactions across all of our lakes, instead of the local lake level. Traits are doubtlessly important for describing species' interactions at a local-scale; however, they may need to be refined from the resolution required for the aforementioned studies. For example, the traits used in this study are typically described at a population, or lake-specific level. This is due, in part, because sampling at an individual level is difficult to do in a survey of this size. However, it means that we are neglecting the contribution of intraspecific variation in these traits which has been shown to be very important in maintaining species coexistence and community structure (see review in González-Varo and Traveset 2016).

In fact, the poor predictive ability of our traits at the local scale suggests that, at least in our study system, a few traits may not be sufficient to predict local realizations of food webs. Instead, which traits are sufficient to predict interactions at such a fine scale are likely species' and location dependent. For example, for a cold-tolerant species such as Brook Trout, overlap in thermal optima may drive interactions at the edges of their range while morphology may drive interactions near the centre. Moreover, the results from the environmental drivers of interaction turnover demonstrated a correlation between environmental drivers and interaction turnover suggesting that synergistic effects of both environmental and ecological drivers may be responsible for local realizations of these regional food webs. Indeed, a recent study by Joffard et al. (2019) outlined a promising technique to study such synergistic effects. Environmental and ecological perturbations are realized at a local scale and thus, reconciling the differences in the predictive capacities of ecological network models at both local and regional scales is paramount for anticipating species-specific responses to change. For example, climate warming could shift habitat utilization by species' highly sensitive to temperature and thus substantially alter network topologies. In a recent study, Guzzo et al. (2017) demonstrated that lake trout in a pristine lake shift habitat utilization in response to yearly fluctuations in temperatures, changing prey types, and in turn, reducing energy acquisition by this top predator.

The consequences of spatial variation in species-specific interactions on individual species are not immediately apparent. Our evidence for the preservation of fundamental species' roles across the large spatial extent of the study, despite high turnover in interactions across lakes, suggests flexibility in prey choice whereby predators select prey species which maintain stabilizing network structures (Fig. 2.4). This is further supported by the large contribution of basal turnover (β_B) to β_{ST} suggesting that predators show high flexibility in prey selection. These findings are similar to those observed by Baker et al. (2015), which demonstrated the resilience of fundamental network structure despite substantial turnover in species in a host-parasitoid system and provided evidence for the reassembling of networks to preserve fundamental roles. Moreover, the preservation of species' roles suggests that the prediction of species interactions could be improved by optimizing predicted interactions based on the over and under expression of different motif profiles (e.g., Bascompte and Melián 2005) to preserve species roles. Using a second null model based on lake-specific species' generality demonstrated that in over half the cases generality could refine predictions of species' roles. Those species which showed significant conservation of their role, however, encompassed the entire range of generality seen in our study. Examining how species' functional guild influences species' roles could provide incredibly useful in predicting local realizations of regional food webs especially if ecological networks truly have a common structural backbone (Bramon Mora *et al.* 2018).

We provide a comprehensive study of spatial turnover in multi-trophic antagonistic freshwater food webs. Despite high overall turnover in interactions across lakes, we demonstrate that ecological drivers are poor predictors of species-specific interactions per lake, but that species' roles are highly conserved across the study region. Our findings demonstrate that incorporating species' fundamental roles into predictive food web models may be essential to improving our predictions of ecological networks at local scales; which is instrumental to anticipating the restructuring of ecological communities as we progress in the Anthropocene.

2.5 Data Accessibility

All data and R code are available on figshare: https://figshare.com/s/63db9179b0ec429e6b00. Due to data privacy issues the fish body size data is not available.

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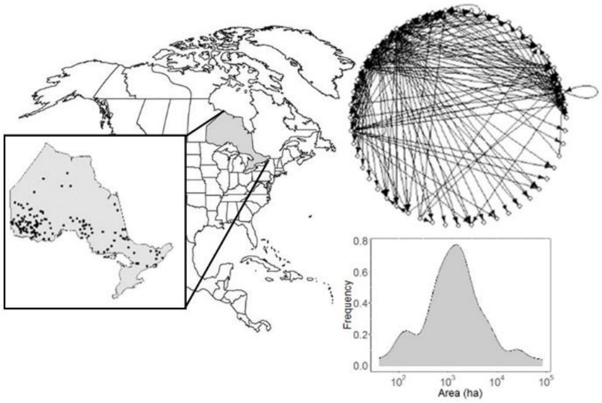

Figure 2.1 Distribution of lakes collected by the Broad-scale Monitoring Survey conducted across Ontario, each highlighted lake is one of the 129 lakes examined, the complete metaweb of species interactions where each circle is a species and each line is an interaction (arrow points from predator to prey), and a density plot of areas (ha) of the study lakes.

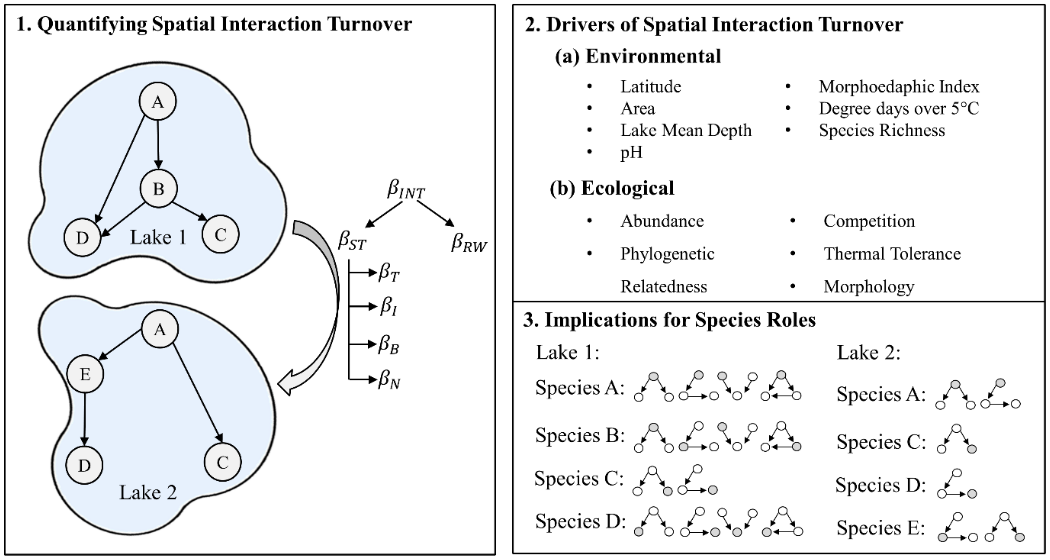

Figure 2.2 Conceptual diagram of analyses of lake food webs. (1) Spatial turnover in interactions across lakes (βINT = 1 in the diagram above) is quantified using Whittaker's dissimilarity index, which is the summation of the turnover in interactions due to rewiring of interactions between species common to both sites ($\beta_{RW} = 0.29$) and the turnover in interactions due to change in species compositions ($\beta_{ST} = 0.71$), which can be further compartmentalized into turnover driven by changes in predator species ($\beta_T = 0$), intermediate species ($\beta_I = 0.71$), prey species ($\beta_B = 0$), and both predator and prey species ($\beta_N = 0$). Here, light grey circles with letters indicate unique species. (2) The contributions of both environmental and ecological drivers to spatial interaction turnover are calculated. (3) The implications of spatial turnover on individual species is determined by examining the fidelity of species roles as measured by their frequency in unique positions of three-species motifs, indicated by light grey circles.

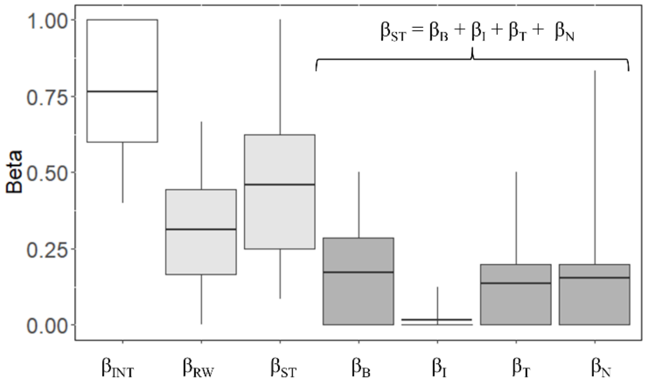

Figure 2.3 Comparison of each interaction turnover component where error bars represent 95% confidence intervals, boxes represent interquartile range, and middle line represents overall mean. Here, βINT represents the overall turnover in interactions between lakes, β_{RW} the turnover in interactions between lakes due to rewiring of the interactions between co-occurring species, β_{ST} the turnover in interactions between lakes due to species turnover, β_T the turnover in interactions due to changes in top species, β_I the turnover due to changes in intermediate species, β_B the turnover due to changes in basal species, and β_N turnover due to changes in both predator and prey species. The grey shading delineate what component of turnover the βs contribute to since $\beta_{INT} = \beta_{RW}+ \beta_{ST}$ and $\beta_{ST} = \beta_T+ \beta_I+ \beta_B+\beta_N$. See Appendix A.3, Fig. A.3.1 for the equivalent figure after the removal of rare interactions.

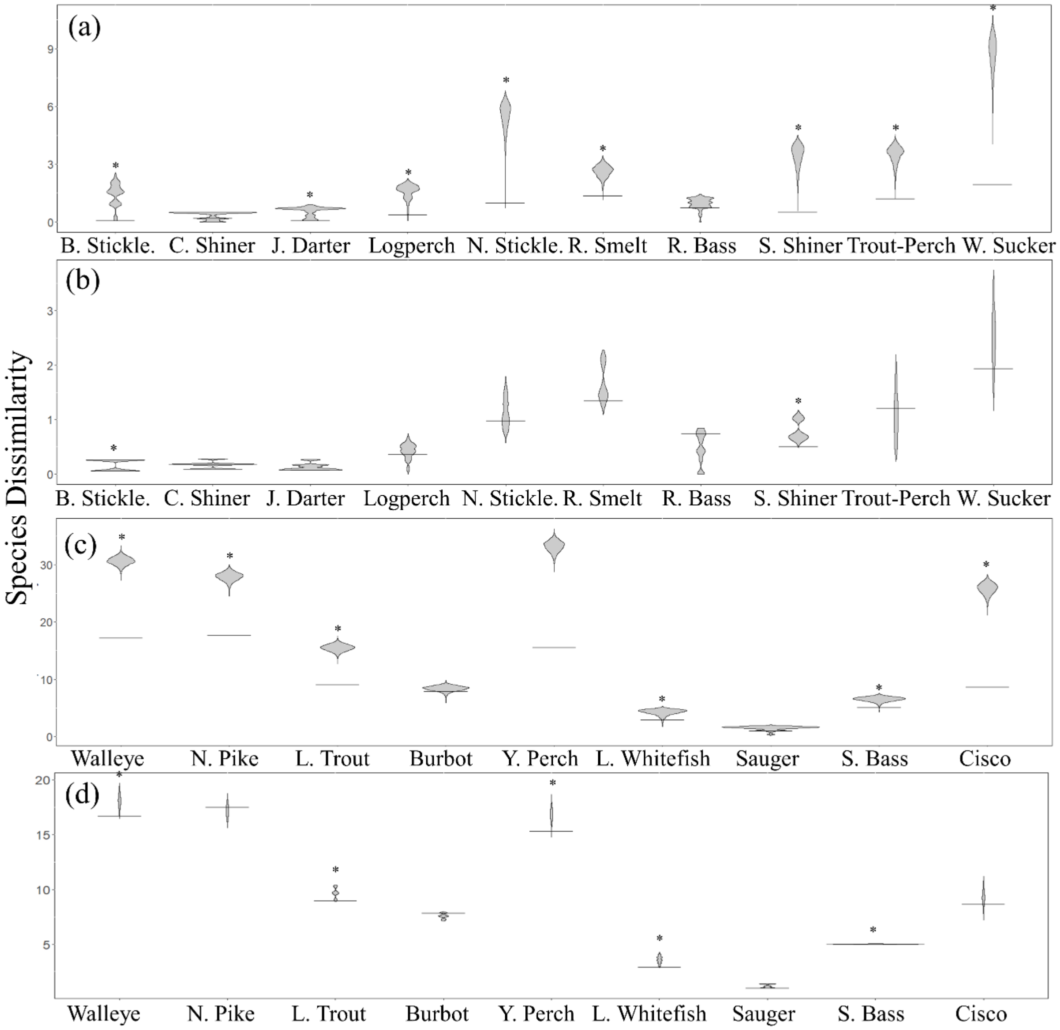

Figure 2.4 Species-specific dissimilarity (dk) index comparing conservation of species' roles between networks for (a & b) prey species, and (c & d) predator species where horizontal lines indicate the observed species dissimilarity index, violin plots show the results of the randomization of species roles, and (*) indicate species for which the observed species dissimilarity index was less than the randomization 5% of the time. Finally, (a & c) represent the random null model results while (b & d) represent the generality null model results. Species' names have been abbreviated with B. Stickle representing brook stickleback, C. Shiner is common shiner, J. Darter is johnny darter, N.

Stickle is ninespine stickleback, R. Smelt is rainbow smelt, R. Bass is rock bass, S. Shiner is spottail shiner, W. Sucker is white sucker, N. Pike is northern pike, L. Trout is lake trout, Y. Perch is yellow perch, L. Whitefish is lake whitefish, and S. Bass is smallmouth bass. Note: here we classify prey species as those species for which we do not have stomach content analyses for since this is a multi-trophic system and all predators are also prey in some cases. See Appendix A.3, Fig. A.3.2 for the equivalent figure after the removal of rare interactions.

Table 2.1 The results from a perMANOVA with distance matrices with 5000 permutations on different community interaction turnover metrics and environmental parameters. Here, values represent adjusted R2s where bolded values indicate $p < 0.05$. The environmental parameters are all lake specific values where TP stands for total phosphorus, and DD5 stands for degree days above 5 °C. The community interaction turnover metrics are defined as follows: β_{INT}: overall interaction turnover between lakes, β_{RW}: turnover in interactions between lakes due to rewiring of interactions between shared species, β_{ST}: turnover in interactions between lakes due to species turnover between lakes, and sub-components of β_{ST}, specifically β_T: turnover in interactions between lakes due to novel top species, β_I: turnover in interactions between lakes due to novel intermediate species, β_B: turnover in interactions between lakes due to novel basal species, and β_N : turnover in interactions between lakes due to both novel predator and prey species (see Appendix A.3, Table A.3.2 for the equivalent table after the removal of rare interactions).

Parameter	β_{INT}	β_{RW}	β_{ST}	β_B	β_I	β_T	β_N
Latitude	**0.063**	-0.042	**0.105**	**0.137**	-0.039	**0.040**	**0.040**
Area	0.008	-0.007	0.013	0.015	-0.013	0.010	0.002
Depth (mean)	**0.116**	-0.046	**0.168**	-0.089	**0.244**	**0.254**	**0.129**
pH	**0.028**	**0.031**	**0.028**	**0.050**	-0.023	-0.012	**0.056**
MEI	0.011	0.022	0.007	0.021	-0.094	**0.051**	-0.016
TP	**0.012**	-0.008	**0.030**	-0.014	0.096	0.011	**0.076**
DD5	**0.024**	0.018	**0.032**	**0.047**	0.038	-0.074	**0.127**
Richness	**0.123**	0.123	**0.121**	0.109	-0.070	0.070	**0.195**

Table 2.2 Results from the Monte Carlo process used to generate lake-specific interactions based on five base ecological interaction probability matrices and all subsequent combinations of those five base ecological models (see Appendix A.3, Table A.3.1 for the equivalent table after the removal of rare interactions).

Model[a]	TSS[b,c]	Sensitivity[d]
AxMxPxT	0.219 (0.142)	0.388 (0.112)
AxPxT	0.214 (0.168)	0.383 (0.132)
AxT	0.211 (0.169)	0.380 (0.132)
AxMXT	0.211 (0.168)	0.380 (0.132)
CxAxMxPxT	0.201 (0.141)	0.372 (0.111)
AxP	0.200 (0.189)	0.368 (0.148)
AxMxP	0.199 (0.188)	0.368 (0.147)
A	0.196 (0.189)	0.366 (0.148)
AxM	0.195 (0.189)	0.365 (0.147)
CxAxPxT	0.192 (0.164)	0.365 (0.129)
CxAxT	0.189 (0.165)	0.362 (0.130)
CxAxMxT	0.188 (0.165)	0.361 (0.129)
CxAxP	0.175 (0.185)	0.348 (0.145)
CxAxMxP	0.175 (0.185)	0.348 (0.144)
CxA	0.171 (0.186)	0.345 (0.145)
CxAxM	0.171 (0.185)	0.345 (0.145)
MxPxT	0.147 (0.210)	0.326 (0.165)
PxT	0.145 (0.210)	0.324 (0.164)
MxT	0.141 (0.211)	0.321 (0.165)
T	0.139 (0.211)	0.319 (0.165)
CxMxPxT	0.116 (0.205)	0.301 (0.160)
CxPxT	0.115 (0.205)	0.299 (0.160)
CxMxT	0.111 (0.205)	0.296 (0.160)
CxT	0.109 (0.205)	0.295 (0.160)
MxP	0.102 (0.231)	0.288 (0.177)
P	0.100 (0.231)	0.286 (0.177)
M	0.096 (0.229)	0.283 (0.176)
Null	0.096 (0.230)	0.283 (0.176)
CxMxP	0.072 (0.223)	0.264 (0.171)
CxP	0.071 (0.222)	0.263 (0.170)
CxM	0.068 (0.221)	0.261 (0.169)
C	0.066 (0.221)	0.259 (0.169)

[a] Letters indicate the interaction probability matrices used based on abundance (A), phylogenetic relatedness (P), competition (C), thermal tolerance (T), and morphology (M).

[b] TSS values demonstrate overall model accuracy between the Monte Carlo process and the observed interaction matrices for each lake

[c] Standard deviations for both TSS and Sensitivity are in brackets

[d] Sensitivity assesses model fit of only interactions which are observed present

CHAPTER 3

The multiple meanings of omnivory influence empirical, modular theory, and whole food web stability relationships

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3.1 Introduction

Recent studies have highlighted the importance that the specific placement of key interactions might have on stabilizing food web dynamics (termed keystone interactions; sensu Kadoya, Gellner, & McCann, 2018) (McCann *et al.* 1998; Neutel *et al.* 2002). Theoretical explorations of trophic modules (called modular theory, hereafter) have identified omnivorous interactions, defined as a consumer feeding on more than one trophic level (Pimm & Lawton 1978; McCann *et al.* 1998; Gellner & McCann 2011), as a possible candidate for these keystone interactions. Whether the stabilizing effect of the omnivore-resource interaction in modular theory is maintained within a complex, whole food web context is unclear, but a growing area of research (Borrelli, 2015; Kondoh, 2008; Stouffer & Bascompte, 2010).

Understanding the effect of omnivorous interactions in whole food webs is complicated by the contrasting definitions of omnivory. For example, while modular theory has highlighted the stabilizing effect of omnivory (e.g. Gellner & McCann, 2011; Holt & Huxel, 2007; McCann et al., 1998), these theoretical modules typically only consider the case where an omnivore and consumer compete for a shared resource, normally a primary producer (called classic omnivory hereafter; e.g. McCann & Hastings, 1997; Fig 3.1a). While examples of classic omnivory are common in nature, the literature is also replete with empirical examples of omnivores and consumers competing for higher trophic level resources (called trophic omnivory hereafter; see Fig. 3.1b). Examples of trophic omnivory range from incidences involving aquatic top predators like *Esox lucius* (northern pike) and *Sander vitreus* (walleye) (e.g. Post *et al.* 2000) to common avian species like *Corvus corax* (ravens; e.g. Kissling *et al.* 2012). Moreover, classic omnivory requires competition between the omnivore and consumer for a shared resource, yet there are many empirical examples where this competition for a resource is absent. For example, ecosystem integrators such as both *Ursus americanus* and *Ursus arctos* (black and grizzly bears, respectively) consume both fish and berries (called multi-resource omnivory, hereafter, but note that it is similar to different-channel omnivory described in Polis (1991); Fig. 3.1c; e.g. Welch *et al.* (1997); see Kratina *et al.* (2012) for more specific examples). Finally, two further cases of omnivory modules outside the classic omnivory module definition are mutual predation, whereby the consumer also feeds upon the omnivore (Fig. 3.1d), and cannibalism - both of which are rarely examined in empirical or theoretical work (Fig. 3.1e; but see Martinez 1991; Palomares & Caro 1999; Rudolf 2007). Theoretical explorations, however, seldom consider these alternatives to classic omnivory, leaving empirical work to draw tenuous parallels between the expression of omnivory in natural communities and theoretical predictions based on classic omnivory alone.

Even if the presence of an omnivorous interaction, irrespective of the type of omnivory module, is sufficient to stabilize trophic modules, these results may not scale to the whole food web context. Indeed, theoretical studies have demonstrated that even the presence of a single additional species, such as the presence of an alternative resource or a top predator, are sufficient to alter the stability of these food web modules (e.g. Holt & Huxel 2007; Hall 2011). These results beg the question of what happens when these modules are embedded within a whole food web context. One of the few studies examining how the presence of omnivory modules within a broader food web context influences food web persistence showed that increasing the number of trophic and classic omnivory modules increased the persistence of whole food webs (Stouffer & Bascompte 2010). This study, however, does not include broader omnivory module types, or quantify the incidence of the omnivore-resource interactions, the very component of the classic omnivory module which is proposed by modular theory to be the stabilizing component.

Here, our objectives are three-fold. First, we explore the prevalence of omnivory within empirical food webs by quantifying both the expression of a broad range of individual omnivory modules and the number of each specific type of omnivore-resource interaction across the food webs (see Fig. 3.1 for types of omnivory). Second, we determine the influence of omnivory on trophic module stability and persistence and third, we examine how these modular theory conclusions scale to a broader whole food web context. Through the integration of empirical food web data, modular theory, and whole food web models we demonstrate that not all omnivore-resource interactions act to stabilize food webs, but rather their influences are dependent on both the module type and the food web in which they are nested. Our analysis suggests that the type of keystone interaction and the scale of analysis (i.e., modular vs whole food webs) may be fundamental to uncovering general relationships between interaction diversity and food web stability.

3.2 Methods

3.2.1 Expression of omnivory modules in empirical food webs

One way of exploring the importance of omnivory in food webs is by determining its prevalence in nature. While the presence of omnivory has been reported across food webs (e.g. Menge & Sutherland, 1987; Polis, 1991), studies determining the frequency of omnivory have differed widely in approach. For example, one study counted the number of omnivores observed (Dunne *et al.* 2004), while others compared the number of individual species in each classic or trophic omnivory module to a random null model (e.g. Arim & Marquet 2004), and still others quantified the number of times the combined classic and trophic omnivory module were expressed within food webs (Bascompte & Melián 2005). Theory suggests, however, that it is the omnivore-resource interaction which stabilizes tri-trophic food chain dynamics, and as such, the omnivore-resource interaction should be over-expressed in empirical food webs (McCann *et al.* 1998; Neutel *et al.* 2002; Gellner & McCann 2011). Thus, instead of comparing the number of omnivores observed, which underestimates the prevalence of the omnivore-resource interactions (Fig. 3.1f), or comparing the number of times the omnivory module is observed, which over-estimates the number of omnivores (Fig. 3.1g), we should be expressly quantifying the prevalence of omnivore-resource interactions within these empirical webs.

To determine the expression of both omnivory modules and omnivore-resource interactions we calculated the number of omnivory modules and the number (and type) of omnivore-resource interactions observed in six high quality, binary food webs from a variety of ecosystems. The six food webs were and their sources were Benguela (Yodzis 1998; Brose *et al.* 2005), Caribbean (Bascompte *et al.* 2005), Weddell Sea (Brose *et al.* 2005), and Ythan Estuary (Cohen *et al.* 2009), Silwood Park (Memmott *et al.* 2000), and St Mark's Seagrass (Baird *et al.* 1998). The latter were both obtained from http://cosinproject.eu/extra/data/foodwebs/WEB.html. We then compared the observed number of omnivory modules and omnivore-resource interactions to null model re-creations of the food webs. The results depend on the null model used to generate the food web randomizations, so we used the same four null models presented in Bascompte & Melián (2005) (see Stouffer *et al.* (2007) and Baiser *et al.* (2016)); the local rewiring algorithm, the niche model, the nested hierarchy I model, and the nested hierarchy II model (see Appendix B.1 in Supplemental Information). In this way, the local rewiring algorithm acts as a random model since it is not based on any biological assumptions, however, does fix the degree (or the number of interactions each species participates in) of each species. The three other models impose more realistic biological constraints in order to better emulate network structure. The niche model uses the biological constraint that species' can be sorted along a single dimension to build a network within this hierarchy whereby predators can only consume prey from those species whose rankings are within a specific niche range of the predator. This model has been shown to be capable of predicting many topological network properties (Williams & Martinez 2000). One of the critiques of the niche model is that it assumes a contiguity of predator diets without any gaps. These gaps, however, have been demonstrated to be pervasive in food webs (Cattin *et al.* 2004). Thus, the nested-hierarchy model was developed to take an evolutionary perspective, building in phylogenetic constraints and adaptation into the base niche model (Cattin *et al.* 2004). This model was further altered to attempt to capture spatial aggregation of consumers that share prey (see Bascompte & Melián, (2005) for more details on this). There are many additional null models which we could have used. We chose these three biologically realistic models because they perform well at predicting different food web metrics (Williams & Martinez 2008), are computationally less intensive, and require only binary interaction matrices. We created 5000 food web randomizations for each null model and each of the six observed food webs. We then compared the frequency of each omnivory module normalized by the total number of modules observed in that food web randomization in a similar manner to Borrelli, (2015) and Stouffer et al., (2007). In this way the adjusted frequency of a module k's observation (p_k) is equal to $\frac{f_k}{\sum_m f_m{}^2}$ where f_k is the frequency of the module (k) and f_m is the frequency of the m other types of omnivory, and the three other most commonly observed food web modules: tri-trophic food chains, apparent competition, and exploitative competition (Bascompte & Melián 2005; Stouffer *et al.* 2007). If the number of omnivory modules or omnivore-resource interactions observed in the empirical web is more (less) than 97.5% (2.5 %) of the null model generations it was classified as over (under) –expressed.

3.2.2 Persistence and stability of omnivory modules

We explored theoretical predictions for the impact of omnivory on the stability of our five types of omnivory modules (Fig. 3.1). We used a multi-species consumer-resource model (Yodzis & Innes 1992) to simulate the dynamics of species biomass over time. The food web module interaction structure is assigned specifically to depict the 2-4 species modules being explored and the species biomass model is parameterized as in previous studies (e.g. Brose, Williams, & Martinez, 2006; Stouffer & Bascompte, 2010; Williams, 2008; see Appendix B.2 in Supplemental Information).

Previous studies have evaluated the impact of omnivore-resource interaction strength on trophic module persistence and stability, where interaction strength included both consumer preference, and the biomass of the consumer and all its prey items (e.g. McCann et al., 1998). Interaction strength, however, is a term fraught with conflicting meanings and very difficult to measure in the field (see Berlow et al., 2004) which is important for empirical tests of ecological theory. For the rest of this study we define interaction strength, w_{ij}, as the relative inverse attack rate of predator i on prey j. In the modular theory case, i is either the omnivore (O) or the consumer (C), and j can be a consumer (C) or resource (R). This definition of interaction strength is similar to previous studies by Montoya & Solé (2003), Stouffer & Bascompte (2010) and Gellner & McCann (2016) as this measure of interaction strength is easy to measure in the field (see Berlow et al., 2004) and easier to scale to broader whole food web models of persistence than those which account for species' biomass (see Stouffer & Bascompte, 2010).

For each module we built on the binary omnivory modules (see Figure 3.1 a-e) by allowing the omnivore-resource interaction strength (w_{OR}, or w_{OC} in the case of trophic omnivory) to vary from 0 to 1, while the equivalent of the omnivore-consumer interaction strength (i.e. omnivore-predator in the case of trophic omnivory or consumer-consumer in the case of cannibalism) is the inverse (e.g. $1 – w_{OR}$). The remaining interaction strengths present in each module are fixed at one.

Just as ecological literature is replete with definitions of interaction strengths, there are also many ways of defining food web persistence and stability (see review in Donohue et al., 2016; Ives & Carpenter, 2007). In this study, a module persists when all species within the module maintain biomass greater than 10^{-30} over the 5000 time steps. We define stability based on the eigenvalues of the Jacobian matrix where modules were homogeneously stable if the real parts of all eigenvalues were less than zero, monotonically stable if they were real numbers, had damped oscillatory dynamics if they had imaginary parts, and otherwise the module exhibits oscillatory or unstable dynamics.

This allows us to determine what interaction strengths are required for both persistence and stable persistence.

3.2.3 Influence of omnivory modules on whole food web persistence

From a theoretical standpoint these two to four species modules are attractive because they are more mathematically tractable offering researchers the opportunity to analyze the systems of differential equations analytically instead of numerically. However, there are far fewer studies determining how these modules interact on a larger scale within broader food web contexts (but see Kondoh 2008; Stouffer & Bascompte 2010; Gellner & McCann 2016; Monteiro & Del Bianco Faria 2017; Kadoya *et al.* 2018). Thus, we used the same multi-species consumer-resource model (e.g. Yodzis & Innes 1992; Williams 2008) described earlier to simulate the dynamics of species' biomass over time and determine the impact of the presence of omnivory modules and omnivore-resource interactions on whole food web persistence. This food web model explicitly incorporates the nonlinearities and the non-equilibrium conditions present in natural ecosystems (Williams & Martinez 2004; Martinez *et al.* 2006). As a result, when scaled up to complex communities this model predicts the persistence and non-persistence stable, cyclic, and chaotic individual population behaviours (Williams & Martinez 2004; Brose *et al.* 2006). Here, we relied on food web persistence, commonly called community stability in other studies of complex food webs, which allows us to consider a range of dynamics including cycles and chaos (e.g. Brose *et al.* 2006; Martinez *et al.* 2006; Kondoh 2008; Stouffer & Bascompte 2010).

To scale the module theory to whole food webs, we created food webs with 50 species and a directed connectance (C) of C ∈ {0.1, 0.15, 0.2} which is within the range typically observed in empirical food webs (Pascual & Dunne 2006). We assigned food web interaction structure using the niche model (Williams & Martinez 2000). The niche model assigns interactions based on observed number of species and average directed connectance (C). Here, we assigned relative inverse attack rates (w_{ij} from the modular methods above) from a log-normal distribution with log-mean $\mu = -3.0$ and log-standard deviation $\sigma = 1.5$ to be more biologically realistic (Bascompte *et al.* 2005). For each combination of S and C we generated 250 different network structures and ran 125 different dynamic simulations which maintain the network structure, but were randomly-assigned interaction strengths, for a total of 93 750 simulations. Finally, we calculated overall average interaction strength for each food web at the start of the simulations and at the end of the simulations to determine the influence of initial, final, and change in interaction strengths on food web persistence.

The numbers of two to four species omnivory modules (see Fig. 3.1) were directly quantified following the formulation of whole food web structure using the niche model. Similar to our modular theory analyses, we define persistence as the frequency of species which have biomasses greater than 10^{-30} at the end of the 5000 time steps. We then used linear regression to measure the relationship of each omnivory module type to whole food web persistence when statistically controlling for the effects of the other modules similar to the method described in Stouffer & Bascompte (2010). An omnivory module's contribution to whole food web persistence is equal to the partial residuals of the model given by $persistence \sim \beta_0 + \sum_l c_l N_l$ where l indicates the different modules, c_l is the influence of the different modules, and N_l is the number of those modules in the given whole food web. It has been shown that exploitative competition, apparent competition, tri-trophic food chain, and omnivory (classic and trophic combined) make up 95% of all three species modules found in nature (Bascompte & Melián, 2005; Stouffer et al., 2007). Thus, we included these three additional modules in the statistical analyses but do not report their results to maintain the focus on the different types of omnivory.

3.3 Results

3.3.1 Expression of omnivory modules in empirical food webs

Overall, when we compared the frequency of each type of omnivory observed in a food web to the total number of omnivory modules observed in that food web, multi-resource omnivory was the most frequently observed omnivory module across the six empirical webs (mean of 44.43 %, range 3.35 – 93.86 %), followed by trophic omnivory (mean 37.70 %, range 0.83 – 80.57 %), while cannibalism and mutual predation were the rarest (mean 4.06 %, range 0.5 – 14.41 % and mean 5.14 %, range 0 – 9.21 %, respectively). Classic omnivory made up on average 12.16 % (range 1.68 – 43.9 %) of omnivory modules observed across food webs.

Patterns of under- or over- expression of the different types of omnivory modules are dependent on both the null model chosen and the food web in question. As expected, patterns from the niche, nested-hierarchy I (NHI) and nested-hierarchy II (NHII) null models were very similar, while the types of omnivory were most distinct for the local rewiring algorithm (LRA) null models. Within a single food web, the null model results differed in whether the observed number of modules was over (under) - expressed or not, but not in the direction of expression (with the exception of the Caribbean food web where NH2 often predicted a different result; Appendix B.1 Table B.1.1). The same is not true when examining patterns across empirical food webs. For example, trophic omnivory is significantly under-expressed in the Ythan and Weddell food webs, but significantly over-expressed in the Silwood food web (Appendix B.1 Table B.1.1). Further, when we examine the expression of classic omnivory, the most well-studied omnivory module in theoretical literature (e.g. Holt & Huxel 2007; Gellner & McCann 2011; Hall 2011), we see that across both empirical food webs and null model type, classic omnivory expression is most commonly not significantly greater or less than expected from the null models. Overall, when all types of omnivory are combined, omnivory shows different patterns of expression dependent on both the null model chosen and the food web demonstrating that omnivorous interactions depend on both the type of omnivory module and the food web community effects.

Often the frequency of omnivory modules gets conflated with the frequency of omnivore-resource interactions but empirically, this is not the case. For example, while there are over 9000 trophic omnivory modules observed in the Caribbean food web there are only 2157 trophic omnivore-resource interactions (Table 3.1 and Appendix B.1 Table B.1.2 for full results). Moreover, while null model comparisons demonstrated an under-expression of trophic omnivory modules within this food web, the trophic omnivore-resource interaction was over-expressed and it is the omnivore-resource interaction and not the frequency of omnivory modules which has been predicted to stabilize food webs (e.g. McCann *et al.* 1998; Hall 2011). The classic omnivore-resource interaction, for example, is frequently over-expressed in most food webs as theory predicts. Further, while there are no consistent differences in the observed frequency of mutual predation or cannibalism omnivory interactions and null model predictions, trophic omnivory interactions show food web dependent differences in expression, and multi-resource omnivory was consistently over-expressed.

3.3.2 Persistence and stability of omnivory modules

The analysis of classic omnivory shows that every case of classic omnivory where all species are persistent is also oscillatory (when $w_{OR} < 0.0710$) or exhibits stable, damped oscillations to a fixed point ($0.0710 < w_{OR} < 0.0736$; see Table 3.2 or Appendix B.3 Fig. B.3.1). Of the different omnivory modules, trophic omnivory is the one that demonstrates the most similarities to classic omnivory dynamics in the region where all species persist. Despite having a larger region of persistence ($w_{OC} < 0.11$ for trophic omnivory vs $w_{OR} < 0.0736$ for classic omnivory where w_{OC} is the omnivore-consumer interaction strength and w_{OR} is the omnivore-resource interaction strength), within this region of persistence trophic omnivory exhibits unstable oscillatory dynamics, similar to classic omnivory (see Table 3.2). Our numerical simulations of multi-resource omnivory modules, on the other hand, demonstrates similarities to classic omnivory when w_{OR} is greater than 0.0736 since for both modules the predation pressure from the omnivore causes the consumer to go extinct and thus the modules are identical. When w_{OR} is less than 0.0736, however, multi-resource omnivory persists, yet exhibits unstable dynamics contrary to the unstable oscillatory dynamics exhibited by the classic omnivory module (Table 3.2; Appendix B.3 Fig B.3.3). Cannibalism, on the other hand, has the widest region of persistence ($\mathrm{w_{OR}} > 0.0642$) and is stable across this parameter space, but this persistence requires very strong omnivore-resource interaction strengths, which is likely rare as weak interaction strengths dominate in nature (e.g. Bascompte et al., 2005; see Table 2). This is likely due, in part, to the fact that the omnivore here acts both as an omnivore and a consumer – hence, the omnivore-resource interaction is also the consumer-resource interaction, trading off with the cannibalism consumer-consumer interaction which cannot be too high as it would lead to the extinction of the consumer. Finally, the mutual predation module never persists, but has a large region of stability depending on whether the omnivore or the consumer outcompetes the other.

3.3.3 Influence of omnivory modules on whole food web persistence

We present only the results for the C = 0.1 food webs, but C = 0.15 and C = 0.2 can be seen in Appendix B.5 in Supporting Information. When we scaled up from module results to whole food web persistence, we observed a very weak positive correlation between the frequency of the classic omnivory module and food web persistence (Appendix B.4 Table B.4.3.a; Fig. 3.2). Indeed, this correlation is the lowest of all types of omnivory (correlation coefficient of 0.025; Appendix B.4 Table B.4.3.a; Fig. 3.2). Moreover, we observed a negative, but weak, relationship (correlation coefficient of -0.141; Appendix B.4 Table B.4.3.b; Fig. 3.3) between the classic omnivore-resource interaction and whole food web persistence. Multi-resource omnivory, on the other hand, had the strongest positive correlation with food web persistence (correlation coefficient of 0.446). This extended to the multi-resource omnivore-resource interaction (correlation coefficient of 0.302).

Perhaps unsurprisingly, mutual predation was not correlated with food web persistence (correlation coefficient of -0.088). Mutual predation omnivore-resource interactions, also were not highly correlated with persistence (correlation coefficient of 0.008). Similarly, cannibalism and cannibalism omnivore-resource interactions had little relationship with food web persistence and was quite rare in our theoretical webs. Lastly, trophic omnivory showed a weak positive relationship with food web persistence (correlation coefficient of 0.169). However, when the trophic omnivore-resource interaction is examined, we see that this interaction is not highly correlated with food web persistence (correlation coefficient -0.067).

Overall, these correlations, while statistically significant, are weak. This is more evident when the results for C = 0.15 and C = 0.2 are examined (Appendix B.5). In these cases, we see that for C = 0.15 both multi-resource and trophic omnivory modules have the strongest correlations with persistence (0.262 and 0.185, respectively; Appendix B.5 Table B.5.4.a), however, classic and trophic omnivory modules have the strongest correlation with persistence (0.325 and 0.268, respectively; Table B.5.4.a). Further, when the omnivore-resource interactions are examined the classic omnivore resource interactions contribute the most to whole food web persistence for C = 0.15 (0.145; Appendix B.5 Table B.5.4.b), while the multi-resource omnivore interaction has the strongest correlation with persistence when C = 0.2 (0.349; Appendix B.5 Table B.5.5.b).

3.4 Discussion

Omnivorous interactions are often advanced as a key stabilizing interaction, but differences in the definition of omnivory combined with the deficit of studies scaling modular theory to whole food web dynamics makes consensus difficult. We integrate data, modular theory, and whole food web models to examine the role of different types of omnivory modules and omnivore-resource interactions on food web stability and persistence. First, our empirical examination of omnivory expression demonstrated that while omnivore-resource interactions depended on both module type and the food web in which they were nested, multi-resource interactions were consistently over-expressed.

Second, the modular theory approach demonstrated module-dependent impacts of omnivory on module persistence and stability with cannibalism having the largest region of both persistence and stability of all five omnivory modules. Finally, the whole food-web model analysis demonstrated that conclusions from modular theory are not generalizable within whole food web contexts. For example, whilst cannibalism had the largest region of both persistence and stability based on the modular theory analysis, multi-resource omnivory had a stronger influence on whole food web persistence. Further, the frequency of omnivory modules, specifically multi-resource omnivory, are more important for whole food web persistence than omnivore-resource interactions. Together, these results suggest that we should revise the current thinking that omnivory is broadly stabilizing, particularly in light of the weak negative correlation between the classic omnivore-resource interactions' contributions to whole food web persistence.

Patterns of expression of omnivory within empirical food webs depend on the null model chosen. While the niche, and nested-hierarchy I and II structural food web models are successful at predicting the summary statistics of networks (e.g. connectance, number of top species), they can be poor predictors of species-specific interactions (e.g., Allesina et al. 2008, Vázquez et al. 2009, Olito and Fox 2015, Simmons et al. 2018). Future analyses should incorporate traits, such as body size, into structural food web models since these models both better predict species-specific interactions (e.g Eklöf *et al.* 2013; Morales-Castilla *et al.* 2015; Brousseau *et al.* 2018) and allow for adaptive changes within these trait values (e.g. seasonality (Vázquez *et al.* 2009)). Of the three marine systems, the Caribbean and Benguela food webs are most similar (Jacob *et al.* 2011), yet only the Caribbean food web had significantly over- or under- expressed omnivory module or omnivore-resource interaction frequency (Table 3.1). A trait-based null model approach may resolve these differences in structural similarities, as each food web may be structured along different trait dimensions. For example, Weddell is structured predominantly by the mobility of the resource, while the Caribbean food web structure is driven by the body mass of the resource (Eklöf *et al.* 2013).

Food web theory that is based on simple representations of trophic compartments (i.e., modular theory, or investigations of the dynamics of three to four species subwebs) has developed a broad range of predictions for how factors like food web configuration, interaction strengths, and body size may impact food web stability (McCann *et al.* 1998; Holt & Huxel 2007; Hall 2011). There is a much smaller body of work, however, examining if these predictions scale to whole food web dynamics (i.e. dynamics of dozens of species), but this research is emerging (e.g. Kondoh 2008; Stouffer & Bascompte 2010; Allesina *et al.* 2015). For example, Stouffer & Bascompte (2010) examined the importance of module frequency on whole food web persistence and observed a significant positive impact of omnivory modules on whole food web persistence. Their results may appear counter to our own, but there are important differences between the studies. Stouffer & Bascompte (2010) did not differentiate between classic and trophic omnivory, thus a direct comparison is difficult, but our results demonstrate a significant positive relationship for both classic and trophic omnivory module frequency and whole food web persistence. Thus, we can infer that combining these two modules would only strengthen these results. Despite these significant, positive relationships we still consider them weak because of the low correlation coefficients, a metric not provided in the aforementioned study. Stouffer &

Bascompte (2010), however, also advise to proceed with caution when scaling modular theory to whole communities. The approach we presented here provides more comprehensive evidence in support of that sentiment. For example, while trophic and classic omnivory modules demonstrated persistent and oscillatory dynamics (Table 3.2) these omnivory interactions actually had a negative impact on whole food web persistence for whole food web models with connectance of 0.1 and 0.2 (Appendix B.4 Table B.4.3.b & Appendix B.5 Table B.5.5.b). Conversely, despite showing unstable but persistent dynamics at weak interaction strengths (Table 3.2, Fig. B.4.3), multi-resource omnivory modules contributed positively to whole food web persistence.

Generalizing module results to the whole food web scale is not entirely a fruitless endeavor. For example, with well-described food webs and the assumption that these food webs were at a stable equilibrium, Neutel et al., (2007) showed that food web stability increased as the maximum weight of positive omnivory feedback loops of length three decreased. In part this is due to the small bottom-up effect of the basal species on the omnivore (Neutel *et al.* 2002, 2007). While omnivory may not be as important for food web persistence as weak interaction strengths, or the presence of feedback loops, the presence of some omnivory modules, in particular multi-resource omnivory, were still correlated with increased whole food web persistence. Despite multi-resource omnivory not being a true loop since there are two resources, this still may explain why multi-resource omnivory had a strong positive effect on whole food web persistence (Figure 3.2 and 3) and is over-expressed within empirical food webs (see Table 3.1). On the contrary, our modular analysis showed that while the multi-resource omnivory module was persistent at low interaction strengths it was unstable (Table 3.2; Appendix B.3 Fig

B.3.3). These results may suggest that multi-resource omnivory disperses the top-down pressure of the omnivore through multiple energy channels in whole food webs (e.g. Rooney & McCann, 2012). While we did not examine the resource types involved in these multi-resource omnivory modules in whole food webs, it is likely that they are actually coupling fast and slow energy channels such as planktonic and detrital food webs within the aquatic environment, or fungi and bacteria in terrestrial environments (e.g. (Rooney *et al.* 2006, 2008). As a next step, a null food web model could be developed to determine if different types of omnivory were over-expressed in select parts of the food webs. For example, multi-resource omnivory coupling different habitats within the community, or classic omnivory being over-expressed only within detrital webs. Alternatively, the over-expression of multi-resource omnivory within the empirical food webs could be an artefact of how we assemble and collect food web data, and instead reflect temporal shifts in topological interactions whereby predators display adaptive prey preferences. This is a phenomena that has been shown to be a stabilizing force within food webs and food web modules (e.g. Oaten & Murdoch, 1975), but is a topological phenomenon that can be difficult to tease out from ontogenetic or seasonal diet shifts (e.g. discussion in Wootton, (2017)). Consequently, an exploration of the prevalence of omnivory modules when an adaptive prey preference is incorporated within a whole food web model could be a promising avenue of research.

The three-pronged analysis undertaken here challenges the broadly held perspective that omnivory stabilizes ecological communities. We offer three potential explanations beyond components analyzed (i.e., type of omnivory, scaling from modular to whole food web theory) here to help interpret our findings and guide future research on this topic. First, previous studies of whole food web models have demonstrated that weak interactions are necessary to ensure food web stability (e.g. May 1972; Allesina & Tang 2012; Allesina *et al.* 2015), while other research has demonstrated that the specific placement of key interactions is sufficient to ensure food web stability irrespective of whole food web interaction strength (e.g. McCann *et al.* 1998; Gellner & McCann 2016; Kadoya *et al.* 2018). Thus, we would expect that it is a combination of both omnivory interaction frequency and the change in interaction strength for each omnivory interaction type which would increase food web stability. However, when we expand our analyses to include a measure of omnivore interaction strength along with interaction frequency, we see that both contribute little to food web persistence (the strongest correlation coefficient is -0.072 for trophic omnivory; Appendix B.4 Table B.4.3.c). Recent research has distilled a species' role within a food web to one based on the frequency with which it appears in each position of all possible 3 species modules (Baker *et al.* 2015; Cirtwill *et al.* 2018). While this approach does not give consideration to the influence of different modules on food web persistence, perhaps by expanding the quantification of a species role (sensu Baker et al., (2015)) to including 4 species modules as well, and prioritizing some modules over others may prove an important step in reconciling these two hypotheses. Second, ecological networks demonstrate the small-world patterns and non-random configurations observed across a wide range of different networks (e.g. Milo 2002; Bascompte & Melián 2005; Stouffer *et al.* 2007). The predictable presence of these sub-graphs, motifs, or modules, has led to the hypothesis that these confer robustness or stability to ecological networks (e.g. Borrelli et al., 2015; Saiz et al., 2017). But recent evidence suggest that these patterns may just be artefacts of assembly with no inherent impact on community stability or robustness (e.g. Monteiro & Del Bianco Faria 2017; Maynard *et al.* 2018). However, these studies rarely include four species' modules (but see Monteiro & Del Bianco Faria, (2017)) and the correlation between multi-resource omnivory modules and whole food web persistence suggests that those species which participate in more multi-resource modules may be integral structures to the persistence of the whole food web. Finally, most studies of whole food webs use persistence, or community stability, as a measure of stability, not the eigenvalue measures which many modular approaches (including ours) use. Reconciling predictions based on different measures of stability is an important challenge when attempting to scale modular theory to whole food web theory (see Ives & Carpenter, (2007) for more discussion on the different measures of stability).

3.5 Conclusions

Anthropogenic activities are irreparably altering the natural world (Ellis & Ramankutty 2008). One way of examining the effects of these changes is through theoretical exploration of persistence and stability of food webs, or networks of antagonistic interactions. Previous studies have demonstrated the importance of omnivory as a key stabilizing force within food web modules. We use a three-tiered approach from empirical data to local and global theory demonstrating that not all omnivory interactions are equal and rather the whole food web context of these interactions is critical for predicting their impacts on whole food web persistence. Our findings suggest that we need to increase our efforts of describing food webs, particularly in vulnerable ecosystems, with particular attention to rare interactions which may be intrinsic to the persistence of the whole food web. Determining the effects of the loss of these interactions is of paramount importance for predicting and anticipating further community stress as the effects of anthropogenic change increase.

3.6 Data Accessibility

All R code are available on figshare: https://figshare.com/s/91ad1117391927c94bc1.

3.7 References

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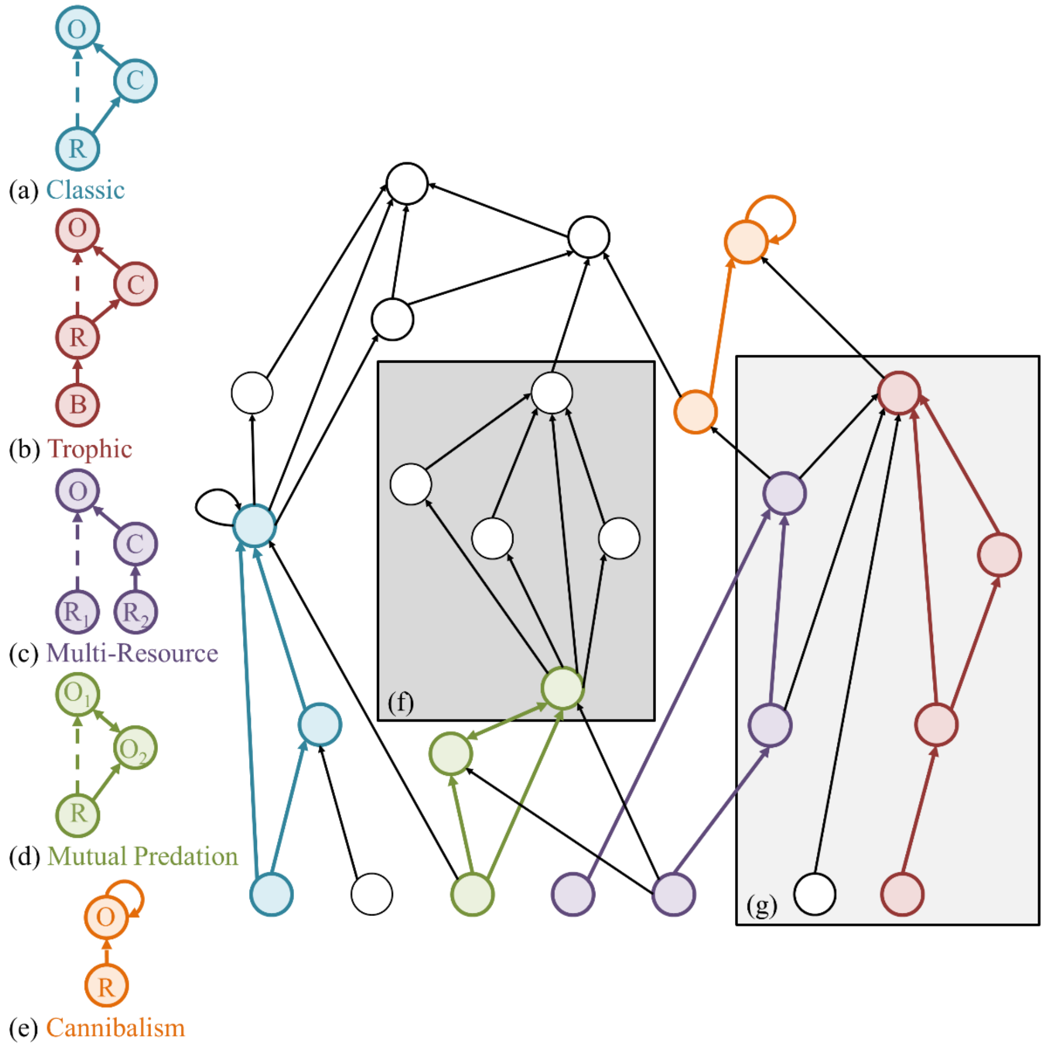

Figure 3.1 The different omnivory modules on left (a-e) where dashed lines indicate the omnivore-resource interaction, arrows indicate the flow of energy, and a sample food web on the right with a sample of each omnivory module type highlighted. (f) An example of the case where the number of omnivory modules (i.e. 3) is greater than the number of omnivore-resource interactions (i.e. 1). (g) An example where the number of omnivores (i.e. 2) is less than the number of omnivore-resource interactions (i.e. 4) involving that omnivore. Note that in (d; mutual predation) the arrow between the two omnivores is double pointed to indicate reciprocal feeding. Here, O stands for omnivore,

C for consumer, R for resource, B for basal resource, with subscripts if there are more than one of each present in the same module.

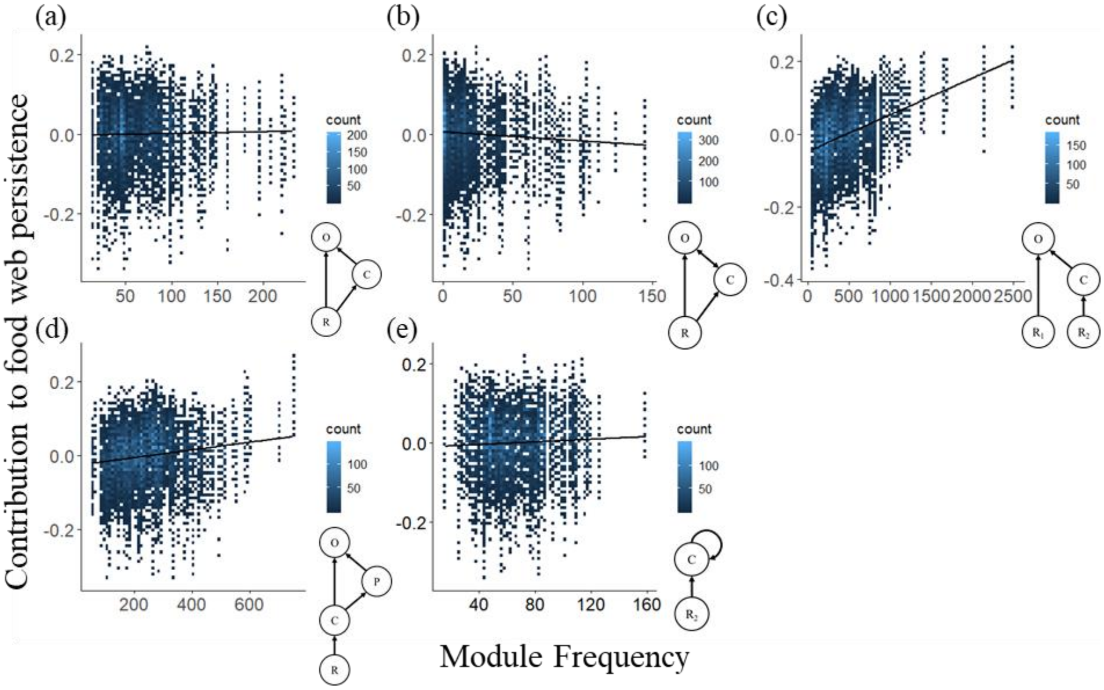

Figure 3.2 Relationship between module frequency and whole food web persistence. (a) The classic omnivory, (b) the mutual predation, (c) the multi-resource omnivory, (d) the trophic omnivory, and (e) cannibalism modules. On the x-axes the frequency of each module type is shown, and on the y-axes the contribution to whole food web persistence when statistically controlling for the effects of the other modules. A module's contribution to whole food web persistence is equal to the partial residuals of the model given by $persistence \sim \beta_0 + \sum_l c_l N_l$ where l indicates the different modules, c_l is the influence of the different modules, and N_l is the number of those modules in the given whole food web.

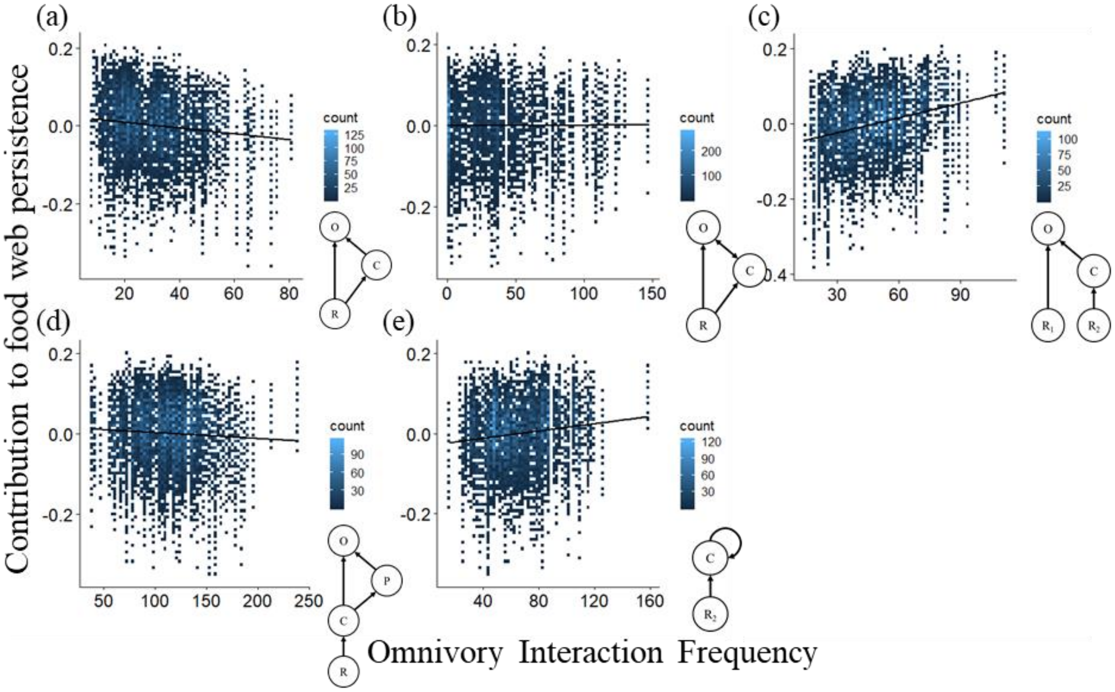

Figure 3.3 Relationship between frequency of module specific omnivore-resource interactions and whole food web persistence. (a) The classic-omnivory, (b) the mutual predation, (c) the multi-resource omnivory, (d) the trophic omnivory, and (e) cannibalism modules. On the x-axes the frequency of each omnivore-resource interaction type is shown, and on the y-axes the contribution to whole food web persistence when statistically controlling for the effects of the other omnivore-resource interaction types. An omnivory interactions' contribution to whole food web persistence is equal to the partial residuals of the model given by $persistence \sim \beta_0 + \sum_l a_l N_l$ where l indicates the different omnivory interaction types, a_l is the influence of the different interaction types, and N_l is the number of those interaction types in the given whole food web.

Table 3.1 Number of observations of each type of omnivory module and each type of omnivore-resource interaction in six classic food webs (Benguela, Caribbean, Silwood, St Marks, Weddell and Ythan) and an example null model reconstructions of these food webs using the niche null model (see Appendix B.3 for results from the four different null models; local rewiring algorithm, niche model, nested hierarchy I, and nested hierarchy II). Here, sig. represents whether the number of modules observed in the empirical web was more extreme than 97.5 % of the null model generations (indicated by over), or less extreme than 2.5 % of the null model generations (indicated by under), with NS indicating cases where there is no difference, and SD represents standard deviation. Finally, overall indicates the total number of omnivory modules observed irrespective of omnivory type.

	Module Frequency			Interaction Frequency		
Food Web	Obs. No.	Niche Mean (SD)	Sig.	Obs. No.	Niche Mean (SD)	Sig.
Classic						
Silwood	209	7.36 (5.42)	NS	64	6.96 (4.99)	Over
Weddell	290	63.08 (28.38)	Over	168	45.13 (17.5)	Over
Benguela	10	60.37 (43.72)	NS	7	18.47 (10.64)	NS
St Marks	65	51.74 (28.94)	NS	32	26.12 (11.52)	NS
Ythan	47	27.77 (14.5)	NS	38	23.37 (11.21)	NS
Caribbean	461	716 (216.33)	Under	125	264.75 (65.27)	Over
Mutual Predation						
Silwood	0	0.1 (0.89)	Under	0	0.24 (1.88)	Under

Weddell	7	4.8 (10.45)	NS	14	9.22 (17.22)	NS
Benguela	55	65.86 (60.55)	NS	80	74.69 (41.36)	NS
St Marks	0	12.41 (19.15)	NS	0	20.87 (24.63)	NS
Ythan	0	1.07 (4.01)	NS	0	2.21 (7.02)	NS
Caribbean	73	169.96 (151.65)	NS	109	230.22 (149.18)	NS
Trophic						
Silwood	136	11.08 (8.75)	Over	65	10.49 (7.92)	Over
Weddell	62	177.36 (77.86)	Under	50	125.66 (44.45)	Under
Benguela	444	379.6 (156.46)	NS	128	113.32 (27.56)	NS
St Marks	173	176.89 (88.01)	NS	95	88.51 (30.07)	NS
Ythan	11	58.09 (30.55)	NS	11	48.67 (22.64)	Under
Caribbean	9628	5236.95 (1241.44)	NS	2157	1867.8 (261.17)	NS
Multi-Resource						
Silwood	120	381.43 (142.6)	NS	13	82.74 (17.46)	Over
Weddell	5928	1560.87 (670.55)	Over	341	139.46 (29.3)	Over
Benguela	2	113.23 (123.57)	NS	1	18.97 (12.99)	NS
St Marks	175	349.02 (240.34)	NS	35	42.34 (15.83)	NS
Ythan	1231	932.14 (369.9)	NS	218	118.38 (24.06)	Over
Caribbean	1579	15728.97 (6762.23)	Under	135	420.88 (89.47)	Over
Cannibalism						
Silwood	11	6.68 (7.26)	Over	11	6.68 (7.26)	NS
Weddell	29	40.81 (25.89)	NS	29	40.81 (25.89)	NS
Benguela	86	82.35 (30.39)	NS	86	82.35 (30.39)	NS
St Marks	10	42.58 (23.89)	NS	10	42.58 (23.89)	NS

Ythan	41	19.28 (15.27)	NS	41	19.28 (15.27)	NS
Caribbean	209	359.3 (123.33)	Under	209	359.3 (123.33)	NS
Overall						
Silwood	476	406.65 (148.15)	NS	153	107.11 (25.71)	NS
Weddell	6316	1846.91 (714.42)	Over	602	360.28 (87.92)	Over
Benguela	597	701.41 (263.26)	NS	302	307.81 (88.34)	NS
St Marks	423	632.64 (299.09)	NS	172	220.42 (72.04)	NS
Ythan	1330	1038.34 (389.07)	NS	308	211.92 (51.24)	NS
Caribbean	11950	22211.18 (7162.54)	NS	2735	3142.95 (460.39)	NS

Table 3.2 Stability and persistence of different omnivory modules within the classic omnivory persistence parameter space. Here, wij represents the interaction strength between predator i and prey j which is varied, R represents the resource, C the consumer, and O the omnivore. Fixed point stability is when the species regain equilibrium values directly following a perturbation, damped oscillations are when the species regain equilibrium values, but after undergoing damped oscillations as they approach equilibrium values, oscillatory when species' biomasses oscillate around the equilibrium values following perturbation, and unstable otherwise. Persistence occurs if all species' within the module have biomasses greater than 10^{-30} after 5000 time steps. See Fig 3.1 for topological depiction of each omnivory type, and Appendix B.3, Fig. B.3.1 – B.3.5 for species' biomass dynamics over time.

Omnivory Type	Region of Stability				Region of Persistence
	Fixed Point	Damped Oscillations	Oscillatory	Unstable	
Classic	$0.0736 \leq w_{OR} < 0.1740$	$0.0710 \leq w_{OR} < 0.0736$ $0.1742 \leq w_{OR} < 0.6428$	$0.000 \leq w_{OR} < 0.0710$ $w_{OR} > 0.6428$	N/A	$w_{OR} < 0.0736$
Mutual Predation	$0.20 \leq w_{OR} < 0.64$ & $w_{CR} < 0.64$ (& vice versa)	$w_{OR} > 0.64$, $w_{CR} > 0.64$, & ($w_{OR} < 0.2$ & $w_{CR} < 0.2$)	N/A	N/A	N/A
Multi-Resource	$0.0734 \leq w_{OR} < 0.1742$	$0.0710 \leq w_{OR} < 0.0734$ $0.1742 \leq w_{OR} < 0.6418$ $0.7622 \leq w_{OR} < 0.8952$	$0.070 \leq w_{OR} < 0.0710$ $0.6418 \leq w_{OR} < 0.7622$ $w_{OR} > 0.8952$	<0.070	$w_{OR} < 0.0734$ $w_{OR} > 0.8952$
Trophic	N/A	$0.1110 \leq w_{OC} < 0.2112$	$w_{OC} < 0.1110$	N/A	$w_{OC} < 0.1100$

			$w_{OC} > 0.2112$		
Cannibalism	$w_{OR} < 0.3496$	$0.3496 \leq w_{OR} < 0.9242$	$w_{OR} \geq 0.9242$	N/A	$w_{OR} > 0.0642$

CHAPTER 4

Multiscale analysis reveals incongruent relationships between network metrics and community, species, and interaction persistence in food webs

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A version of this chapter is in review at Journal of Animal Ecology.

4.1 Introduction

Ecologists have long been fascinated with describing the complex communities observed in the natural world. These communities can be described as collections of species, interactions, and the networks of interactions which emerge from these building blocks (e.g. Niquil *et al.* 2020). Empirical studies have occurred at each of these levels; from the studies of abiotic effects on snowshoe hare populations at the species level (Wolff 1980) to lynx-snowshoe hare cycles at the interaction level (Stenseth *et al.* 1997), and finally, studies of boreal food web dynamics at the community level (Strong & Leroux 2014). Theoretical research, on the other hand, has mainly focused on communities - for example what happens to communities following the loss of species (e.g. community viability analysis; Ebenman & Jonsson 2005 but see Williams 2008). These studies have highlighted the importance of network metrics, such as modularity, on community persistence (Stouffer & Bascompte 2011) as compartments can buffer against the propagation of extinctions. While other studies have highlighted the importance of weak interaction strengths in stabilizing communities (May 1972), or the importance of a diverse basal trophic level for community persistence (Williams 2008). It remains to be seen, however, whether a) these metrics are important simply for the maintenance of networks, or are sufficient predictors of community persistence and b) whether these metrics scale to predicting persistence of species and interactions in a network.

Ecological networks are abstractions of community dynamics which allow us to distill these complex collections of species and interactions into singular metrics (see review in Delmas *et al.* 2019). Studies have demonstrated that even slight changes in these metrics impact community persistence (e.g. Ebenman & Jonsson 2005; Dunne & Williams 2009; Curtsdotter *et al.* 2019). For example, it has been demonstrated that community persistence is weakest when autotrophs are removed, while largely unaffected when a top predator is removed (Borrvall *et al.* 2000). These results are dependent on the amount of functional redundancy within a food web – those food webs which have a large number of species in each functional group are less affected by species loss, regardless of the properties of the species being lost (Borrvall *et al.* 2000). Predominantly, however, these studies have demonstrated which metrics are important for the maintenance of communities, sometimes called community viability analysis (e.g. Ebenman & Jonsson 2005) instead of identifying the importance of metrics for predicting the persistence of networks. This is an important, albeit nuanced distinction.

Community viability analyses examine the relationship between community resistance to a species deletion and food web structure (e.g. Borrvall *et al.* 2000; Borrvall & Ebenman 2006). Studies examining a metrics importance for community resistance either focus on the persistence of a network after a specific species is removed (e.g. species removal alters network metrics in Curtsdotter *et al.* 2011; Gilljam *et al.* 2015) or conduct paired simulations whereby network structures, interaction strengths, and initial conditions are identical, but in one network a species is removed altering network metrics (e.g. Stouffer & Bascompte 2011). For example, in a study highlighting the importance of modularity for network maintenance, Stouffer & Bascompte (2011) considered two sets of model simulations in parallel where the second set is identical in all ways to the first, but one species has been removed. They demonstrate that between these sets of simulations an increase in modularity resulted in a higher number of preserved species

(Stouffer & Bascompte 2011). Community viability analyses, such as this one suggest that if network structure is known *a priori* then a change in modularity following a species extinction or extirpation may be used to assess community resilience to that change. Unfortunately, more often than not, we only have network structure for one time point and thus identifying metrics for predicting the persistence of communities is critical.

Communities are assemblages of species and interactions between these species, thus understanding which properties predict the persistence of specific species and interactions is just as important. These aforementioned community viability analyses examine how species properties influence whole community persistence through direct and indirect effects, but studies determining if similar properties are useful for identifying which species and interactions will or will not persist have yet to be done. Empirical data has demonstrated that network-level properties are largely invariant across both temporal (e.g. Olesen *et al.* 2008; Petanidou *et al.* 2008) and spatial scales (e.g. Tylianakis *et al.* 2008; Nielsen & Totland 2014) suggesting that these network-level properties may be too coarse to predict species and interaction level persistence. Ecological networks, however, emerge from these community ensembles of species and interactions. Thus, successful predictions of species and interaction persistence should translate to improved predictions of community persistence.

Finally, it is critical to not only consider those network-level metrics which have been shown to be important previously (e.g. interaction strength - May 1972; McCann *et al.* 1998; Neutel *et al.* 2002 and modularity - Stouffer & Bascompte 2011), but to also compare metrics common across the organizational scope to assess whether the metrics which best predict community persistence are also strong predictors of species and interaction level persistence. One promising technique is motif analysis. Networks can be deconstructed into smaller subgraphs composed of a specific number of nodes. Most commonly studied are three species subgraphs, termed motifs, since there are only 13 possible, compared to 64 possible 4 species subgraphs (e.g. Milo 2002; Kashtan *et al.* 2004; Borrelli 2015). These motifs are often termed the building blocks of networks, and the frequency of each of them describes the makeup of communities. Indeed, recent work has suggested that if the identity of the constituent species are ignored, based on motif frequency alone, networks can be re-aligned into common backbones of interactions (Bramon Mora *et al.* 2018). Just as communities can be described by the frequency with which each three species' motif is observed across the entire community, nodes can be described by their participation in the 30 unique positions represented by these motifs, termed species' roles (see Figure 4.1). Finally, the pairwise interactions between species can also be described by their participation in the 24 unique interactions described by these 13 motifs. Unfortunately, while there have been numerous studies examining the expressions of these motifs in natural communities (Bascompte & Melián 2005; Stouffer *et al.* 2007), much less work has been done examining the expression of each of the 30 unique species' positions and 24 unique interaction positions within these motifs in communities (but see Baker *et al.* 2015). From an applied perspective there is great interest in understanding how network metrics relate to community, species, and interaction persistence because it is easier to focus on protecting species than interactions, or harder still, communities of interactions. Network metrics which highlight those species least likely to persist can help isolate which species conservation efforts should prioritize in order to ensure persistence of whole communities (see review in Tylianakis *et al.* 2010).

Here, we used a well-studied dynamic food web model to determine the relationships between current network metrics and community, species, and interaction-level persistence. Following from previous research (e.g. May 1972), we predict that interaction strength will be the single strongest predictor at each level of study, but that high frequency of the three species motifs shown to be over-represented in food webs, and low frequency of those motifs shown to be under-represented in food webs will also be strong predictors of community persistence. Moreover, we expect that those structures which are strong predictors of community persistence will also be strong predictors of interaction and species' persistence since community persistence inherently hinges on the persistence of both interactions and species (for specific predictions see Table 4.1).

4.2 Methods

4.2.1 Model

We measured the relationship between different metrics and motifs on the persistence of community, species, and interactions with a classic multi-species consumer-resource model (Yodzis and Innes, 1992). To facilitate comparisons across studies, we used the same parameterization as in other studies (e.g. Brose *et al.* 2006; Williams 2008; Stouffer & Bascompte 2010). In brief, the change in biomass of species *i* over time can be described as:

$$\frac{dB_i}{dt} = r_i\left(1 - \frac{B_i}{K}\right)B_i - x_iB_i + x_iB_i\sum_{j=prey}^{n} y_iF_{ij} - \sum_{k=pred}^{n}\frac{x_ky_kB_kF_{ki}}{e_{ki}} \tag{1}$$

where r_i is the mass-specific growth rate ($r_i = 0$ if species *i* is not a primary producer), *K* is the carrying capacity (similar to r_i, if species *i* is not a primary producer than K is inconsequential), x_i is the mass-specific metabolic rate, y_i is a species' maximum consumption rate relative to its metabolic rate, F_{ij} is a type II functional response describing the impact of species *i* on prey *j*, and e_{ij} is the fraction of biomass of species *j* that is actually metabolized by predator *i*.

The functional response, F_{ij}, is then described as follows:

$$F_{ij} = \frac{w_{ij}B_j}{B_0+\sum_{k=prey}^{n} w_{ik}B_k} \qquad (2)$$

where w_{ij} is the relative inverse attack rate for predator *i* on prey *j*, in our case it is used as a proxy for interaction strength (Berlow *et al.* 2004; Bascompte *et al.* 2005) and B_0 is the half-saturation density.

As in other studies, time scale was normalized to the mass-specific growth rate of the basal species. In this way,

$$r_i = 1 \qquad (3)$$

$$x_i = \frac{a_x}{a_r}\left(\frac{M_i}{M_0}\right)^{-1/4} \qquad (4)$$

$$y_i = \frac{a_y}{a_x} \qquad (5)$$

Where a_i are the allometric constants, M_i is the body size of species i, and M_0 is the body size of the basal species (see Brose *et al.* 2006). Body size was then assigned based on fixed predator-prey body mass ratios Z (e.g. Brose *et al.* 2006; Otto *et al.* 2007; Williams 2008). That is:

$$M_i = Z^T \qquad (6)$$

where T is the prey-averaged trophic position of species i and calculated using the R package netIndices and $Z = 42$ (see Brose *et al.* 2006). The other parameters which represent realistic scenarios for many communitis (see description in Yodzis & Innes 1992) are $e_{ij} = 0.85$, $K = 1$, $M_b = 1$, $a_r = 1$, $a_x = 0.2227$, and $a_y = 1.7816$ (as per Brose *et al.* 2006 with parameters from the original model, Yodzis & Innes 1992, and updated allometric parameters from Brown *et al.* 2004).

We used this model to simulate the biomass dynamics of species over time. We created food webs with 50 species and a directed connectance of 0.1, 0.15, and 0.2, which are within the realm of nature (e.g. Pascual & Dunne 2006), but also control for the impact that both number of species and number of interactions have on persistence (e.g. May 1972). We assigned food web structure using the niche model (sensu Williams & Martinez 2000) and generated 250 different network structures with 125 different dynamic simulations maintaining this structure, but randomly assigning interaction strength from a log-normal distribution with log mean, $\mu = -3$, and a log standard deviation, $\sigma = -1.5$ (e.g. Bascompte *et al.* 2005). Species initial biomasses were randomly assigned from a uniform distribution in the range [0.5, 1] (e.g. Otto *et al.* 2007). Persistence is the response variable in our analyses. We measured community persistence as the number of species that had biomasses greater than 10^{-30} at the end of 5000 time steps, species-level persistence as either species presence (i.e. biomass greater than 10^{-30})

or absence at the end of 5000 time steps, and interaction-level persistence as interaction presence or absence at the end of 5000 time steps (e.g. Otto *et al.* 2007).

4.2.2 Metrics

We tested how a series of community, species, and interaction-level metrics correlate with community, species, and interaction persistence.

4.2.2.1 Community Level

Community metrics included interaction strength, degree, modularity, and frequency of three species motifs. Specifically, at the community level interaction strength was measured as the average interaction strength (w_{ij}) across all interactions in the network at the beginning of the simulations. Average out/in degree and modularity were calculated using the iGraph package in R, frequency of multi-resource omnivory was calculated using the associated R code, and the initial frequency of each of the 13 motif types was calculated using the pymfinder package (see Figure 4.1). Since the frequency of motifs increases with connectance, we control for the effect of these additional interactions by normalizing the frequency of motifs by the total number of motifs in that network (including multi-resource omnivory). That is,

$$p_k = \frac{f_k}{\sum_{j=1}^{j=13} f_j} \qquad (7)$$

where p_k is the normalized motif profile for motif k and f_k is the frequency of motif k in a network.

4.2.2.2 Species Level

Species-level metrics included frequency of each species in each unique species' position for all community metrics described above. Specifically, species-level metrics included frequency of each species in each unique species' position in the 13 possible three species' motifs calculated using the pymfinder package, unique position within the multi-resource omnivory motif calculated using associated code (see Figure 4.1), degree calculated using the associated code, trophic position calculated using the NetIndices package, and average interaction strength. Average interaction strength was calculated as the average of all initial interaction strengths (w_{ij}) of a given species. Since the frequency of motifs increases with connectance, we control for this effect by normalizing the frequency of a species position by the total number of unique positions in that network (including multi-resource omnivory).

4.2.2.3 Interaction Level

Interaction-level metrics include interaction betweenness, frequency of each interaction in each unique interaction position, and interaction strength. Specific, interaction betweenness was calculated using the iGraph package, interaction strength, and frequency of each interaction in each unique interaction position within the 13 possible three species motifs calculated using the pymfinder package and frequency of each interaction in each unique interaction position with the multi-resource omnivory motif calculated using the associated code (see Figure 4.1). Since the frequency of motifs increases with connectance, we control for this effect by normalizing the frequency of an interaction position by the total number of unique interaction positions within that network

4.2.3 Statistical Analyses

We predicted that interaction strength, exploitative competition, apparent competition and motifs M98, M74, M14, M102, M78 and M110 would all have negative effects on community persistence (see Table 4.1 for more details). While modularity, out degree, frequency of multi-resource omnivory, tri-trophic food chains, and M108, M46, and M238 would all have positive effects on community persistence (see Table 4.1 for more details). We tested this by determining the effect of each metric on community persistence (i.e., persistence ~ metric) using a general linear model. We hypothesized the same relationships for these metrics on species persistence. In this case we fit 38 generalized linear models with a binomial error structure and a logit link for species level persistence (species persist [1], or does not [0]). Finally, we hypothesized the same relationships for interaction level persistence, with the exception of the omnivore-resource interaction in the omnivory motif which we predicted would negatively affect interaction persistence. Again, we fit 29 generalized linear models with a binomial error structure and a logit link of interaction persistence (interaction persists [1], interaction does not [0]). Due to the large number of predictive metrics (e.g. there are 30 unique species positions), performing model selection across all metrics was unwieldy. Instead we took the top five models (i.e., metrics) based on their R^2 values for each level of analysis (i.e., community level persistence, species level persistence, and interaction level persistence), removed variables with significant correlations (i.e. correlation coefficient > ± 0.4), and then used AIC model selection to compare across all additive combinations of the remaining metrics. We report model estimates for community persistence and model-averaged odds ratios (i.e., the exponential of variable coefficients) for species and interaction persistence. Positive model estimates indicate a positive correlation between metric and community persistence, while odds ratios higher than one, or a positive log odds ratio, indicates that metric correlates with higher odds of species or interaction persistence. We also reported effect sizes (R^2) instead of p-values as p-values should not be used in simulation studies with large sample sizes (White *et al.* 2014). Note that most other studies of community viability or metric-community persistence use p-values, so comparisons must be done carefully.

4.3 Results

4.3.1 Community Persistence

At the community level we observed a positive relationship between all metrics and community persistence, with the exception of modularity, apparent competition, exploitative competition, and M98 (in all cases slope estimates do not overlap zero; Appendix C.1 Table C.1.1). However, these relationships are variable (e.g. R^2 range from 0 for closeness centrality and M12 to 0.068 for M36). The top five predictors for community persistence are exploitative competition motif (M36), average interaction strength, apparent competition, out/in degree, and omnivory motif (M38) (R^2 of 0.07, 0.04, 0.03, 0.03, and 0.03, respectively; see Figure 4.2). Contrary to expectations, average interaction strength had a positive influence on community persistence (estimate: 2.92 ± 0.051), while in/out degree (estimate: 0.005 ± 0), omnivory (estimate: 0.213 ± 0.004), exploitative competition (estimate: -0.422 ± 0.005), and apparent competition (estimate: -0.389 ± 0.007) all had the predicted positive relationship with community persistence (Figure 4.2). After removing average interaction strength and omnivory because of their strong correlations with the other 3 predictors, our model selection analysis demonstrated that incorporating out/in degree, frequency of exploitative competition, and frequency of apparent competition is the top ranked model based on AIC with an R^2 of 0.09 (Table 4.2).

4.3.2 Species Persistence

In contrast, at the species level we observed mainly negative relationships between metrics and species persistence (see Appendix C.1 Table C.1.4). For example, the only positive predictors of species persistence are frequency with which species appear at positions S1 and S2 in the exploitative competition motif, S3, S4 and S5 in the tri-trophic food chain motif, S9 and S10 in the apparent competition motif, S21 in motif M98, S30 in M238, R1, R2, C1 and O in the multi-resource omnivory motif and interaction strength (in all of the positive cases the slope estimates do not overlap zero; Appendix C.1 Table C.1.4). Relationships were very variable demonstrated by their low R^2 values (R^2 ranges from 0 for metrics such as S30 to 0.0015 for degree). The top five predictors of species persistence are degree, S2, TL, S10, and S11 (R^2 = 0.0015, 0.0007, 0.0006, 0.0005, and 0.0005, respectively; see Figure 4.3). Contrary to predictions, degree had the strongest relationship with species persistence (log odds estimate is -0.009 ± 0.00). S2 (log odds estimate is 21.881 ± 0.59), S10 (log odds estimate is 8.936 ± 0.31), S11 (log odds estimate is -38.651 ± 1.20) and TL (log odds estimate is -0.043 ± 0.001) all had the predicted relationships with species persistence, with the exception of TL since there were no predictions for its influence on species persistence (see Table 4.1 and Figure 4.3). After removing S10 from further analyses because of high correlations with the other four predictors, our model selection analysis demonstrated that the top ranked model based on AIC involved all four predictors. Incorporating all four predictors, however, only improved the R2 to 0.003 (see Table 4.3).

4.3.3 Interaction Persistence

Lastly, at the interaction level we observed all positive relationships between metrics and interaction persistence with the sole exception being those interactions involved in the multi-resource omnivory motif. All of these metrics had slopes which did not overlap zero, and had R^2 values which, while lower than those for community level persistence predictions, were higher than those for species persistence predictions (R^2 values ranged from 0 for metrics such as interaction strength, to 0.034 for E8; see Appendix C.1 Table C.1.7). The top five predictors of interaction persistence are E8 (log odds estimate is 602.28 ± 1.64, $R^2 = 0.03$), E7 (log odds estimate is 537.06 ± 1.56, $R^2 = 0.03$), E6 (log odds estimate is 144.47 ± 0.46, $R^2 = 0.02$), E9 (log odds estimate is 349.82 ± 1.25, $R^2 = 0.02$), and E19 (log odds estimate is 1361.83 ± 5.22, $R^2 = 0.02$) (Figure 4.4). These metrics all had a positive relationship with interaction persistence, despite predictions that E6 would be negatively correlated with persistence (Figure 4.4). After removing E6 from further analysis because of high correlations with the other four predictors, our model selection analysis demonstrated that the top ranked model based on AIC involved all four predictors ($R^2 = 0.08$).

4.3.4 Cross-level Comparisons

When the importance of the top five predictors are compared across organizational level we see that parameters which are important for community persistence are not necessarily important for species or interaction persistence (Figure 4.5). For example, average interaction strength has a positive influence on community persistence, but was not an important predictor for species or interaction persistence. Further, the direction of impact a metric has on persistence is dependent on what level is being investigated. While M36 has a negative impact on community persistence, the frequency of S10 and E6 are both correlated with increased species and interaction persistence, respectively.

4.4 Discussion

Ecological networks are composed of ensembles of species within communities interacting with one another. Network metrics take these complex communities and distill them into single metrics characterizing their structure. Despite this reduction in complexity, network metrics have been shown to be integral for maintaining community persistence from the role of weak interactions (e.g. Neutel *et al.* 2002) to modularity (e.g. Stouffer & Bascompte 2011). Our results demonstrate that those metrics which are important for predicting community viability (sensu Ebenman & Jonsson 2005; e.g. modularity; Stouffer & Bascompte 2011) are not necessarily those metrics which are important for predicting community persistence. Moreover, it is a logical conclusion that those metrics which are critical for the persistence of the entire network should also be important predictors for the persistence of the key components of these networks (i.e. the nodes and interactions from which networks emerge), however, our analysis reveals that this is not the case.

Despite species and interactions being essential components of communities, those metrics which are important predictors of community persistence are not necessarily the same metrics which are important for predicting species or interaction persistence (e.g. apparent competition; see Figure 4.5). Moreover, and perhaps more importantly, those structural features which are important predictors of community, species, and interaction persistence may have a positive or negative relationship depending on the level of persistence (Figure 4.5). For example, increased frequency of omnivory is related to increased community persistence, while the frequency of the omnivore (S11) within an omnivory module is negatively correlated to the persistence of a species. Omnivory is an interesting example of conflicting results depending on the level of persistence being examined because the scientific literature lacks a clear consensus about the role of omnivory in communities (e.g. Kratina *et al.* 2012). In particular, there is a body of theoretical research demonstrating that omnivory ranges from being an important stabilizing force within food webs (e.g. McCann & Hastings 1997; Neutel *et al.* 2007) to being largely unstable (e.g. Levins 1974; Pimm & Lawton 1978; May 2001). Moreover, when the expression of omnivory in empirical webs is examined the message is just as ambiguous with studies stating omnivory is found more often than expected in natural communities (e.g. Menge & Sutherland 1987; Arim & Marquet 2004), to being less prevalent than expected (e.g. Cohen *et al.* 1990). Here, however, we demonstrate that omnivory modules are important for network level persistence, but while omnivory may enable community persistence, being an omnivore may come at a cost for an individual species. This tension between the differential importance of omnivory for community and species persistence is resolved at the interaction level where being involved in an omnivory interaction increases the probability that an interaction persists. In particular, this suggests that being an omnivore is costly for a species, but beneficial for the community, thus we would expect to see fewer omnivores, but more omnivory modules (e.g. Dunne *et al.* 2004).

There has been a growing body of research developing species' specific network properties which can describe temporal and spatial variation in species' interactions over time. This includes metrics such as species' centrality which has been used to identify potential keystone species (e.g. Martín González *et al.* 2010) and species' roles which quantify a species' position within a network (e.g. Baker *et al.* 2015). Interestingly, research on spatial and temporal empirical networks has suggested that these motif position profiles are preserved despite changes in the species' identities (e.g. Baker *et al.* 2015; McLeod *et al.* 2020). In fact, this preservation of species' roles across spatial scales suggests they may reveal integral stabilizing architectures contributing to species' persistence within communities. Overall, however, our results demonstrate that while network metrics influence whole network persistence, they are poor predictors of individual species persistence. The poor predictive power of these species roles for predicting species persistence within a dynamic food web model suggests that factors other than species' roles (e.g. initial biomass of individual species) may be better predictors of species' persistence.

Networks, however, are assembled from species and network persistence by its very definition hinges on species persistence (e.g. Niquil *et al.* 2020). However, our network metrics all emerge from the direct effects that species have on one another through consumption, ignoring the influence that indirect effects may have on species' persistence. For example, in a study of marine rocky intertidal food webs, Menge (1995) demonstrated that changes in a species biomass could propagate quickly through the food web contributing to unexpected declines in biomass further away within the food web. The importance of indirect effects for resisting perturbations in communities has also been demonstrated in a theoretical exploration of empirical webs, however, with a linear, equilibrium model whereby the inverse Jacobian matrix could be used to quantify indirect effects (e.g. Montoya *et al.* 2009). However, without doing exhaustive deletion perturbations within the non-linear food web models (e.g. Zhao *et al.* 2016), such as those presented here, it is difficult to quantify indirect effects.

Conservation efforts are typically focussed on conserving species, rather than the complex communities in which they are embedded (e.g. Runge *et al.* 2014). The recognition that anthropogenic changes can alter community structure (e.g. Albrecht *et al.* 2007; Aizen *et al.* 2008) while species richness is maintained (e.g. Tylianakis *et al.* 2007) has led to more recent calls to conserve interactions. Despite the recognition of the importance of preserving community structure (e.g. McCann 2007), which interactions should be prioritized is often unclear. In fact, how interaction metrics vary between nodes within metrics are some of the least studied (but see Cirtwill & Stouffer 2015). Here we have provided some metrics which can assess the probability an interaction will not persist. Interestingly, these metrics are almost as good at predicting interaction persistence as the metrics which predict community persistence (e.g. top model R^2 =0.075 for interaction persistence and 0.092 for community persistence). Nor are our relationships predicting community persistence significantly different than other studies examining metrics which affect community persistence. For example, in a similar study which only examines community persistence, Williams (2008) demonstrated that in a weak generalist web, with a weak type III functional response (i.e. each B_i in the functional response has an exponent of 1.2 instead of 1), trophic level was the most important predictor of network persistence (R^2 = 0.21), however in a strong generalist web it became one of the weakest predictors of community persistence ($R^2 = 0.008$). Despite the variable nature of these relationships, research such as this does suggest some network and interaction properties which will help us to predict the future persistence of networks as we continue to alter natural communities.

Network level metrics take a reductionist approach, distilling these complex networks involving tens to hundreds of species and hundreds to thousands of interactions (e.g. Polis, 1991) into single, network-wide metrics (e.g. Paine 1988; Allesina & Pascual 2009). Thus, at first glance we might expect them to be poor predictors of food web persistence. Despite their coarseness, however, community viability analyses have demonstrated that these network-level metrics can provide important insights into the robustness of communities to change. Our results demonstrate that those metrics which are important for the maintenance of communities from community viability analyses are not necessarily those which are important for predicting the persistence of networks. For example, while other studies have demonstrated the importance of modularity for community maintenance (Stouffer & Bascompte 2011), our results demonstrate that within the natural variation of different network topologies, different interaction strengths, and different initial conditions, modularity is not a top predictor of community persistence. This demonstrates a key distinction – if network structure is known *a priori,* change in modularity following a species extinction or extirpation may be used to assess community resilience to that change. More often than not, however, we are only able to collect food web data post anthropogenic change. Consequently, future work assessing predictive abilities of network metrics for the persistence of communities, species, and interactions, especially modeling persistence of empirical webs, should provide testable predictions for evaluating community vulnerability.

4.5 Data Accessibility

All data and R code are available on figshare: https://figshare.com/s/d374724f60ddbefa1178.

4.6 References

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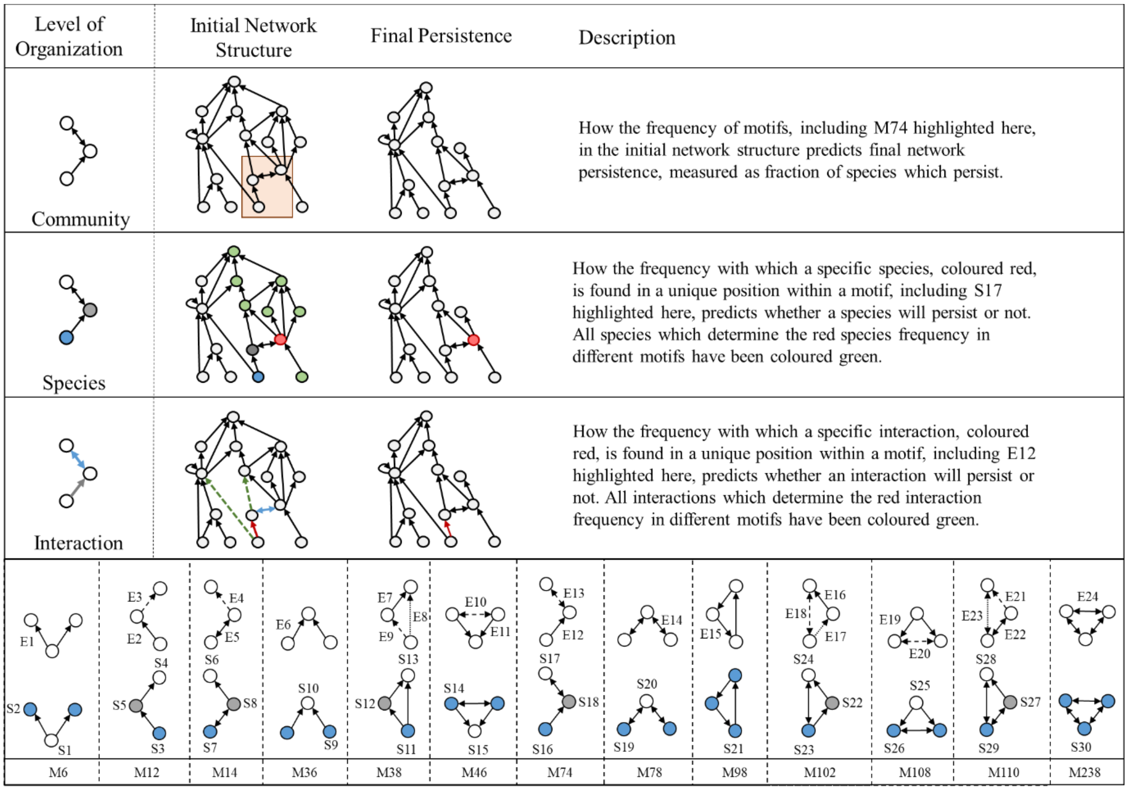

How the frequency of motifs, including M74 highlighted here, in the initial network structure predicts final network persistence, measured as fraction of species which persist.

How the frequency with which a specific species, coloured red, is found in a unique position within a motif, including S17 highlighted here, predicts whether a species will persist or not. All species which determine the red species frequency in different motifs have been coloured green.

How the frequency with which a specific interaction, coloured red, is found in a unique position within a motif, including E12 highlighted here, predicts whether an interaction will persist or not. All interactions which determine the red interaction frequency in different motifs have been coloured green.

Figure 4.1 Conceptual diagram demonstrating how network metrics are used to predict community, species, and interaction persistence. The top panel demonstrates the nested structure of M74 within a full network, while the bottom panel demonstrates the 13 different motifs, the 30 different species positions, and the 24 different interaction positions within these motifs. In our analysis we started with an initial network structure (750 different network topologies with 125 further iterations of these with different interaction strength distributions) after the end of 5000 time steps we measure final persistence. Final persistence is either the fraction of species which persist at the community level, whether the species persists at the species level, and whether the interaction persists at the interaction level.

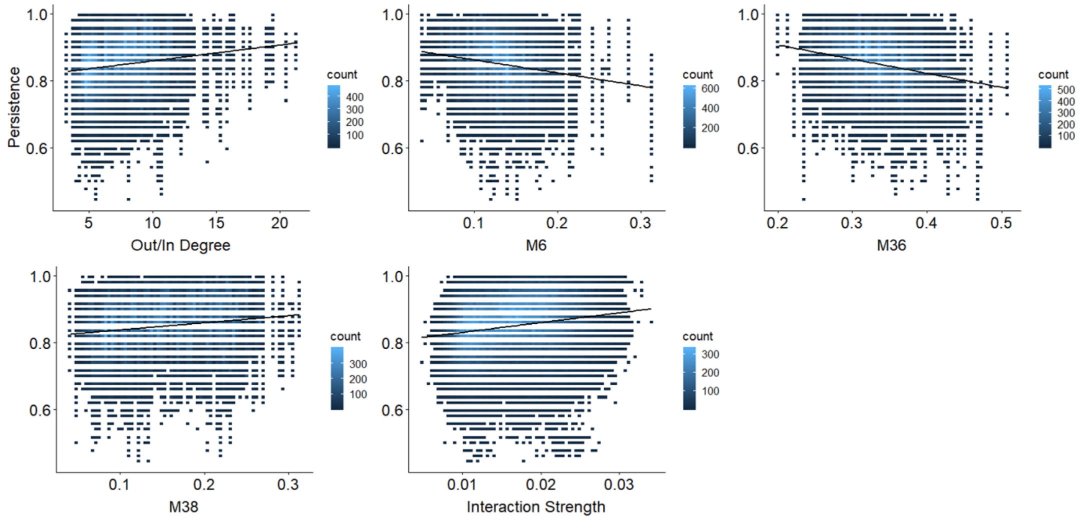

Figure 4.2 The influence of the top five predictors on community persistence. Here, the x-axis is either normalized number of motifs, average out/in degree across the network, or average initial interaction strength. Colour of the dots indicates the density of points in an area, and the line of best fit is shown in black.

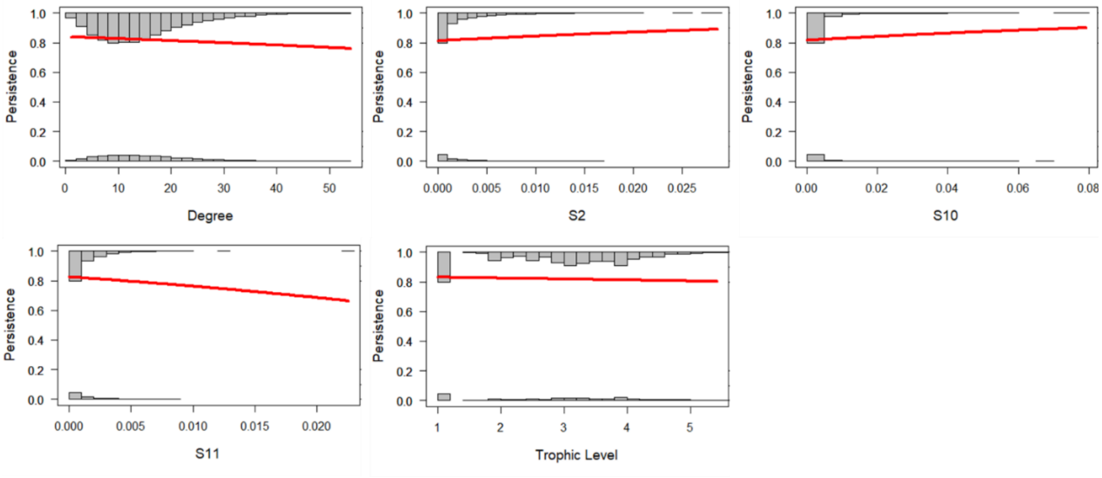

Figure 4.3 The influence of the top five predictors on species persistence. Here, the distribution of points are demonstrated using a histogram at one for those species which persisted, or zero for those species which did not. The logistic regression is shown in red.

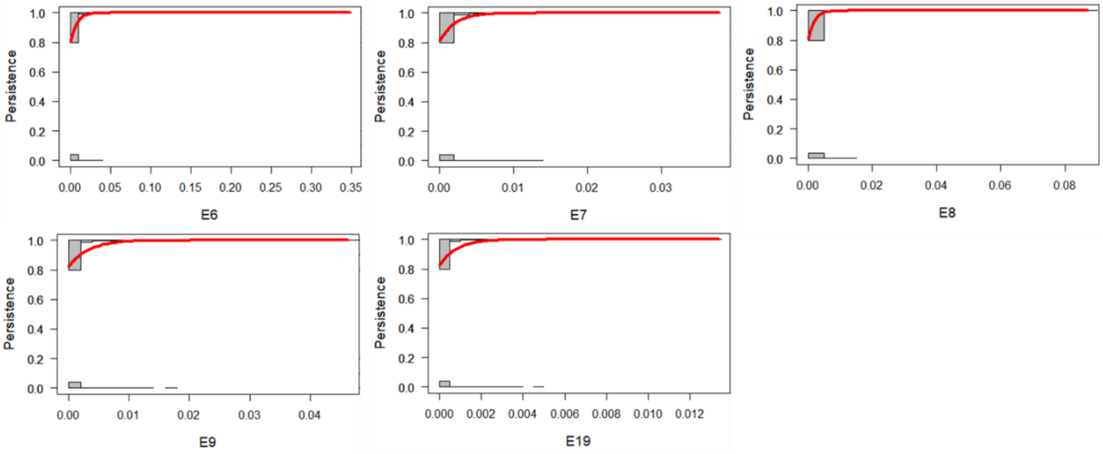

Figure 4.4 The influence of the top five predictors on interaction persistence. Here, the distribution of points are demonstrated using a histogram at one for those species which persisted, or zero for those species which did not. The logistic regression is shown in red.

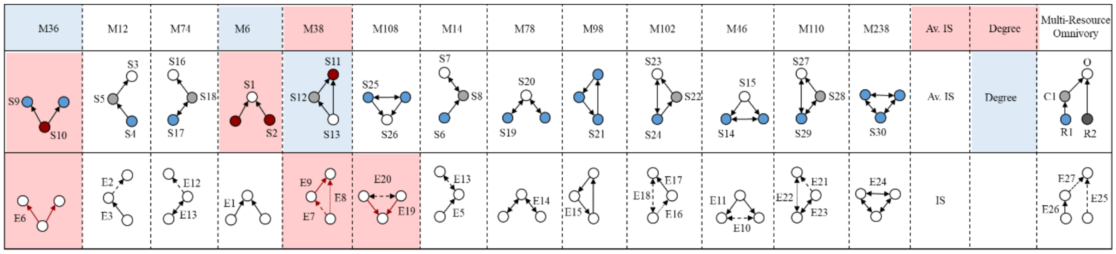

Figure 4.5 Comparison of top five predictors across organizational level where colour indicates direction of relationship. The colour of the interaction or node indicates which is in the top five, and colour denotes direction (e.g. E19 is red because it has a positive effect on persistence, while E20 is black because it has no effect). Note that trophic level is missing from this chart because it was only measured for species, but it had a negative impact on persistence. Here, Av IS stands for average interaction strength, while IS just stands for interaction strength.

Table 4.1 Predictions for the influence of each metric and motif on community persistence, species persistence, and interaction persistence and citations where appropriate. Note, if there are no citations than the prediction is an extension of the community level prediction.

Metric	Community Level	Species Level	Interaction Level
Interaction Strength	Negative[a]	Negative	No relationship[b]
Modularity	Positive[c]	---	---
Out Degree	Weak Positive[d]	No relation	---
Multi-Resource Omnivory	Positive	---	---
Motifs			
Omnivory	Positive[e]	Positive	Negative
Food Chain	Positive[e]	Positive	Positive
Exploitative Competition	Negative[e]	Negative	Negative
Apparent Competition	Negative[e]	Negative	Negative
M108, M46, M238	Over-expression suggests positive correlation with persistence[f]	Positive	Positive
M98, M74, M14, M102, M78, M110	Under-expression suggests negative correlation with persistence[f]	Negative	Negative

May 1972[a]; McCann *et al.* 1998b[b]; Stouffer *et al.* 2007[c]; Williams & Martinez 2008[d]; Stouffer & Bascompte 2010[e], 2011[f]

Table 4.2 Results for the top two models from AIC model selection for community, species, and interaction persistence. For full model results see SI Table S3, S6, and S8. Here, TL stands for trophic level, OD stands for out/in degree, and R^2 is Nagelkerke's R^2.

Persistence	Model	AIC	Dev. Expl	LogLik	R^2	ΔAIC	Aikaike weights
Community	OD+M6+M36	-213532	9.181	106771.2	0.092	0	1
	M6+M36	-213373	9.019	106690.6	0.090	159.28	0
Species	Degree + S2 + S11 + TL	2971176	0.233	-1485583	0.004	0	1
	Degree + S2 + TL	2971265	0.230	-1485629	0.004	89.90	0
Interaction	E8 + E9 + E19 + E7	8401906	5.111	-4200948	0.075	0	1
	E8 + E7 + E9	8432254	4.769	-4216123	0.070	3.0×10^5	0

CHAPTER 5 Incorporating abiotic controls on animal movements in metacommunities

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A version of this chapter is in review at Ecology.

5.1 Introduction

Processes operating across broad spatial scales have large impacts on local scale dynamics (e.g. Levin 1992; Chase & Leibold 2002). In particular, spatial flows of energy, materials, and species between local systems can influence coexistence of complex competitive communities (Leibold *et al.* 2004), persistence of multi-trophic food webs (Gravel *et al.* 2016), and the role of abiotic processes and elemental cycling (Loreau *et al.* 2003) amongst many other ecological phenomena. Meta-ecology (sensu Schiesari *et al.* 2019), or the study of such flows, arose in part from concerns about increasingly fragmented landscapes composed of disparate communities of species and how spatial coupling between fragmented patches can allow the persistence of species (see review in Haddad *et al.* 2015). For example, the movement of species between local communities alters local adaptation and gene flow (Kawecki & Holt 2002; Urban *et al.* 2008), species interactions (Pillai *et al.* 2010; Thompson & Gonzalez 2017), population dynamics (Koelle & Vandermeer 2005; Acevedo & Fletcher 2017), and community composition (Holyoak *et al.* 2005; Baiser *et al.* 2013). As such, much attention has been paid to the role of species movement on community and ecosystem processes (e.g. Briggs & Hoopes 2004; Amarasekare 2008; Massol *et al.* 2011). Yet, traditional meta-ecology theory represents movement in very simple ways which are independent of the abiotic environment.

Metacommunity studies have focused primarily on types of dispersal (e.g. reaction-diffusion or density dependent; (Briggs & Hoopes 2004; Amarasekare 2008). Movement, however, is comprised of dispersal, foraging, and migration which differ in their frequency and timing within an organism’s life-cycle. Dispersal, for example, is empirically classified as when an organism settles away from its natal habitat (e.g. Massol *et al.* 2017). Foraging movements, on the other hand, can be more frequent and tracks the movement of an organism in its search for resources across multiple habitats (e.g. Subalusky *et al.* 2015). And finally, migration encompasses both life-cycle and seasonal migrations whereby organisms shift habitats in response to changes in their ontogeny (e.g. mayfly emergence in aquatic environments) or perform seasonal dependent movements between habitat patches (e.g. the diurnal migration of zooplankton in the water-column in aquatic environments or the cross continent migrations of monarch butterflies in terrestrial environments) (Bauer & Hoye 2014). Incorporating diverse types of movement is a major frontier in metacommunity theory (Guzman *et al.* 2019). But, a critical part of the metacommunity dynamics remains overlooked—the movement of organisms between patches is governed by the interplay between both a species' ability to move, irrespective of movement type, and the abiotic controls on this movement (Gounand *et al.* 2018, Fig. 5.1). For example, two lakes may share a geographic proximity, but without a river connecting them even the most mobile fish species will be unable to move between them whilst many insects and birds species may cross easily (Fig. 5.1). By ignoring abiotic controls on species movement we are neglecting a crucial piece of movement dynamics.

These abiotic controls can be as simple as creating asymmetries in connectivity between patches; that is, the probability of moving from patch *i* to patch *j* is not necessarily the same as moving from patch *j* to patch *i*. For example, a fast-flowing river only connects an upstream lake to downstream lakes for aquatic organisms which move passively (Fig. 5.1). While it is often assumed in metapopulation models that there is fixed, symmetric dispersal between patches, it has been shown that relaxing these assumptions can have substantial effects on metapopulation dynamics (e.g. Armsworth & Roughgarden 2005; Vuilleumier *et al.* 2010; Acevedo & Fletcher 2017). Moreover, it has been suggested that even at the metapopulation level symmetry in the dispersal of species among patches is rarely observed in nature (e.g. Prokopy & Owens 1983; Cowen *et al.* 2006; Siegel *et al.* 2008), and when it is, it is typically time-dependent (e.g. there are only symmetric flows between patches for a couple days of the year). Consistent with this expectation, Salomon *et al.* (2010) in one of the few studies to apply the idea of asymmetric dispersal, albeit in competitive metacommunities, showed that asymmetric dispersal is sufficient to ensure species persistence even for a poorer competitor, regardless of whether that dispersal is disproportionately towards patches where that species may have some kind of competitive advantage. Thus, it is reasonable to assume that when we consider the dynamics of multiple interacting species, incorporating species-specific connectivity of patches across the spatial landscape will substantially alter our predictions about the persistence, stability, and resilience of metacommunities.

Despite the origins of the metacommunity concept as a method of developing specific, testable hypothesis about the role of landscape alterations on community persistence (e.g. Leibold *et al.* 2004), metacommunity theory focuses on biotic interactions. These interactions, however, do not occur in isolation from the abiotic environment. Here, we propose a framework that builds conditional dependence of biotic interactions and movement on the abiotic environment (i.e. landscape structure and physical flow). We derive a novel metacommunity model to demonstrate how species-specific movement capabilities and abiotic conditions, which together we refer to as species-specific connectivity, interact to influence metacommunity stability. This framework is complementary to recent progress on integrating differential dispersal ability (e.g. Pedersen *et al.* 2016; Guzman *et al.* 2019) and asymmetric dispersal (Salomon *et al.* 2010) by filling the gap in understanding the intersection between organism movement and landscape.

5.1.1 Empirical evidence of the influence of abiotic conditions on species movement

Species-specific movement among local communities can emerge via physical flows, landscape structure or the combination of both. Animals can move passively or actively. Animals that move passively are dependent solely on environmental and physical flows, while animals which move actively can control their movement trajectories.

5.1.1.1 Physical flows

For organisms which move passively, physical flows—such as wind current (McInturf *et al.* 2019)—can drive their movement and result in asymmetries in species-specific patch connectivity. Indeed, the literature is replete with examples of how physical flows, such as wind and water currents, alter the distribution and dispersal of organisms across both terrestrial and aquatic systems (e.g. Kneitel & Miller 2003; Levin *et al.* 2003; Nathan *et al.* 2008; Vanschoenwinkel *et al.* 2008). For example, wind activity is known to carry dormant propagules, such as seeds, and distribute them according to wind flow patterns across the landscape (Minami & Azuma 2003). Such movement mediated by physical flows can occur over small spatial extents like the dispersal of seeds directly around a parent tree to continental-level extents. For example, aerodynamic currents have been shown to disperse bacteria and fungi between continents in dust clouds generated by storm activity (Kellogg & Griffin 2006). Organisms which move actively, on the other hand, have developed locomotor sensory systems allowing them to exhibit controlled movement trajectories, but can still be impacted by physical flows. Wind, for example, carries volatile chemical signals from vegetation causing organisms which move actively, such as many insect species, to direct their movement upwind tracking these environmental cues (Prokopy & Owens 1983). This is not unique to terrestrial systems—freshwater systems are affected by both aerodynamic processes, through wind dispersal of invertebrates such as zooplankton (Vanschoenwinkel *et al.* 2008), and hydrodynamic processes. These hydrodynamic processes are, perhaps, most obvious in oceans whereby ocean circulation has a pronounced effect on pelagic larval dispersal, even for larvae which exhibit well-developed swimming capabilities (Siegel *et al.* 2008). For example, larvae can use ciliary or musculoskeletal movement to change positions in the water column to capitalize on oceanic currents (e.g. Metaxas 2001). Moreover, it has been shown in coral reef systems, for example, that the effects of biophysical characteristics, such as tidal patterns and ocean currents, combined with biological factors, like the larva's developing motor and sensory capabilities, create highly variable and species-specific larvae dispersal (James *et al.* 2002; Cowen *et al.* 2006; Siegel *et al.* 2008).

5.1.1.2 Landscape structure

Landscape structure describes the physical architecture which connects habitats. This ranges from patches connected by habitat corridors facilitating movement through an inhospitable matrix (e.g. Gonzalez *et al.* 1998), to situations where the matrix may be inhospitable for some organisms, but not for all (Vandermeer & Carvajal 2001). This is most easily envisioned in the lake example above whereby rivers are required for mobile fish species to move between them (see Fig. 5.1). An aquatic species, however, may require more than just a stream or river to be present to movement between lakes or ponds. It also requires that the river have the characteristics that fit its environmental requirements - that is, for example, for it to have depth, oxygen, and temperature profiles within its species niche. Other aquatic species, however, with different sets of requirements may be able to move between lakes connected by stagnant ditches or shallow streams (e.g. amphibians; Reh & Seitz 1990). Moreover, there may be physical obstacles, such as dams or waterfalls, which prevent the movement of highly mobile fish species, but are not impediments for the movement of birds and aquatic invertebrates. Or, are only impediments for specific life stages of a species. Nor do physical flows or landscape structures act independently to shape species-specific landscape connectivity. Rather, communities and ecosystems are made up of the cumulative effects of these abiotic properties creating complex patterns of connectivity between patches.

The above examples provide evidence that a) abiotic conditions (i.e. physical flows and landscape structure) can impact animal movement and b) the combination of abiotic conditions and biotic properties can influence organisms differently. Taken together, this suggests that species-specific connectivity is the rule rather than the exception - yet there is little theory incorporating species-specific connectivity. Next, we derive a multi-trophic metacommunity model that incorporate abiotic controls and biotic properties.

5.2 Building a multi-trophic metacommunity model with species-specific connectivity

In this section we lay the foundation for a multi-trophic metacommunity model. We begin by describing local patch dynamics, then connect these disparate patches in a regional metacommunity. Next we introduce a framework to incorporate species-specific connectivity within this regional metacommunity.

5.2.1 Local dynamics

At the local level we have a three species multi-trophic food chain which can be described using Rosenzweig-MacArthur consumer-resource equations. The resource (*R*) has a logistic growth, growing with rate r and saturating at carrying capacity (*K*). The resource is consumed by a herbivore (*H*), which has a Holling Type II functional response based on the herbivore's attack rate for the resource (a_R) and handling time (h_R). The herbivore has an efficiency (e_H) with which it converts energy obtained from the resource into biomass. Herbivore biomass is lost by both consumption by predators (P) and by mortality other than predation (d_H). Predator consumption is also governed by a Holling Type II functional response, where a_H is the predator's attack rate for the herbivore, h_H is the predator's handling time for the herbivore, and e_P is the efficiency with which the predator converts energy obtained from the herbivore into its biomass. Finally, predator biomass is lost by mortality (d_P). In this way, local patch dynamics (*L*), in the absence of spatial linkages can be described as:

$$\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - \frac{a_R H R}{1 + a_R h_R R} \qquad (1)$$

$$\frac{dH}{dt} = e_H \frac{a_R H R}{1 + a_R h_R R} - \frac{a_H P H}{1 + a_H h_H H} - d_H H \quad (2)$$

$$\frac{dP}{dt} = e_P \frac{a_H PH}{1+a_H h_H H} - d_p P \qquad (3)$$

5.2.2 Regional dynamics

At the regional level, multi-trophic food chains are connected by passive diffusion of species between patches. The movement matrix (*M*) is a $k \times k$ matrix where k is the number of species' in the local food web—in our case $k = 3$. It is a diagonal matrix where the diagonal elements describe the movement rate of each species, and the off-diagonals are zeros. The way in which the patches are linked is then described by the connectivity matrix (*C*) which is an $n \times n$ matrix where each c_{ij} describes whether patch *i* is connected to patch *j* (note that patch connectivity does not have to be symmetric, but it is identical for all species). Finally, element c_{ii} normalizes the matrix so that no organisms are lost during movement between patches (i.e. $\sum_j c_{ij} = 0$ for all *i* and $c_{ii} \leq 0$).

5.2.3 Metacommunity dynamics

When we combine local and regional dynamics we describe the change in biomass of a multi-trophic metacommunity. For example, if we consider a three patch system with symmetric connectivity between patches and resource, herbivore, and predator movement rates described by m_R, m_H, and m_P, respectively. We end up with the following equations describing species' biomass in patch *i*:

$$\frac{dR_i}{dt} = rR_i\left(1 - \frac{R_i}{K}\right) - \frac{a_R H_i R_i}{1+a_R h_R R_i} - m_R \sum_{j=1}^{3} C_{ij} \qquad (4)$$

$$\frac{dH_i}{dt} = e_H \frac{a_R H_i R_i}{1+a_R h_R R_i} - \frac{a_H P_i H_i}{1+a_H h_H H_i} - d_H H_i - m_H \sum_{j=1}^{3} C_{ij} \qquad (5)$$

$$\frac{dP_i}{dt} = e_P \frac{a_H P_i H_i}{1+a_H h_H H_i} - d_p P_i - m_P \sum_{j=1}^{3} C_{ij} \qquad (6)$$

5.2.4 General connectivity metacommunity framework

In a metacommunity with two patches and three species equations (4-6) are manageable, but as we incorporate both more species and more patches we have to keep track of $k \times n$ equations which can quickly add up. Instead, if the local patch (L) is stable in the absence of spatial dynamics, it has been proven that the stability of the local patch when spatial dynamics are incorporated can be described using the eigenvalues of matrix $V(i)$ where $V(i)$ is:

$$V(i) = J(L) + \lambda_i M \quad i = 1, \ldots, n \tag{7}$$

where J is the Jacobian matrix of local food web dynamics (L) in the absence of spatial processes and λ_i is the i^{th} eigenvalue of the connectivity matrix, C (Jansen & Lloyd 2000)(see Fig. 2). Here, stability is defined as fixed point stability, however, this could be extended to oscillatory stability using Floquet multipliers (see discussion in Jansen & Lloyd 2000). Note that despite having n patches, n eigenvalues of C, and n matrices $V(i)$, each $V(i)$ cannot be thought of patch specific, in particular because of the way that C is defined λ_1 will always be 0 and represent the dynamics in the absence of space (i.e. when $\lambda_1 = 0$ then $V(i) = J$ (Jansen & Lloyd 2000)). Finally, metacommunity dynamics are stable as long as each $V(i)$ is stable.

5.2.5 Incorporating species-specific connectivity

We can then extend this general connectivity metacommunity framework one step further to allow species-specific connectivity of patches simply by allowing each species (s) its own connectivity matrix (C_s) according to the physical flows and landscape structure (see Fig. 2). In the modified approach we have species-specific connectivity matrices (C_s), where C_s is an $n \times n$ connectivity matrix describing how the n patches are connected for species *s*. Recall that in the general connectivity formulation *C* was identical for all species, or a special subset of the species-specific connectivity. In this way we now have a vector of λ_i's which are the i^{th} eigenvalues for each species. And, equation 7 becomes:

$$V(i) = J(L) + \begin{pmatrix} \lambda_{1,i} \\ \vdots \\ \lambda_{k,i} \end{pmatrix} M \quad i = 1, \dots, n \qquad (8)$$

This represents a way of incorporating species-specific connectivity, which is ubiquitous in nature, into metacommunity models while retaining the tractability of the original formulation (see Appendix D.2 for proof).

Below we apply this novel metacommunity model to explore how incorporating species-specific connectivity influences metacommunity predictions.

5.3 Effect of species-specific connectivity on food web stability

To explore how species-specific connectivity influences the distribution of biomass and metacommunity stability we provide two case studies.

5.3.1 Case Study I

First, we consider a system with three patches and three species. We contrast the general connectivity scenario with a species-specific scenario using equations 4-6. For general connectivity, C is as follows:

$$C = \begin{pmatrix} -1 & \frac{1}{2} & \frac{1}{2} \\ \frac{1}{2} & -1 & \frac{1}{2} \\ \frac{1}{2} & \frac{1}{2} & -1 \end{pmatrix}$$

For species-specific connectivity, on the other hand, both the resource (R) and the herbivore (H) have the same connectivity (i.e. $C_R = C_H = C$), while the connectivity matrix for the predator (P) is as follows:

$$C_P = \begin{pmatrix} -\frac{1}{2} & \frac{1}{2} & 0 \\ \frac{1}{2} & -\frac{1}{2} & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

Each species' also has a species-specific movement rate. In this case $m_R = 3.5$, $m_H = 0.01$, and $m_P = 0.1$. We start at equilibrium biomasses, calculated using Mathematica (Wolfram Research 2020), perturb the Resource equilibrium biomass and then run the model using lsode from deSolve package (Soetaert *et al.* 2010) in R (R Core Team 2017) for 2000 time steps, and report biomass dynamics from time 500 to 2000 using the same parameters as used in McCann *et al.* (2005): $K = 2.75$, $a_R = 2.5$, $a_H = 8.75$, $h_R = 0.4$, $h_H = 1.15$, $e_H = 0.8$, $e_P = 0.8$, $d_H = 1$, $d_P = 0.4$, $r = 1$ as they are commonly used, biologically realistic values (see derivations in (Yodzis & Innes 1992).

This analysis demonstrates that species-specific connectivity results in two major differences in metacommunity dynamics (Fig. 5.3). First, we observe a decrease in total biomass for the resource across all patches, but we also observe changes the stability of species' dynamics from one of fixed stability to one with oscillatory behaviours for all species. The oscillatory behaviours likely emerge from the reduced movement of the predator and thus unequal predation pressures across the three patches. Here, we have illustrated the influence of species-specific connectivity on patch dynamics using an example when the predator has restricted movement compared to the prey (e.g. some shark species on atolls; Lea *et al.* 2016). Further permutations of these species-specific connectivities are presented in Appendix D.1 Fig D.1.1, demonstrating a range of fixed and oscillatory dynamics depending on the species-specific connectivities.

5.3.2 Case Study II

Here, we expand on Case Study I by applying the framework outlined here to investigate how patch stability of the tri-trophic food chain model changes as we incorporate species-specific landscape connectivity matrices. We follow the same basic analysis, using the local patch dynamics described in equations 1-3, and the same parameter values as in Case Study I (i.e., $K = 2.75$, $a_R = 2.5$, $a_H = 8.75$, $h_R = 0.4$, $h_H = 1.15$, $e_H = 0.8$, $e_P = 0.8$, $d_H = 1$, $d_P = 0.4$, $r = 1$), however, there are two major differences between this case study and Case Study I. First, only the resource (R) and the predator (P) can move between patches. For example, two lakes connected by shallow streams which promote the movement of plankton between patches, but inhibit the movement of fish whilst birds can access all patches irrespective of stream connectivity. And second, we apply our metacommunity framework to explore how abiotic conditions influence metacommunity stability in a more general sense. To this end, we do not fix movement rates of either the resource (m_R) or the predator (m_P), nor do we fix the number of patches. Instead, we explore the dynamics for three different minimum λ_R values—in other words there is a fixed connectivity for R which could correspond to various patch layouts (see examples in Fig. 5.4)—when $\lambda_P = \lambda_R$ and when $\lambda_P \neq \lambda_R$**.**

First, we observe that under a general connectivity scenario, where both the predator and the resource have the same landscape connectivity (i.e. $C_P = C_R$ which implies that $\lambda_P = \lambda_R$), there is a tradeoff whereby a high predator movement rate (m_P) is stable only when the resource movement rate is low ($m_R < 0.25$; Fig. 5.4, dark grey). Likewise, when there is high resource movement (m_R) the system is only stable when the predator movement rate remains low ($m_P < 0.25$). However, when we introduce species-specific connectivity matrices (i.e. $\lambda_P \neq \lambda_R$), we observe stable dynamics when both m_P and m_R are highly mobile. In this case λ_R was always fixed, however, the same pattern holds as we decrease λ_R from -2 to -4/3 (see Fig. 5.4 a-c. Note: λ_i is mathematically constrained between 0 and -2). Consequently, we observe that incorporating species-specific connectivity in this case actually expands the parameter space and patch orientations for which stable metacommunity dynamics are observed.

The movement of resources and predators between patches inaccessible to the herbivore may seem counter to paradigms of the hierarchies of dispersal, but there are many natural occurring examples of such non-hierarchical dispersal (see discussion in Pedersen *et al.* 2016). Moreover, an important application of metacommunity theory is in developing hypotheses about the role of habitat fragmentation on food web stability. In aquatic systems this includes both the fragmentation of river corridors by dams (e.g. Grill *et al.* 2015), but also the subsequent loss of water bodies and transitioning of water bodies from permanent to seasonal states (e.g. Pekel *et al.* 2016). In particular, Case Study II highlights what happens when dams are built which decrease flow and water levels in connecting streams, obstructing the movement of fish between habitat patches, but allowing for the passive movement of resources with water currents and leaving avian predators unaffected. In fact, it suggests that overlooking the impediments to herbivore movement may in fact suggest instability, when removing this assumption of a general connectivity of patches for all species points to all patches remaining stable.

5.4 Future directions and implications

5.4.1 Experimental and observational studies

It is not enough to merely recognizing the importance of abiotic conditions, such as physical flows and landscape structure, for influencing species-specific patch connectivity in theoretical explorations. Rather, we need to extend this perspective into our experimental and observational studies as well. According to a recent meta-analysis most experimental designs for metacommunity studies manually emulate dispersal between patches, transferring water containing aquatic organisms or transferring organisms explicitly between patches (Logue *et al.* 2011; Grainger & Gilbert 2016). The rest of the experimental designs reviewed in Grainger & Gilbert (2016) connect patches directly through a fixed set up of corridors or tubes fixing the connectivity of patches for all species able to move (Grainger & Gilbert 2016). Theoretical explorations in metacommunities have informed the experimental designs used, thus as theoretical treatises examine distinct patches with well-defined borders and uniform connectivity across species, experimental designs have attempted to replicate this (see Logue *et al.* 2011, for more discussion). By recognizing the species-specific connectivity of the landscape and developing a framework to investigate the consequences of this we can transition from these simple patch models to the examination of the more complex metacommunities observed in nature. Moreover, recent advances in genetic techniques have made it easier for us to directly quantify species-specific connectivity (see Baguette *et al.* 2013 for a discussion on scaling up from single species' to multi-species connectivity using genetic tools).

5.4.2 Coexistence perspective

Theoretical metacommunity research has largely been focused on competitive communities to date (see Guzman *et al.* 2019 for more discussion), highlighting the importance of a competition/colonization trade off where asymmetries in competition and colonization (that is the better competitor is a poorer colonizer) leads to coexistence of species across the metacommunity (e.g. Nee & May 1992; Tilman 1994; Calcagno *et al.* 2006). These communities use Lotka-Volterra competition models to approximate dynamics, typically within a trophic level whereby the resource for which the species' pairs are competing are ignored. Moreover, it is often thought that mechanistically modeling competition as additive process occurring between species' pairs is sufficient to capture most of the important details of competitive interactions. And, despite recognizing the possibility for the examination of nonlinearities in competition this is seldom done (but see Amarasekare 2004, for a mutualism example), in part because of the intractable nature of these problems. By using the described framework, however, we simplify the challenge of integrating complex local competition dynamics within a spatial arena. For example, the framework presented here specifically described a multitrophic, antagonistic community with non-linearities in the functional responses, however, the dynamics of the local system (L) could just have easily described a consumer-resource competitive community. For example, taking a standard Lotka-Volterra competition model:

$$\frac{dN_f}{dt} = r_f N_f \left(1 - \sum_{g=1}^{k} \alpha_{fg} N_g\right) \qquad (9)$$

where r_f is the per capita intrinsic rate of increase of species *f*, α_{fg} is the competition coefficient describing the effect of species *g* on species *f*, and N_f is the biomass of species *f*, we can incorporate an intraspecific higher order interaction, for example, by including a quadratic term. In this way, the standard Lotka-Volterra competition model now becomes:

$$\frac{dN_f}{dt} = r_f N_f \left(1 - \sum_{g=1}^{k} \alpha_{fg} N_g - \sum_{g=1}^{k} \beta_{fgg} {N_g}^2\right) \qquad (10)$$

where the cumulative impacts of intra-specific interactions on species *f* are described by β_{fgg}. For more examples of ways to incorporate higher order interactions into the Lotka-Volterra competition model see Letten & Stouffer (2019).

5.4.3 Ecosystem perspectives

Thus far we mainly restricted ourselves to the discussion of biotic, or organism, flows between patches, however, this is not a necessity. Rather, as we alluded to in the introduction, an ecosystem model could also be applied to this approach, changing it from a metacommunity to a metaecosystem perspective. This could be as simple as simple as adding a limiting nutrient and tracking stocks of that nutrient in the food chain instead of biomass (e.g. Marleau *et al.* 2014). Indeed, this could potentially be very illuminating as nutrient feedback loops can lead to unintended consequences. For example, it has been shown that the flow of nutrient resources between ecosystems has the potential to induce trophic cascades in the recipient ecosystem (e.g. Leroux & Loreau 2008). These effects need not just be the result of flows of nutrient resources. From an ecosystem perspective biota can act as ecosystem integrators recycling nutrients in the form of faeces (e.g. whales; Roman *et al.* 2014) and as carcasses (e.g. salmon; (Helfield & Naiman 2001) as they move across the landscape. And, the effects of nutrient recycling via carcasses may be more important in the inhospitable matrix habitats where organisms enter the detrital pool—for example whales grounding on beaches (Roman *et al.* 2014), or airbolown zooplankton landing in terrestrial habitats (Rose & Polis 1998), providing a nutrient pulse as they decay. Here we have provided a novel framework which can start bridging empirical evidence and theoretical progress (see more discussion in Gounand *et al.* 2018).

5.4.4 Edge and matrix effects

While the above examples all apply this framework to well-defined patches surrounded by an inhospitable matrix, the inhospitability of the matrix is species' dependent. From a conservation perspective understanding how species perceive this presumed inhospitable matrix between patches is of pressing concern (e.g. Vandermeer & Carvajal 2001). For example, one strategy to lessen the negative impacts of habitat fragmentation is by creating corridors, or narrow strips of similar habitat joining two patches. These corridors are intended to restore dispersal between otherwise isolated patches thus preserving diversity (Rosenberg *et al.* 1997; Beier & Noss 1998). Not all species use these corridors, however, choosing to disperse through the presumed inhospitable landscape matrix habitat instead (e.g. habitat generalist butterflies; Haddad, 1999), while still other species disperse along the matrix edge of habitat corridors (e.g. bluebirds; Levey *et al.* 2005). Thus, these matrix habitats must be more hospitable than otherwise assumed, and theoretical explorations of how matrix quality may influence species' persistence and community stability are integral. Moreover, this treatment of communities as patches scattered across an inhospitable matrix ignores the evidence that, in some cases, these matrix habitats can be surprisingly species' rich (e.g. the spillover of primary forest species into neighbouring matrices of pasture and regenerating forests in the Amazon (Gascon *et al.* 1999); and see further discussion in Tscharntke *et al.* 2012).

5.5 Conclusions

Community ecology has come a long way since scientists first started recognizing the impact that processes operating at broad spatial scales can have on local dynamics (Levin 1992; Chase & Leibold 2002). Arising, in part, from a concern about anthropogenic effects contributing to increasingly fragmented landscapes, metacommunity studies have focussed predominantly on the interplay between species' movement capabilities and habitat loss. Anthropogenic change, however, influences more than just the loss of a habitat. Instead, it is the disappearance of migratory corridors linking habitat refugia, it is the damming of rivers isolating lakes, and the creation of canals linking otherwise disparate riverine systems. And, it is the change in temperatures shifting wind patterns and altering coastal oceanic currents - changing the physical flows which may have been linking habitat patches for centuries, if not millenia. For example, it has been shown that changes in climate are altering the strength and variability of coastal currents leading to the reorganization of coastal metacommunities solely due to altered larval dispersal pattern (e.g. Aiken *et al.* 2011). Thus, as anthropogenic changes continues to alter landscapes and physical flows across the globe creating a patchwork of increasingly more disjointed communities from deforestation and urbanization in terrestrial environments to damming and habitat destruction in aquatic environments (e.g. coral bleaching and dredging) understanding how species-specific movement patterns connect communities is critical for predicting and preserving structure and function of ecological communities.

5.6 Data Accessibility

All the R code are available on figshare: https://figshare.com/s/0bf4ef23fb83d9bbde22.

5.7 References

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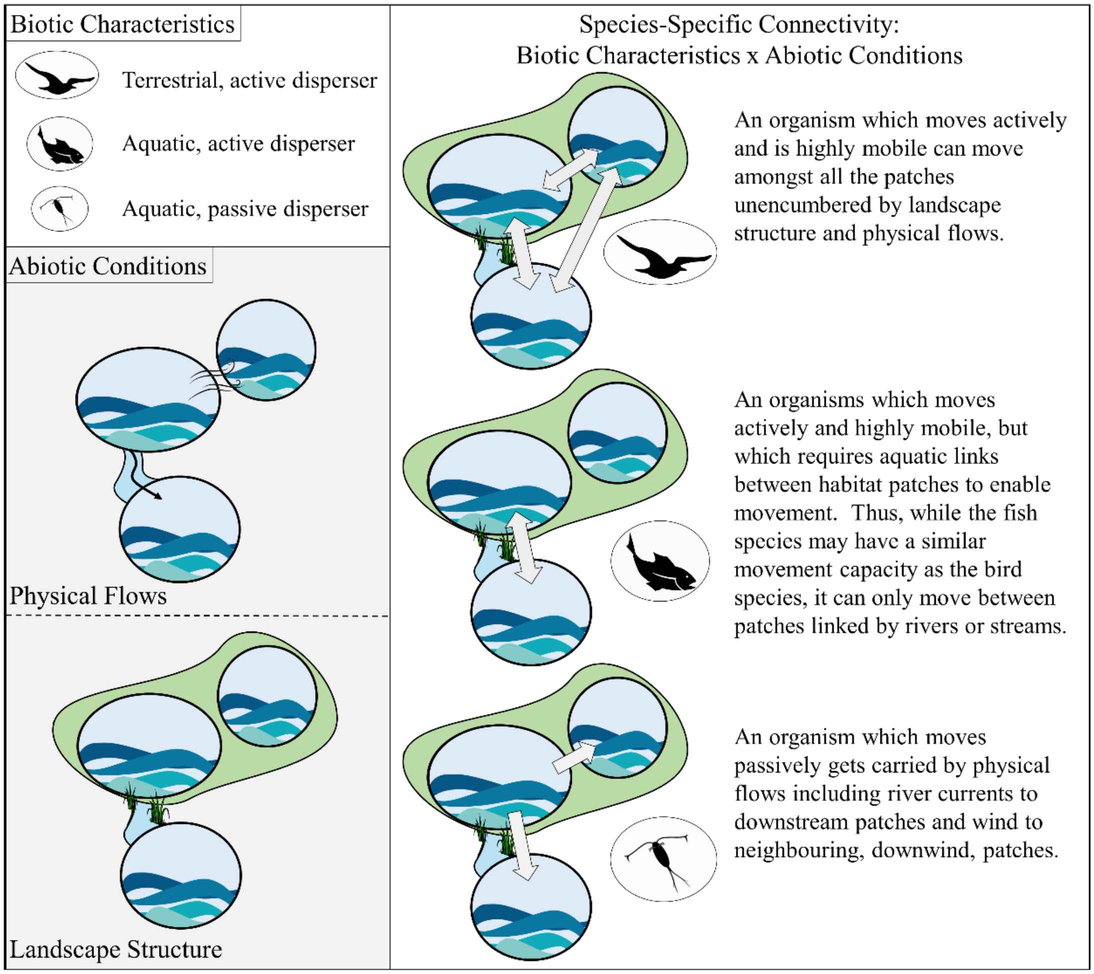

Figure 5.1 Example of how biotic characteristics and abiotic conditions interplay to create species-specific patch connectivity. For example, prevalent wind patterns connect the top two lakes for organisms which move passively, while riverine currents connect other lakes. Organisms which move actively, on the other hand, may rely on the river as a landscape structure connecting two of the lakes.

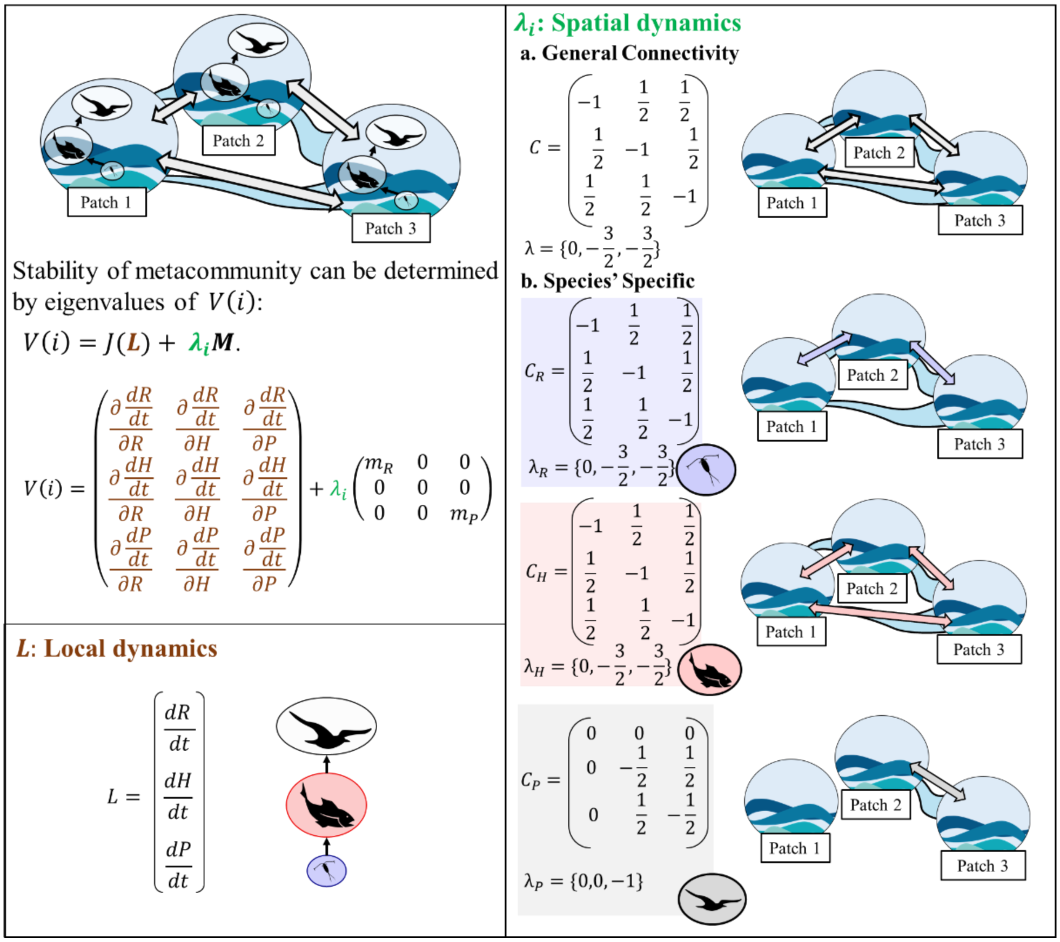

Figure 5.2 The stability of the metacommunity is determined by the eigenvalues of matrix V where, V(i) = J(L) + λ_iM. Here, J(L) is the Jacobian of the system of equations describing the dynamics of local community (L; e.g. equations 1-3), λ_i is the i^{th} eigenvalues of C, each c_{ij} describes the connection from patch j to patch i, and M is the movement matrix. Since $m_H = 0$ in the example, the herbivore does not move between patches.

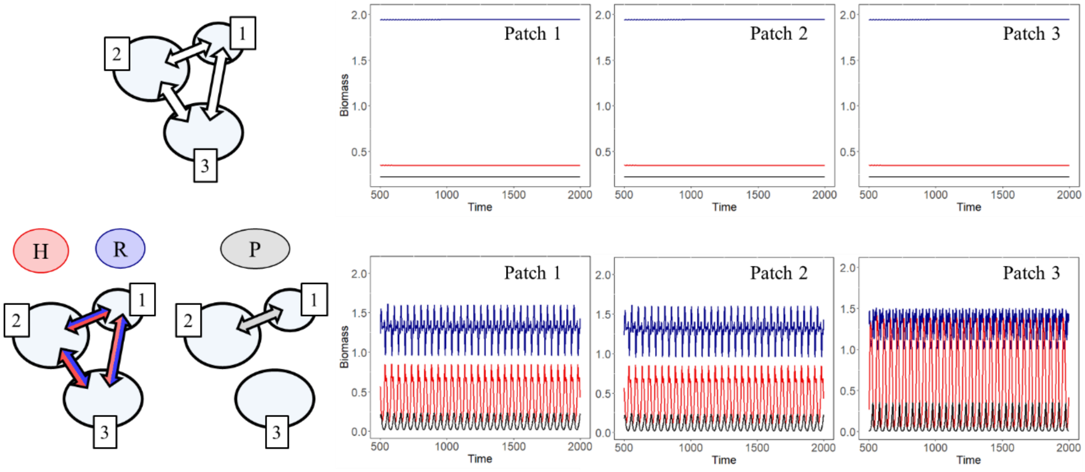

Figure 5.3 Assuming a three patch system and a tri-trophic food chain we can contrast biomass dynamics depending on whether we assume a species' specific connectivity of patches, or the scenario where the connectivity of patches is identical for all species'. First, we use a standard tri-trophic food chain model (e.g. equations 4 - 6) and observe that biomasses are stable (and the same across species) across all patches. When we modify the model to consider species-specific connectivity by preventing predators from accessing patch 3, we observe that biomass now oscillate across patches, resource biomass are lower than in the case where all patches are connected, and Patch 3 demonstrates different dynamics than patch 1 or 2. Here, the resource (R) is in blue, the herbivore (H) is in red, and the predator (P) is in black (Parameters are the same as in McCann *et al.* (2005): $K = 2.75$, $a_R = 2.5$, $a_H = 8.75$, $h_R = 0.4$, $h_H = 1.15$, $e_H = 0.8$, $e_P = 0.8$, $d_H = 1$, $d_P = 0.4$, $r = 1$ and spatial parameters are $m_R = 3.5$, $m_H = 0.01$, and $m_P = 0.1$).

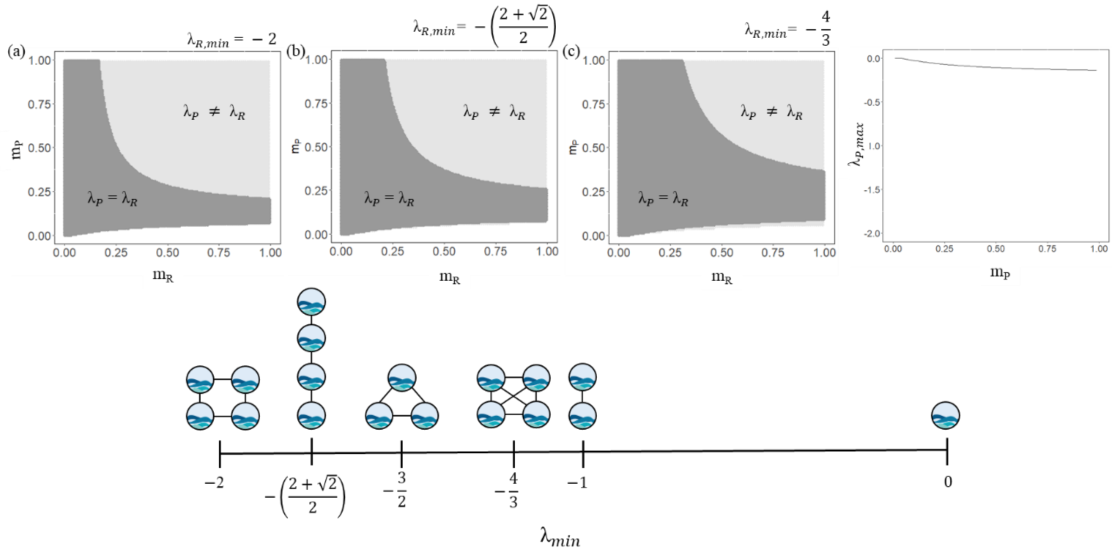

Figure 5.4 Stability of the equilibrium of a tri-trophic food chain depending on movement of the resource (m_R) and movement of the predator (m_P). The dark grey region represents the area where both general connectivity across all species (i.e. $\lambda_R = \lambda_P$) and species-specific connectivity are stable, while the light grey region represents the region where the predator and the resource have independent, or species-specific, connectivity and patch dynamics are stable (i.e. $\lambda_R \neq \lambda_P$). In this case, stability dynamics are driven by the minimum λ, so (a - c) represent three different minimum λ connectivity scenarios. Examples of patch connectivities which correspond to these minimum values are on the number line below. Finally, (d) demonstrates the maximum λ_P, when $\lambda_P \neq 0$ for which species-specific connectivity is stable. Parameters are the same as in McCann *et al.* (2005): $K = 2.75$, $a_R = 2.5$, $a_H = 8.75$, $h_R = 0.4$, $h_H = 1.15$, $e_H = 0.8$, $e_P = 0.8$, $d_H = 1$, $d_P = 0.4$, $r = 1$.

CHAPTER 6 Summary

Food webs are a fundamental part of community organization used to anticipate community responses to changes such as species loss. In fact, simple food webs were described as early as Darwin's Origin of Species (Darwin 1859), while graphical depictions were created as early as 1880 (see translated reference Camerano 1994). These early depictions were used to assist in the eradication of plant pests (Pierce *et al.* 1912), determine productivity of marine communities (Petersen 1915), and were firmly established in ecological literature in Charles Elton's Animal Ecology (Elton 1927). From these early beginnings of food web studies, ecological network research has proliferated with an increase in the number of highly resolved webs (e.g. in a recent study Brose *et al.* (2019) presented a compilation of 290 food webs representing 5736 species), metrics describing the complex networks (e.g. those 5736 species are involved in 222 151 feeding interactions), and a refinement in the interpretation of these webs (see review in Delmas *et al.* 2019). While historically food web studies were focussed on distilling and describing network structure, including the commonalities in food web metrics across disparate ecosystems, we now have the tools and data to examine how network structure changes along spatial and temporal gradients. Investigations which may potentially allow us to predict future food web structure.

The four objectives of my thesis were to i) examine drivers of spatial turnover in food web interactions, ii) comprehensively explore the consequences of omnivory on food-web stability and persistence, iii) determine whether network-level, species-level, and interaction-level metrics can predict persistence at each of these scales, and iv) investigate the role of abiotic controls on organismal flow on food web stability. I found that:

i) There was a high degree of interaction turnover across lakes. This turnover was driven primarily by changes in basal species, but also from the rewiring of interactions among shared species. Overall, interaction turnover was explained, in part by underlying environmental gradients (e.g. species richness), but a large amount of variation in food web structure remained unexplained. Moreover, contrary to previous food web models applied at the regional scale, none of the largely trait-based ecological drivers considered were effective predictors of site-specific food web structure. However, despite the high amount of spatial turnover in interactions, species' roles were highly conserved across the study lakes. Taken together, these results suggest two things. First, while trait-based food web models are effective predictors of forbidden links at the regional scale, they are not sufficient at local extents. Second, even though the species may be changing, the fundamental structures of food webs remain preserved.

ii) The expression of omnivory within empirical food webs and the persistence and stability of omnivory in food web models was highly context dependence. First, the expression of omnivory in empirical webs depended both on type of omnivory and the food web within which it is nested. Multi-resource omnivory interactions, however, were frequently over-expressed. Moreover, this importance of multi-resource omnivory scaled to whole food web model persistence where increased multi-resource omnivory resulted in an increased whole food web persistence. This result was mirrored at the module scale, whereby multi-resource omnivory demonstrated a wider region of persistence and stability than classic omnivory, however, it was the only type of omnivory to show this consistency between theoretical scales. These results demonstrate how module results may not scale to whole food webs. However, my results do suggest that multi-resource omnivory may act as a keystone module ensuring the persistence of communities.

iii) Despite emerging from collections of species linked by interactions, network metrics are most successful predictors of whole network persistence and least effective as predictors of individual species persistence. Interestingly, those whole network metrics which have emerged as important for ensuring food web persistence were not as effective predictors as less well studied metrics. For example, modularity has been widely demonstrated to influence network persistence, however, degree of initial food web modularity was not as strong a predictor of whole food web persistence as average in/out degree. Moreover, those structures which were successful predictors of network persistence were not the same structures which were successful predictors of interaction persistence. These results demonstrate that metrics which influence community persistence are not necessarily those metrics which promote interaction persistence. Indeed, in some cases, those metrics which are negatively correlated with community persistence are positively correlated with interaction persistence.

iv) My investigation into species movement and landscape effects on food web stability across space demonstrates that abiotic controls (i.e. landscape structure and physical flows) and species ability to move combine to lead to species-specific connectivity of patches. Indeed, I demonstrate that the previous assumption in meta-ecology - that patch connectivity is dependent only on the species' movement ability - is the exception rather than the rule. Through a novel mathematical framework incorporating species-specific connectivity into a multi-trophic metacommunity framework I demonstrate how species movement capabilities and abiotic conditions interact to change metacommunity stability. This opens up novel directions for further developments of meta-ecological theory from coexistence of complex communities to ecosystem function.

My thesis advances research on food web structure and persistence from both an empirical and theoretical perspective. It presents important evidence on the relationship between food web structure and persistence, including the variation in species interaction along spatial gradients, the importance of community effects, including indirect effects, on module stability, and the role of the landscape on species movement. In addition, insights gained in my thesis help build specific directions for the future including improving predictions of local community changes, and incorporating both spatial and temporal components into food web theory.

6.1 Bridging the gap between regional theory and local reality

Predicting food web structure is a central question in ecology. It is not just essential for describing and characterizing complex communities, but allows us to explore important theoretical questions regarding the influence of perturbations or species' extinctions on species co-existence and persistence. Currently, there are numerous food web models based on species' abundances, trait distributions, and optimal foraging practices which successfully predict food web structure (e.g. allometric diet breadth model predicts 5-65% of links, body size 13 -76 %; Gravel *et al.* 2013). These models, however are typically validated in highly resolved networks encompassing large geographic areas. These food webs are also typically constructed under the assumption that species' interactions are scale invariant; species A will always consume species B wherever they co-occur (e.g. Cohen *et al.* 2003; Blanchet *et al.* 2020). These topological food web models effectively narrow the field of all possible food web interactions to only those that are probable (e.g. frugivorous birds can only eat those fruits which fit in their mouths; González-Varo & Traveset 2016). At a regional scale, their extent may be broad enough to include all probable interactions at least once (e.g. (Eklöf *et al.* 2013; Brousseau *et al.* 2018). However, results from my second chapter demonstrate that even in an aquatic system with heavily size structured food webs (e.g. Woodward *et al.* 2005; Gravel *et al.* 2013), these topological, trait-based models are poor predictors of locally realized species interactions.

The gap between potential interactions predicted at regional scales and realized interactions in local food webs is an important one (e.g. Kondoh (2003) for a theoretical example of how foraging adaptation impacts food web stability). But, is this distinction simply an artefact of sampling effort? Historic approaches to developing food webs are based on the assumption that potential interactions are not realized because sampling was inadequate in some respect. Existing empirical evidence, however, suggests that species should adapt their feeding interactions depending on biotic and abiotic cues. For example, in a common garden experiment examining the impact of drought and temperature on bromeliad food webs, Amundrud and Srivastava (Amundrud & Srivastava 2019) demonstrated that drought conditions alone made tipulid larvae become omnivorous, a relationship that became stronger with increasing temperature. In this example, the fundamental tipulid niche includes predatory interactions, however, the realization of this interaction is dependent on the abiotic environment (e.g. drought) instead of biotic cues (e.g. presence of mosquitoes). Thus, the absence of a potential interaction actually gives researchers important information about the influence of the abiotic environment. Unfortunately, until recently we lacked the high quality, local food web data compiled from direct observation of species interactions to examine these questions. This is not trivial. Environmental and ecological perturbations are realized at a local scale. Thus, reconciling the differences in the predictive capacities of ecological network models at both local and regional scales is paramount for anticipating species-specific responses to change.

One way that we may be able to achieve better predictions at the local scale is to treat the compiled regional web of species interactions collected from a variety of direct and indirect sources, also called the metaweb (see Gravel *et al.* 2019), as the complete set of potential food web interactions. It represents a compilation of feeding interactions in which a species is morphologically and physiologically capable of engaging. This suite of interactions, however, may never be observed on a local scale. Our current trait-based approaches may be too coarse to capture the local realizations for two main reasons. First, these trait-based topological food web models are based on the assumption that the same model will work universally across species and sites (i.e. lakes) in a gradient. However, the role of traits is likely species dependent. For example, temperature may be a more important physical barrier for a cold water predator, while competition is more important for a warm water predator. Second, lake specific differences, and lake type (i.e. Tonn 1990) may drive the importance of model effects on food webs. For example, lakes within the same watershed likely have similar colonization histories, and thus may have different drivers of feeding interactions than lakes outside the watershed (e.g. priority effects - Fukami 2015). Thus, understanding processes structuring species interactions is aided by considering the specific history of the community in conjunction with environmental and species dependent traits. The combined effects of environmental and ecological factors on ecological network structure are beginning to be explored (e.g. Joffard *et al.* 2019), however this is still in its infancy.

This extends to structural properties as well. Currently, there is a dearth of experimental studies testing the impact of interaction strength on food web stability for complex food webs. Food webs represent complex community dynamics and as such are often hard to measure empirically (Jordano 2016). Validating theoretical predictions, particularly the importance of weak interactions, within natural systems is a critical next step for implementing appropriate conservation strategies. One challenge of putting theory to the test is the difficulties in amassing the kind of data required to measure interaction strength in natural communities, including feeding preference and biomass estimates (see Berlow *et al.* 2004). The approach taken in Chapter 3 & 4, however, demonstrates that frequency of consumption alone is sufficient to predict whole food web persistence. However, approaches to food web construction have emphasized the creation of cumulative, food web approaches, combining data from multiple direct and indirect sources assuming that co-occurrence implies interaction, into a binary network of observed interactions (e.g. Cohen *et al.* 2003). The six empirical webs presented in Chapter 3 are great examples of this, where there is a high resolution of the species interacting but little information on the frequency or preference with which species interact (but see Bascompte *et al.* 2005). The compiled food web approach is convenient because it does not require the heavy sampling needed to develop highly resolved webs based on direct evidence of interactions alone, however, building detailed webs based on direct evidence is becoming even more achievable with current technological advances. For example, advances in DNA barcoding allow researchers to resolve gut contents consistently to a species scale (e.g. Valentini *et al.* 2009), increasing the opportunity for rigorous experimental tests of persistence.

These techniques will also prove instrumental in constructing empirical food webs across communities. The results from Chapter 3 highlight that empirical food webs show no consistent patterns of omnivory prevalence across food webs, however, this could be due to sampling inconsistencies. In particular, our results demonstrate that multi-resource omnivory modules have a stronger impact on food web persistence than other omnivory modules. Multi-resource omnivory, however, is hard to observe in nature because of poor trophic resolution, especially at lower trophic levels (Hall & Raffaelli 1991). The artefacts of poor trophic resolution are likely the cause of the under-expression we found in multi-resource omnivory even within these well described webs. It is not enough, however, to just construct empirical food webs. Instead, these food webs should be constructed with similar sampling efforts at measured time intervals (Jordano 2016).

There is an inherent trade-off between collecting highly resolved food webs and collecting a broad range of food webs, particularly when attempting to answer questions about spatial drivers of species interactions (e.g. Banašek-Richter *et al.* 2004; Cattin *et al.* 2004). However, my results suggest that there is greater merit in characterizing a few food webs more thoroughly. One of the consequences of anthropogenic changes is that species' interactions are changing at a much greater rate than species are being extirpated. If these interactions are truly being lost and not just rewired (e.g. Gilljam *et al.* 2015; Bartley *et al.* 2019) or becoming more infrequent, then our results suggest this food web thinning and the resultant increase in frequency of consumption will cause a decrease in food web persistence, potentially leading to extinction cascades (Jacob *et al.* 2011). Without rigorously sampling food webs at multiple time points we risk missing these initial changes in food web structure where we can still mitigate interaction loss.

6.2 Importance of space for improving model complexity and predictions across scales

The antagonistic, trophic interactions presented in this thesis are not the only type of interactions important for food web persistence and stability (see Ings *et al.* (2009) for a comparison of ecological networks). They are not even the only type of antagonistic interaction, but rather a consumptive subset. While historically it has been common to distill whole communities into their mono-network building blocks like food webs, pollination, and non-trophic networks (e.g. refuge provisioning (positive) or predator interference (negative)), attention is turning to describing communities as compilations of their multi-layered parts (see Pilosof *et al.* 2017). For example, Kéfi *et al.* (2016) compiled an impressive multi-layered network for the Chilean coast including trophic, positive non-trophic and negative non-trophic interactions. This is one of the first well-described networks of its kind, but exhibits clear, predictable structure driven primarily by species traits (Kéfi *et al.* 2016). The resources and effort required to create highly resolved food webs is enormous, so constructing multi-layered networks is even more daunting, but it is doubtlessly an important piece of the ecological puzzle. The study of multi-layer networks is still in its infancy, but theoretical explorations of trophic and mutualist networks demonstrate that the impacts of network structure on stability depend on the type of network (Thébault & Fontaine 2010). How our predictions for ecological stability and resilience develop as we incorporate further interaction types into network theory is a fruitful avenue of research. In particular, the role of keystone modules within a multi-layer framework may reveal unintuitive feedback loops between species with direct interactions in only one layer of the ecological network.

Research suggests that the consideration of multi-layer networks as a delicate balance of conflicting forces will prove integral to illuminating patterns and processes governing persistence of communities (Pilosof *et al.* 2017). Critical to these advances, however, is the integration of both space and time as connective layers within these networks. We tend to view food webs, and ecological networks, as homogeneous mixtures of species interacting based on predictable sets of rules (e.g. Allometric Diet Breadth Model; Petchey *et al.* 2008, or Niche Model; Williams & Martinez 2000). In particular, we often consider food webs as discrete communities of species confined by clear recognizable borders, often landscape attributes. Species, however, do not necessarily recognize these borders. The artefacts imposed by these artificially assigned borders are now being recognized as we scale up to food webs coupled in macro-space (e.g. Warren 1989; Tscharntke *et al.* 2012; Timóteo *et al.* 2018); however, considering species specific micro-space use is just as important. If two species do not share the same micro-habitat then are they still competing for the same resources?

This question is not as rhetorical as it seems. For example, in the exploration of the impacts of seal culling on the Benguela ecosystem, the structural food web lumps lower trophic level species into broad categories such as phytoplankton, bacteria, microzooplankton, and detritus (Yodzis 1998). This example is not to highlight the systemic need for more highly resolved food web data – that has been addressed numerous times in the past (see Paine 1988; Hall & Raffaelli 1991; Cohen *et al.* 1993; Schmid-Araya *et al.* 2002). But rather, it has been chosen to illustrate the arbitrary unit of species and the arbitrary boundaries of space in food web literature. For example, phytoplankton community composition in Benguela has been shown to depend on a variety of factors including distance from the shoreline, and water column depth (Walker & Peterson 1991). This variation in community composition in turn influences average size of phytoplankton cells and food-chain efficiency (Walker & Peterson 1991). As such, the interspecific competition between phytoplankton species cannot be considered consistent across the large food web classified as Benguela. Further, the predation pressures on phytoplankton will change depending on the phytoplankton species identity and predator identity (e.g. goby, anchovy, or macrozooplankton). If instead, we focussed on micro-space habitats within the Benguela food web, building the community up to the broad system commonly used as a case study in food web research (e.g. Allesina & Pascual 2008, 2009; Petchey *et al.* 2008), we may find the scalable patterns and universality of theory that food web ecologists search for to properly understand these complex networks.

Predicting how space alters the food web structure is challenging. For example, while it might seem intuitive that dispersal should stabilize populations through recolonization-rescue dynamics following extinction of subpopulations, the process is more complicated. Instead, dispersal amongst populations can have a strong stabilizing influence only if populations remain asynchronous, otherwise dispersal can be destabilizing (e.g. see Abbott (2011) for a review). Similarly, in a spatially explicit model involving a resource, a superior consumer, an inferior consumer, and a predator which prefers the superior consumer, Gouhier *et al.* (2010)demonstrated that high dispersal (here a passive diffusion process for all species in the module) causes strong and synchronous food web fluctuations. Interestingly, weak environmental stochasticity can stabilize the food web fluctuations in this case, but when low dispersal is stabilizing the food web, weak environmental stochasticity then destabilizes it (Gouhier *et al.* 2010). Moreover, as demonstrated in Chapter 5, considering space alone is not enough – even within a simple tri-trophic food chain, incorporating species-specific connectivity amongst patches can lead to food web destabilization. Yet the importance of space remains an understudied frontier in theoretical food web research (but see Guzman *et al.* 2019).

6.3 Conclusions

In this thesis, I started by exploring how food web interactions change across a broad spatial gradient (Fig. 6.1a). After observing a high degree of interaction turnover, but the preservation of species roles, I conclude that there were key structural features present in food webs which contribute to their preservation (Fig. 6.1b). I then explored the importance of both omnivory and other, less studied structures on network persistence. However, I made a critical assumption that structures repeating across a spatial gradient are meaningful along a temporal gradient. Instead, the importance of both space *and* time on these structures should be examined as a variety of spatial dynamics (e.g. source-sink dynamics) could be important for the persistence of these structures across time, irrespective of their role as stabilizing architectures. To this end, I introduce a framework to incorporate species specific connectivity in a tractable way (Fig. 6.1c). This approach, however, still treats species interactions as fixed across time. Instead, interactions should be considered as ephemeral both across time and space (e.g. Fig. 6.1d). Integrating multilayer network approaches (e.g. De Domenico *et al.* 2016) should allow the flexibility in both spatial and temporal linkages between species in a network, allowing us to reconstruct communities in a more realistic pattern, potentially illuminating scalable, predictable patterns, and making global conclusions more tangible.

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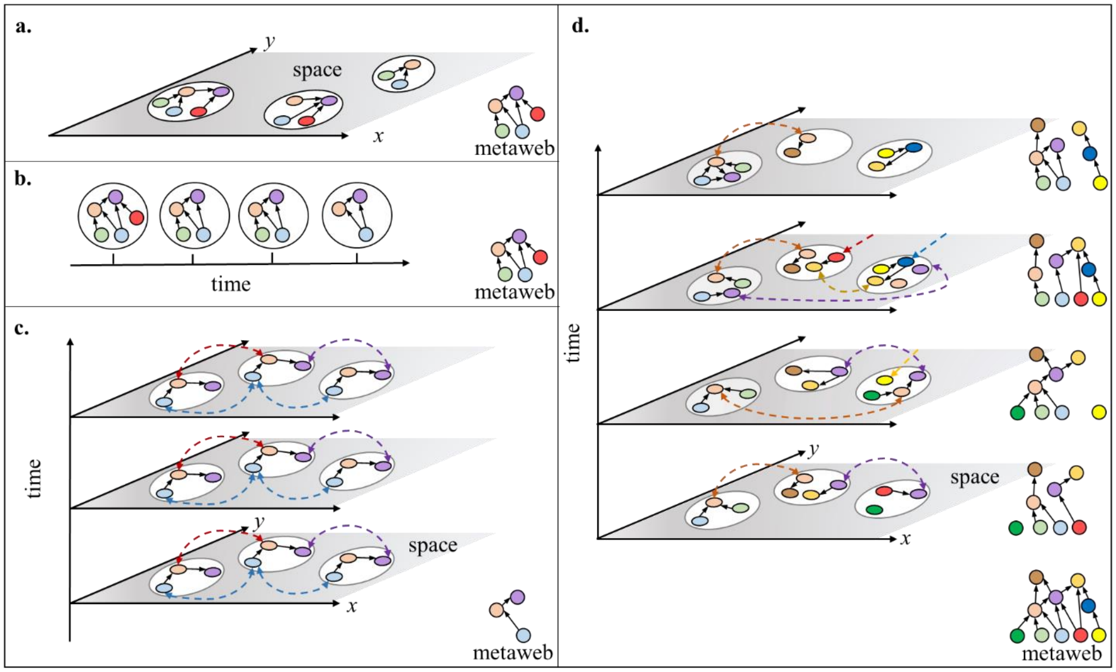

Figure 6.1 Visual representation of the relationship between time and space investigated in my thesis (a-c), followed by a visual depiction of the need to consideration both spatial and temporal linkages between species (d). Here, coloured circles represent populations, arrows indicate direction of antagonistic interactions, the metaweb depicts the overall network structure across space (a,c,d) or time (b,d). Shaded grey area represents a spatial gradient, and larger white circles indicate patches.

APPENDICES

APPENDIX A

Appendices for Chapter 2: Effects of species traits, motifs profiles, and environment on spatial variation in multi-trophic antagonistic networks

Appendix A.1 Data collection

In this appendix we describe the details of the Broad-scale Monitoring Sampling program and how we quantified sample effort to minimize sampling bias.

Data were collected as part of the Broad-scale Monitoring program by the Ontario Ministry of Natural Resources and Forestry (Sandstrom *et al.* 2013). In brief, two types of gill nets were used (1) a large mesh gill net that targeted fish > 20 cm in length, and (2) a small mesh gill net that targeted smaller fish. The large mesh gill nets consisted of two 24.8 m long nets (8 mesh sizes with 3.1 m panels) joined together. The mesh sizes were 38 mm, 51 mm, 64 mm, 76 mm, 89 mm, 102 mm, 114 mm, and 127 mm. The small mesh gill nets consisted of two 12.5 m long nets (5 mesh sizes with 2.5 m panels) joined together. The mesh sizes were 13 mm, 19 mm, 25 mm, 32 mm, and 38 mm. Nets were set when surface water temperatures were greater than 18 °C perpendicular to the shore across lake depths. Set time was a minimum of 12 hours for small mesh, and 16 for large mesh, up to a maximum of 22 hours. To ensure this, nets were set from 13:00 – 17:00 and lifted from 8:00 – 11:00 and sampling effort was standardized to the size of the lake. Fish were identified and total lengths were obtained for all fish sampled, while round weight, sex, gonad condition, otoliths (for aging fish) and stomach contents were collected for the first 50 individuals of the primary species (brook trout (*Salvelinus fontinalis*), lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), northern pike (*Esox* *lucius*), smallmouth bass (*Micropterus dolomieu*), and walleye (*Sander vitreus*)), and first 20 individuals of the secondary species (black crappie (*Pomoxis nigromaculatus*), bluegill (*Lepomis macrochirus*), largemouth bass (*Micropterus salmoides*), sauger (*Sander canadensis*), white sucker (*Catostomus commersonii*), and yellow perch (*Perca falvescens*)), all muskellunge (*Esox masquinongy*) caught, and all dead lake sturgeon (*Acipenser fulvescens*). Using the effort data for each lake along with the number of fish caught, catch-per-unit effort can be approximated and abundance data estimated in a similar way to Stasko et al. (2015).

Water samples were taken during the spring for each of the lakes and processed for nutrients by the Ontario Ministry of Environment and Climate Change. Temperature and dissolved oxygen profiles were obtained using digital YSI meters at 1 m intervals at the deepest location in the lake. Similarly, Secchi depths were obtained at these same locations. In summary, the following lake characteristics were measured at each lake: area, mean depth, lake volume, total dissolved solids, pH, total phosphorus, number of growing degree days, and temperature profiles.

Stomach content analyses from the first 50 primary species (brook trout, lake trout, lake whitefish, northern pike, smallmouth bass, and walleye), and first 20 secondary species (black crappie, bluegill, largemouth bass, sauger, white sucker, and yellow perch) were performed. Because of the nature of stomach content analyses some of these stomachs were empty, or contained unidentifiable items and items which were only identifiable down to a general group (e.g., fish, invertebrates). However, due to the nature of our hypotheses, we removed the stomachs which were empty, any stomach content item which was unidentifiable, and any stomach content item which was only identifiable down to a general group from our analysis. In the end, we constructed fish-only food webs.

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Appendix A.2 Rarefaction analysis

To minimize sampling bias in our dataset we calculated Chao1, an abundance-based richness estimator, to select lakes which indicated that sampling efforts detected a sufficient amount of interactions occurring in each lake (Chao 1987; Chiu *et al.* 2014). Chao1 was calculated as:

$$S_{Chao1} = S_{obs} + \frac{a_1(a_1-1)}{2(a_2+1)} \qquad \text{(S1)}$$

where a_i is the number of interactions observed i times, S_{obs} is the number of observed interactions, and S_{Chao1} is the number of predicted interactions. We retained lakes which had more than 5 observed interactions and a sampling effort sufficient to detect a minimum of 75% of the pairwise interactions occurring in each lake ($S_{\text{Obs}}/S_{\text{Chao1}}$ x 100). These values are consistent with, or higher than sampling efforts reported in other recent studies (Trøjelsgaard & Olesen 2013; Olito & Fox 2015; Trøjelsgaard *et al.* 2015; CaraDonna *et al.* 2017). We used the Vegan package in R to estimate Chao1 (Oksanen *et al.* 2016). Ultimately, 129 lakes consisting of 30 different species and 1793 interactions met our criteria for inclusion.

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Appendix A.3 Results with rare interactions removed

In this appendix we describe the results after rare interactions (i.e., those interactions occurring once in a lake) were removed and the analyses repeated. As reported in the main text, all results were qualitatively the same when rare interactions were removed.

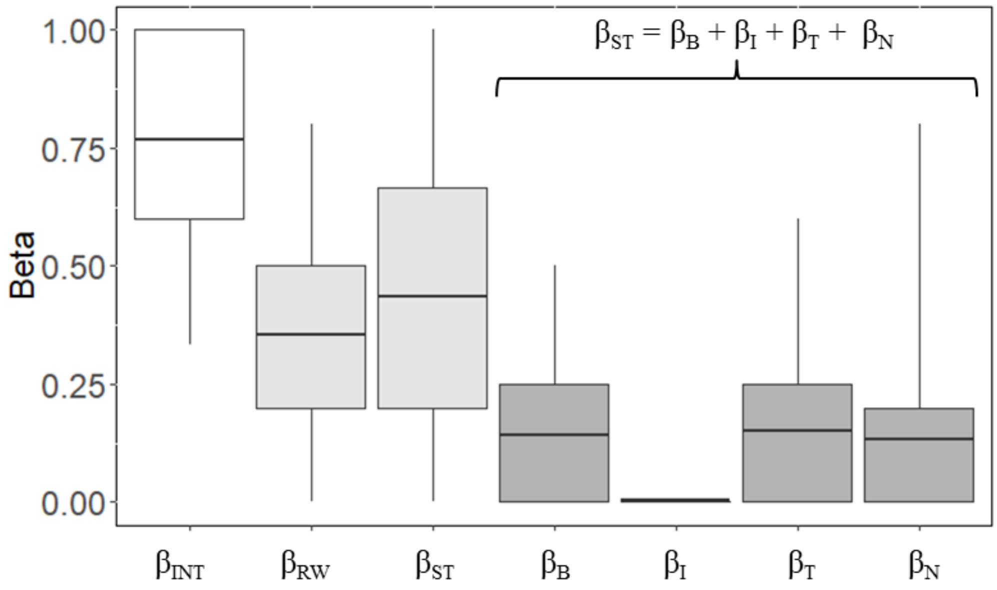

Figure A.3.1. Comparison of each interaction turnover component after the removal of rare interactions where error bars represent 95% confidence intervals, boxes represent interquartile range, and middle line represents overall mean. Here, β_{INT} represents the overall turnover in interactions between lakes, β_{RW} the turnover in interactions between lakes due to rewiring of the interactions between co-occurring species, β_{ST} the turnover in interactions between lakes due to species turnover, β_T the turnover in interactions due to changes in top species, β_I the turnover due to changes in intermediate species, β_B the turnover due to changes in basal species, and β_N turnover due to changes in both predator and prey species. The grey shading delineate what component of turnover the βs contribute to since $\beta_{INT} = \beta_{RW} + \beta_{ST}$ and $\beta_{ST} = \beta_{T} + \beta_{I} + \beta_{B} + \beta_{N}$.

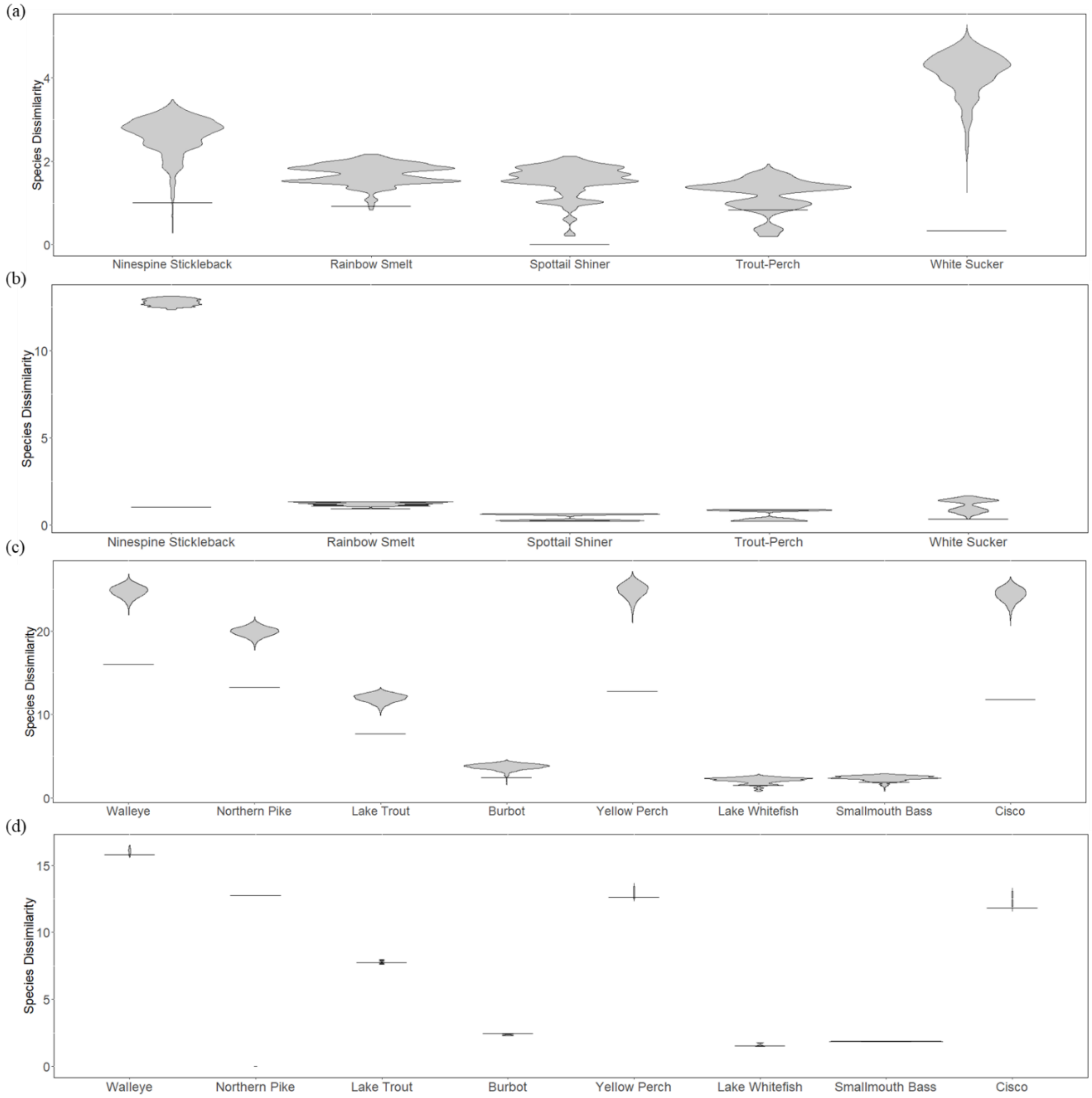

Figure A.3.2. Species-specific dissimilarity (dk) index comparing conservation of species’ roles between networks after the removal of rare interactions for (a & b) prey species, and (c & d) predator species where horizontal lines indicate the observed species dissimilarity index. Here, (a & c) demonstrate results from the random null model, while (b & c) demonstrate results from the generality null model. All species had an observed species dissimilarity index that was less than the random null model 5% of the time except trout-perch (*Percopsis omiscomaycus*; 13%), lake whitefish (5.48%), and smallmouth bass (5.84%). On the other hand, the only species which had an observed species dissimilarity index that was significantly less than the generality null model 5% were burbot, cisco, rainbow smelt, and white sucker. Note: here we classify prey species as those species for which we do not have stomach content analyses for since this is a multi-trophic system and all predators are also prey in some cases.

Table A.3.1. Results from the Monte Carlo process used to generate lake-specific interactions after the removal of rare interactions based on five base ecological interaction probability matrices and all subsequent permutations of those five base ecological models where A is an abundance based interaction probability matrix, P is a phylogenetic relatedness interaction probability matrix, C is a phylogenetic competition interaction probability matrix, T is a thermal tolerance interaction probability matrix, and G is a morphology interaction probability matrix. TSS values demonstrate overall model accuracy between the 5000 iterations of the Monte Carlo process and the observed interaction matrices for each lake, and Sens assesses model fit of only interactions which are observed present, avoiding the problem of false absences. Here, standard deviations for both TSS and Sens are in brackets.

	TSS	Sens
AxMxPxT	0.207 (0.21)	0.318 (0.184)
AxPxT	0.191 (0.234)	0.303 (0.203)
AxMXT	0.186 (0.234)	0.299 (0.203)
AxT	0.186 (0.235)	0.298 (0.204)
CxAxMxPxT	0.181 (0.208)	0.294 (0.182)
CxAxPxT	0.164 (0.228)	0.279 (0.198)

AxMxP	0.162 (0.249)	0.275 (0.214)
AxP	0.162 (0.249)	0.274 (0.215)
CxAxT	0.159 (0.228)	0.274 (0.199)
CxAxMxT	0.159 (0.228)	0.274 (0.198)
AxM	0.157 (0.247)	0.27 (0.213)
A	0.156 (0.247)	0.269 (0.213)
CxAxP	0.136 (0.243)	0.251 (0.209)
CxAxMxP	0.135 (0.242)	0.25 (0.209)
CxA	0.131 (0.242)	0.247 (0.208)
CxAxM	0.131 (0.241)	0.247 (0.208)
MxPxT	0.106 (0.253)	0.224 (0.219)
PxT	0.103 (0.252)	0.221 (0.218)
MxT	0.099 (0.252)	0.218 (0.217)
T	0.096 (0.251)	0.215 (0.216)
CxMxPxT	0.08 (0.243)	0.201 (0.209)
CxPxT	0.078 (0.243)	0.199 (0.209)
CxMxT	0.073 (0.24)	0.195 (0.207)
CxT	0.072 (0.24)	0.194 (0.206)
MxP	0.061 (0.25)	0.182 (0.212)
P	0.059 (0.249)	0.181 (0.211)
M	0.056 (0.247)	0.178 (0.209)
Null	0.054 (0.246)	0.177 (0.208)
CxMxP	0.041 (0.238)	0.165 (0.201)
CxP	0.04 (0.238)	0.164 (0.201)
CxM	0.037 (0.236)	0.162 (0.199)
C	0.035 (0.235)	0.16 (0.198)

Table A.3.2. The results from a permutational multivariate analysis of variance with distance matrices with 5000 permutations on different community interaction turnover metrics and environmental parameters *after the removal of rare interactions*. Here, values represent R^2s where bolded values indicate $p < 0.05$. The environmental parameters are all lake specific values where TP stands for total phosphorus, MEI stands for morphoedaphic index, and DD5 stands for degree days above 5 °C. The community interaction turnover metrics are defined as follows: β_{INT}: overall interaction turnover between lakes, β_{RW}: turnover in interactions between lakes due to rewiring of interactions between shared species, β_{ST}: turnover in interactions between lakes due to species turnover between lakes, and sub-components of β_{ST}, specifically β_{T}: turnover in interactions between lakes due to novel top species, β_{I}: turnover in interactions between lakes due to novel intermediate species, β_{B}: turnover in interactions between lakes due to novel basal species, and β_{N} : turnover in interactions between lakes due to both novel predator and prey species.

Parameter	β_{INT}	β_{RW}	β_{ST}	β_{B}	β_{I}	β_{T}	β_{N}
Latitude	**0.057**	-0.022	**0.076**	**0.105**	0.006	**0.054**	**0.029**
Area	0.007	0.007	0.007	0.008	-0.034	0.016	-0.001
Depth (mean)	**0.129**	-0.046	**0.201**	-0.035	0.165	**0.331**	**0.146**
pH	**0.015**	0.011	**0.027**	**0.037**	-0.014	0.004	**0.060**
MEI	0.008	0.029	-0.003	0.005	-0.215	0.007	-0.017
TP	**0.018**	-0.002	**0.037**	0.013	0.044	0.014	**0.078**
DD5	**0.021**	0.007	**0.032**	**0.061**	0.135	-0.107	**0.101**
Richness	0.111	0.077	0.115	0.068	-0.219	0.133	0.173

Appendix A.4 Environmental drivers of interaction turnover

In this appendix we provide specific predictions and figures demonstrating the relationship between different environmental variables and spatial interaction turnover in Ontario lakes (Fig S3 a - c) and a table presenting the correlation coefficients between each environmental variable (Table S3).

Latitude: Morris et al. (2014) show that the structure of antagonistic networks does not vary consistently across latitudinal gradients. However, Blanck and Lamouroux (2007) demonstrate that latitude has an impact on intraspecific variation in life-history traits of freshwater fish in Europe, thus potentially leading to trait mismatch between predator and prey (e.g. Olesen et al. 2011) with latitude increasing β_{RW} and by proxy, β_{INT}.

Area: Post et al. (2000) show that larger lakes support longer food chains caused by the addition of a top predator, suggesting a positive correlation between area differences between sites and β_{INT}. In addition, Robinson and Tonn (1989) show positive correlation between surface area and species richness in Albertan lakes which should influence β_{ST} primarily and β_{INT} by extension.

Lake Mean Depth (where mean depth is the ratio of volume to area; Rawson 1952): Lake mean depth is highly correlated with other measures such as thermal conditions, productivity, and euphotic-zone depth (Ryder *et al.* 1974). Further, depth is an important predictor of fish assemblages and species richness in north-central North American lakes (Johnson *et al.* 1977; Tonn & Magnuson 1982; Robinson & Tonn 1989). Thus, at the very least, mean depth should influence β_{ST}, but the connection to thermal conditions implies that mean depth should influence β_{RW} as well since increases in lake mean depth increases habitat separation within lakes.

pH: In Albertan lakes, pH and species richness are positively correlated (Robinson & Tonn 1989). In north-central North America, pH is an important predictor of fish assemblages and species richness (Johnson *et al.* 1977; Tonn & Magnuson 1982; Eadie *et al.* 1986). Thus, we expect that pH would be correlated with increased β_{ST} and β_{INT} by extension.

Morphoedaphic index (MEI): The MEI is a measure of productivity in lakes (e.g., Ryder et al. 1974) and productivity is a dominant driver of fish diversity (e.g., Guégan, Lek, & Oberdorff, 1998). Hence, we expect MEI to be positively correlated with β_{ST}.

Degree Days over 5 °C (DD5): Degree days over 5 °C is inherently linked to system productivity so as with MEI, we would expect DD5 to be positively correlated with β_{ST} given that productivity is a dominant driver of fish diversity (e.g. Guégan, Lek, & Oberdorff, 1998).

Species Richness: Increases in species richness increases the number of interactions possible in a system and thus should be positively correlated with β_{ST} and by extension β_{INT} (Burkle *et al.* 2016).

RESULTS:

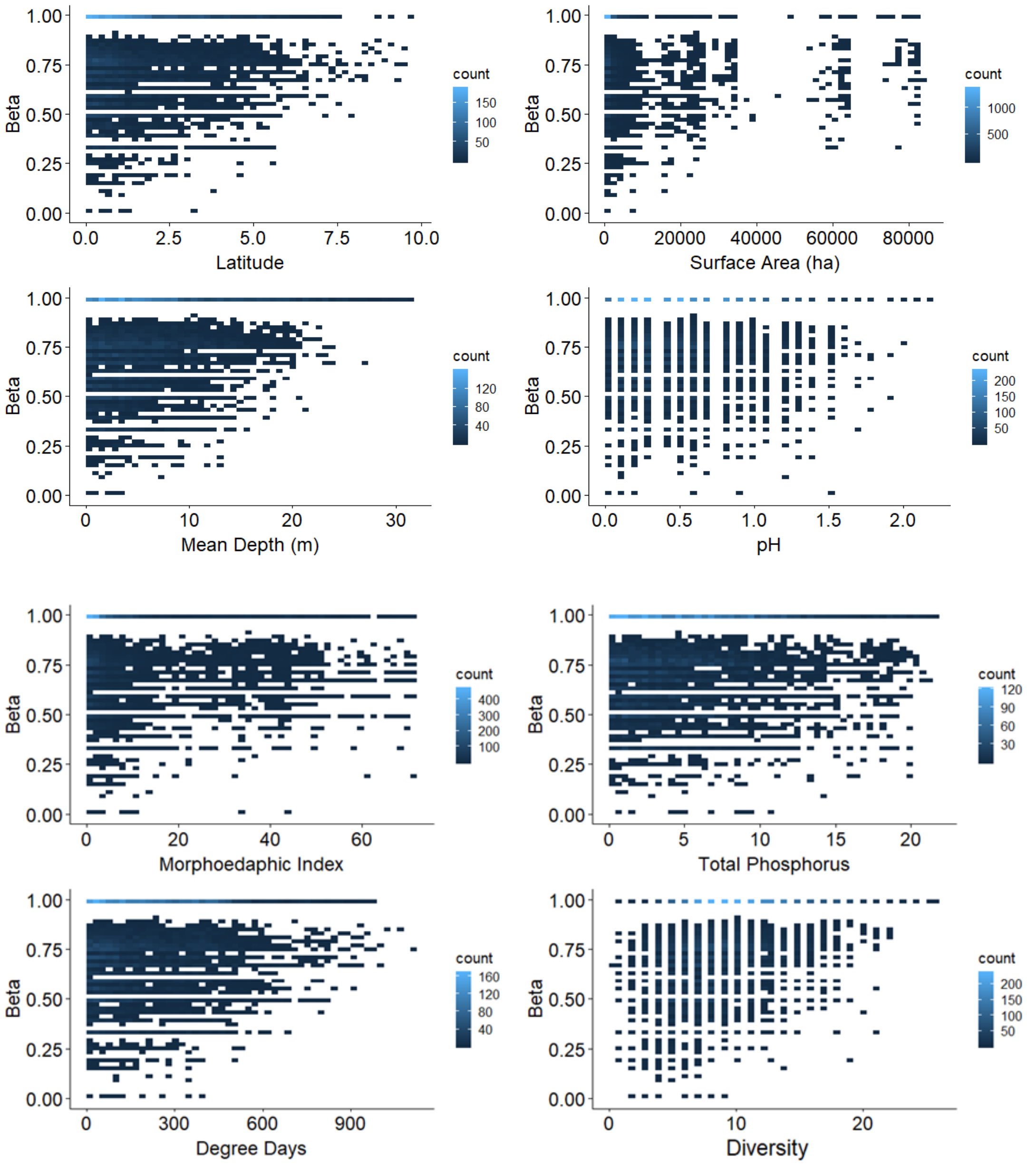

Figure A.4.3a. The relationship between βINT and environmental parameters where each point represents a lake-to-lake (n = 8256) comparison. Here the environmental parameters are represented by the absolute distance between the measured metrics for the lakes in question.

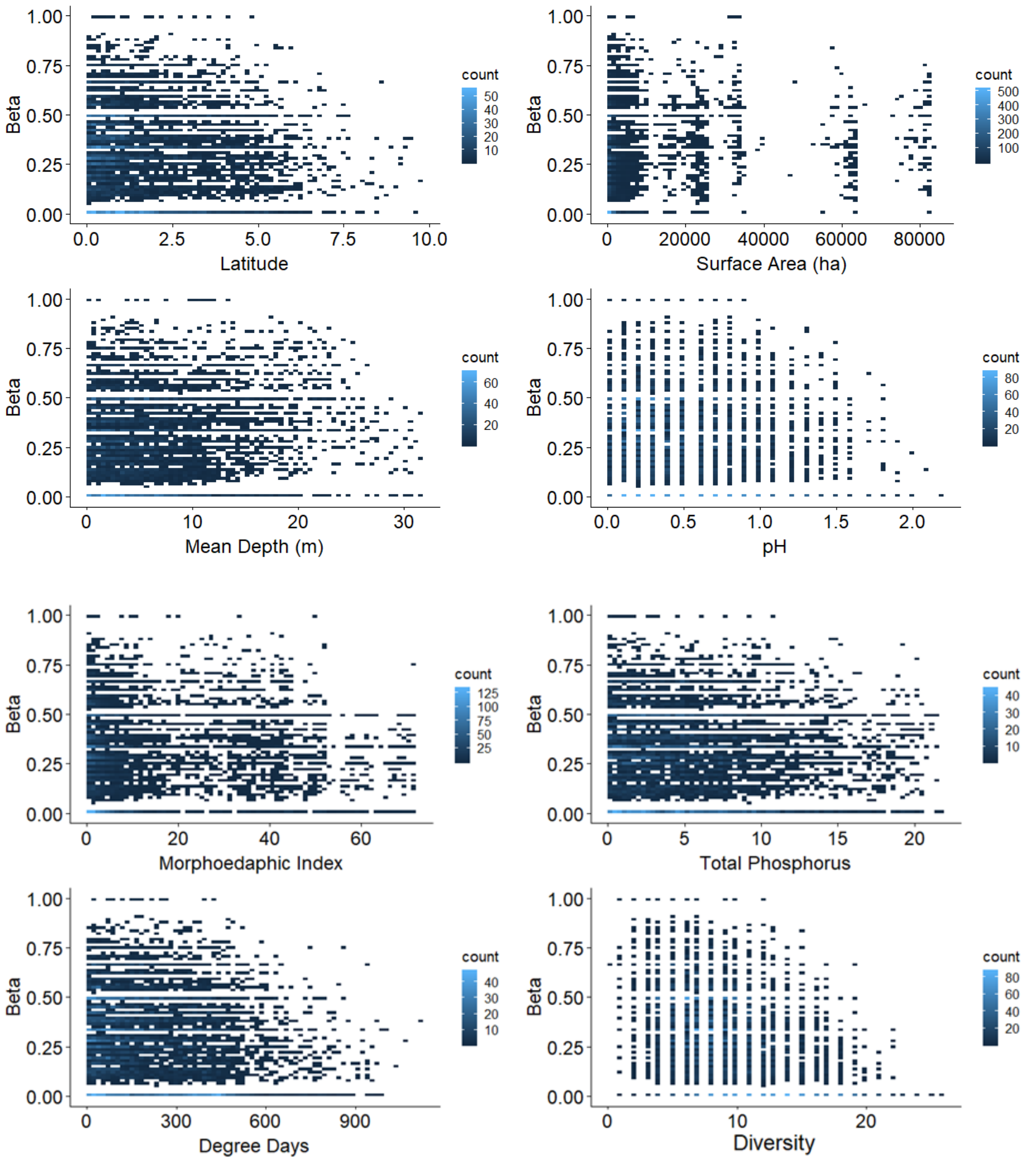

Figure A.4.3b. The relationship between βRW and environmental parameters where each point represents a lake-to-lake (n = 8256) comparison. Here the environmental parameters are represented by the absolute distance between the measured metrics for the lakes in question.

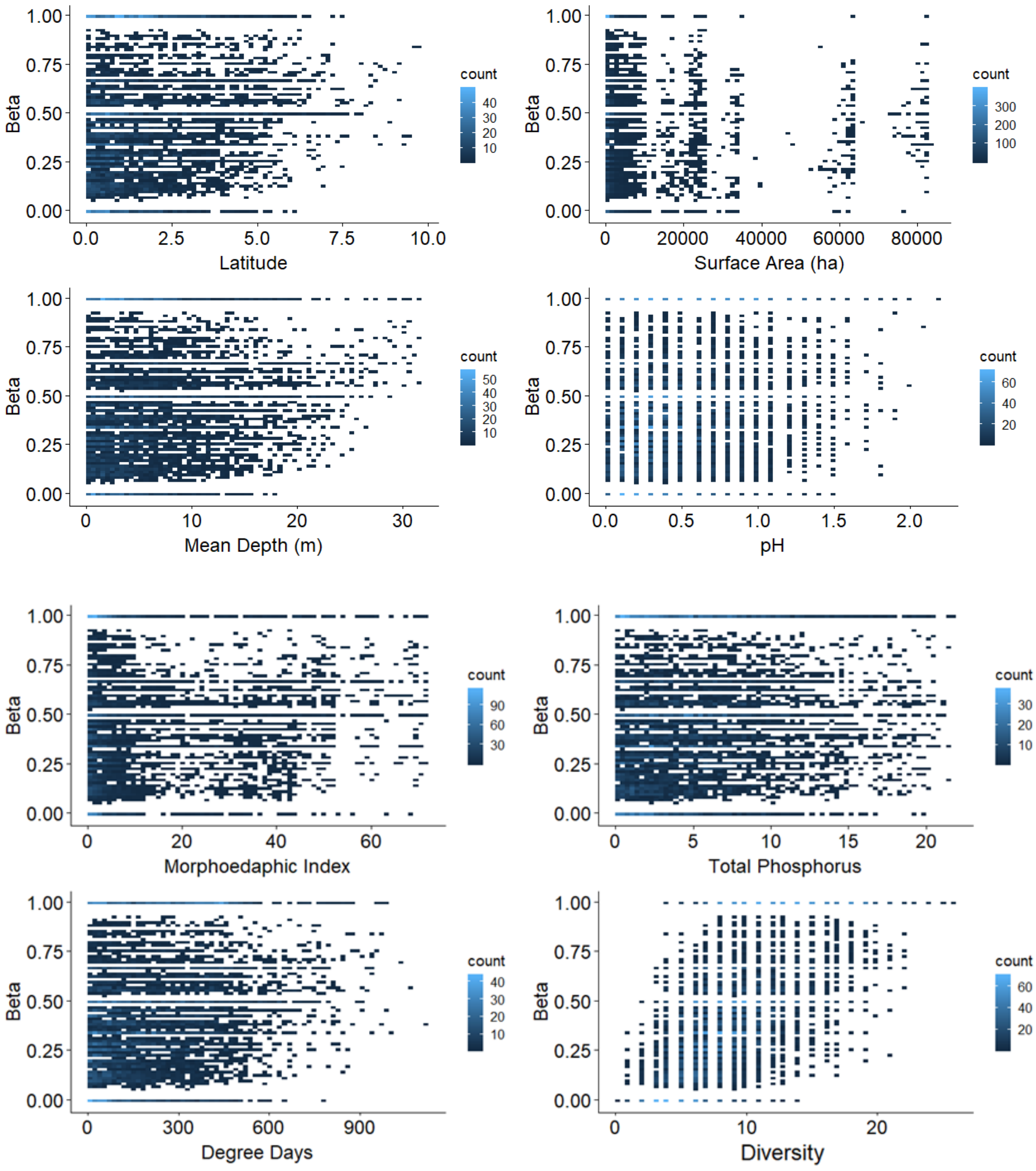

Figure A.4.3c. The relationship between βST and environmental parameters where each point represents a lake-to-lake (n = 8256) comparison. Here the environmental parameters are represented by the absolute distance between the measured metrics for the lakes in question.

Table S3. Correlation coefficients describing the relationship between each environmental parameter. The environmental parameters are all lake specific values where TP stands for total phosphorus, MEI stands for morphoedaphic index, and DD5 stands for degree days above 5 °C. Here, bolded and italicized values are ones that are greater than the |0.35| correlation threshold.

	Lat.	SA	Depth	pH	TP	Degree Days	MEI	Species Richness
Lat.	1	0.14	-0.09	-0.02	-0.05	***-0.58***	-0.29	-0.16
SA	0.14	1	0.00	0.12	0.05	-0.12	-0.00	0.35
Depth	-0.09	0.00	1	-0.23	***-0.43***	0.21	***-0.51***	0.31
pH	-0.02	0.12	-0.23	1	0.29	-0.13	***0.55***	0.15
TP	-0.05	0.05	***-0.43***	0.29	1	0.09	***0.37***	-0.03
Degree Days	***-0.58***	-0.12	0.21	-0.13	0.09	1	0.04	0.35
MEI	-0.29	-0.00	***-0.51***	***0.55***	***0.37***	0.04	1	-0.04
Species Richness	-0.16	0.35	0.31	0.15	-0.03	0.35	-0.04	1

Table A.4.4. The results from a perMANOVA with distance matrices with 5000 permutations on different community interaction turnover metrics and environmental parameters after total phosphous, morphoedaphic index, and degree days above 5 °C were removed. Here, values represent adjusted R^2s where bolded values indicate $p < 0.05$. The environmental parameters are all lake specific values. The community interaction turnover metrics are defined as follows: β_{INT}: overall interaction turnover between lakes, β_{RW}: turnover in interactions between lakes due to rewiring of interactions between shared species, β_{ST}: turnover in interactions between lakes due to species turnover between lakes, and sub-components of β_{ST}, specifically β_T: turnover in interactions between lakes due to novel top species, β_I: turnover in interactions between lakes due to novel intermediate species, β_B: turnover in interactions between lakes due to novel basal species, and β_N : turnover in interactions between lakes due to both novel predator and prey species.

Parameter	β_{INT}	β_{RW}	β_{ST}	β_B	β_I	β_T	β_N
Latitude	**0.063**	-0.042	**0.105**	**0.137**	-0.039	**0.040**	**0.040**
Area	0.008	-0.007	0.013	0.015	-0.013	0.010	0.002
Depth (mean)	**0.116**	-0.046	**0.168**	-0.089	**0.244**	**0.254**	**0.129**
pH	**0.028**	**0.031**	**0.028**	**0.050**	-0.023	-0.012	**0.056**
Richness	0.120	0.116	**0.134**	0.101	-0.057	0.070	**0.258**

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Appendix A.5 Detailed methodology on ecological drivers structuring interactions

In this Appendix we describe our method for constructing the metaweb and how we applied our hypothesized ecological drivers to this metaweb to predict species interactions at a lake specific level (see Fig. S4. for a visual representation of ecological drivers and hypotheses).

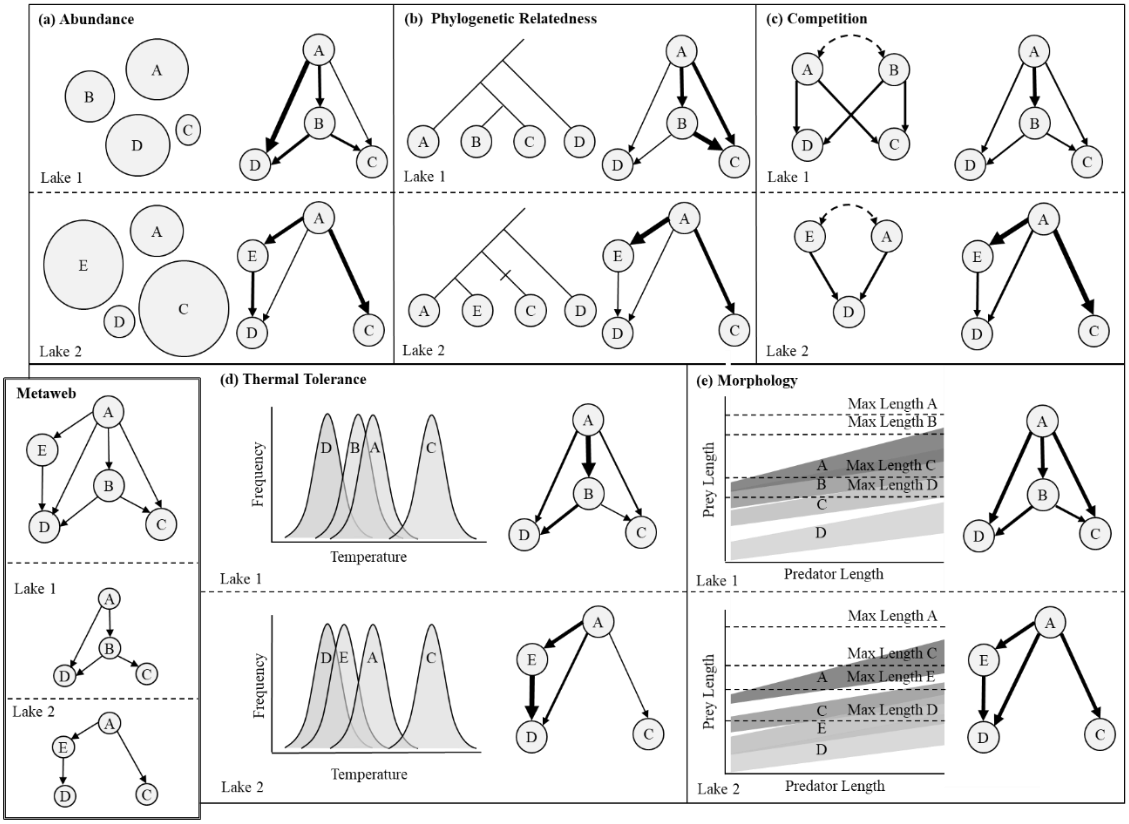


Figure A.5.4. The ecological drivers structuring interactions where size and direction of arrows indicate the strength of the relationship between predator and prey. The inset depicts the metaweb created from all interactions observed in the regional pool and the two local webs – lake 1 and lake 2. The metaweb constrains all interaction predictions, i.e. since E and C do not interact in the metaweb no trait combination will ever permit an interaction. In this way a trait approach is used to predict local realizations of the metawebs. (a) The influence of abundance, where the size of each circle is proportional to the abundance of that species within that lake, (b) the influence of phylogenetic relatedness, where the lines represent the phylogenetic relationship between the species present in that lake, (c) the influence of competition where dashed arrows indicate competition between closely related predators, (d) the influence of thermal tolerance where shaded distributions represent the thermal optimum for a given species, and (e) the influence of total length, where shaded bars represent the optimal prey length for a given predator length, and the dashed lines indicate the maximum size of each species sampled in that lake. The predator can still consume prey that are smaller than its optimal range, just at a lower probability.

We constructed a metaweb for species interactions using all observations of interactions across the 741 lakes in Ontario, and then used this metaweb as a base predictor of species interactions. In this way, interactions may exist between species pairs that were never observed to interact in a specific lake. The five interaction probability matrices presented below (and all possible permutations of those matrices; see Fig. S5) were then combined with the lake-specific realizations of the metaweb. Each lake-specific interaction probability matrix was normalized so that the matrix sums to one similar to the conceptual framework developed by Vázquez, Chacoff, & Cagnolo (2009) and applied by CaraDonna et al. (2017).

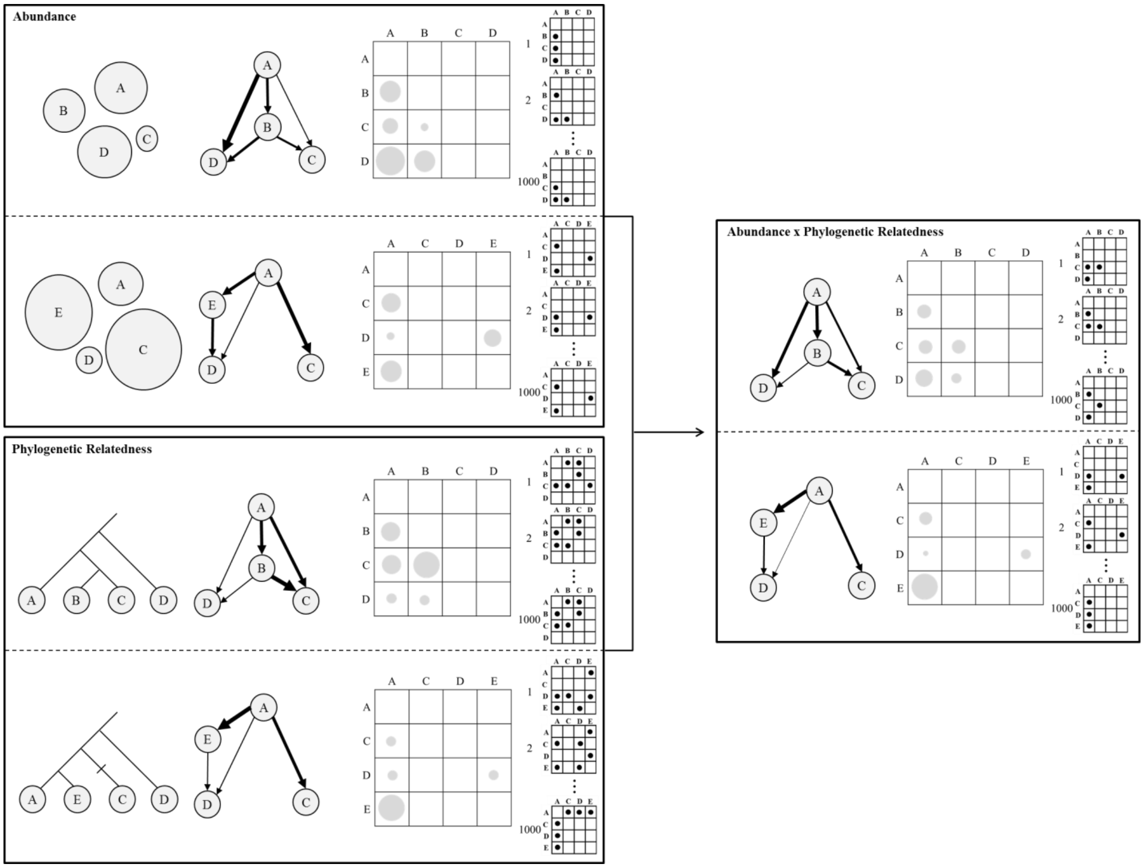


Figure A.5.5. A hypothetical example of the permutation analysis for abundance, phylogenetic competition, and abundance x phylogenetic competition. In each matrix the size of the grey circles indicates the probability of that species' interaction (where matrices are square and columns species consume row species) and the absence of a grey circle indicates a zero probability of that interaction occurring (e.g. a basal resource consuming a predator). Finally, in the right matrices, the black circles represent the presence of an interaction, while the empty squares represent the absence of an interaction. Interaction matrices were generated 5000 times based on abundance probabilities, and True Skill Statistics (TSS) and Sensitivity were calculated for each iteration.

Abundance:

The abundance matrix was developed using a catch per unit effort equation adapted from Hovgêrd and Lassen (2008).

$$N_{Sp} = \frac{C_{Sp,small}}{S_{sp,small}E_{small}} + \frac{C_{sp,large}}{S_{sp,large}E_{large}} \qquad \text{(S2)}$$

where $C_{sp,small}$ is the number of individuals of species *sp* caught in a small net, $C_{sp,large}$ is the number of individuals of species *sp* caught in a large net, E_{small} (or E_{large}) is the fishing effort (number of small, or large, nets set multiplied by the length of the net, in meters), $S_{sp,small}$ (or $S_{sp,large}$) is the selectivity of a small (or large) net for that species. In other words, it is the proportion of fish caught in the small (or large) nets and is consistent across all lakes (the number of individuals of a species caught in a small net across all the lakes adjusted by the total number of individuals of a species caught in any size net across all the lakes). The abundance of each species was then multiplied by the abundance of each other species sampled in the lake resulting in a matrix of potential species interactions based purely on the abundance of species in a lake. The cell values were then normalized by dividing each cell value by the matrix sum so that the normalized matrix sums to one, and each product abundance is expressed as a probability. This is similar to the conceptual framework developed by Vázquez et al. (2009) for plant-pollinator networks. One important issue that is unique to antagonistic food webs generated through observed stomach content data is when a species is observed in the stomach contents of a predator, but not captured in the gill net sample. In this case the abundance is set to zero under the assumption that the species was too rare to be caught in the gill net. We acknowledge, however, that this scenario could also arise because the prey item was too small to be effectively sampled by a gill net; however, this should be adjusted for by the selectivity correction factor.

Phylogenetic Relatedness:

We assembled a fish phylogeny using information from the sequence data available within the BCF and BCFB project files in BOLD (www.barcodinglife.org; Hubert et al. (2008)). We followed the steps outlined in (Hubert *et al.* 2008) to align sequences, and then used the phangorn package in R to calculate molecular distances between species (Schliep 2011). All of our species were present in the barcode database with the exception of the hybrid species, Splake (*Salvelinus namaycush x Salvelinus fontinalis*) which were approximated using the average of Lake trout (*Salvelinus namaycush*) and Brook trout (*Salvelinus fontinalis*). These molecular distances were then subtracted from 1 to create a similarity matrix of probabilities because more closely related species have been shown to have a higher probability of interaction (Cattin *et al.* 2004; Rezende *et al.* 2009; Eklöf & Stouffer 2016). Lake-specific phylogenetic matrices were then normalized to one by dividing each cell by the matrix sum. It is important to note here that this ecological driver is slightly different than the others since the phylogenetic relationship between fish will not vary between lakes, instead what varies is the realization of this variation which ultimately makes each lake-specific interaction matrix unique.

Competition:

The metaweb was used to determine shared predators for a prey. The number of shared predators present in a lake were used to calculate the lake specific probabilities that a predator would interact with a prey. For example, if three shared predators are present in a lake then each predator would have a 1/3 probability of interacting with the prey species because of exploitative competition. Conversely, if only one predator is present then it has no competitors and, thus, a higher probability of interacting with the prey.

Thermal Tolerance:

The amount of time a species spends in the range of temperatures covered by their thermal niche can be described with a normal distribution where the mean is the species-specific thermal optimum and the standard deviation is 2.02 °C (Magnuson *et al.* 1979). If thermal tolerance is the driver for interaction turnover, the probability of two species interacting can be measured by looking at the overlap between the thermal distributions of two species. Both the amount of overlap, and the individual species distributions depend on the thermal profile of the lake, so by bounding the two distributions by the maximum and minimum temperatures in the thermal profiles collected from each lake at the time of sampling, these distributions become lake specific. Probability of interaction was then defined as the area of overlap divided by the total area of that species' thermal distribution in that lake (see Fig. S6).

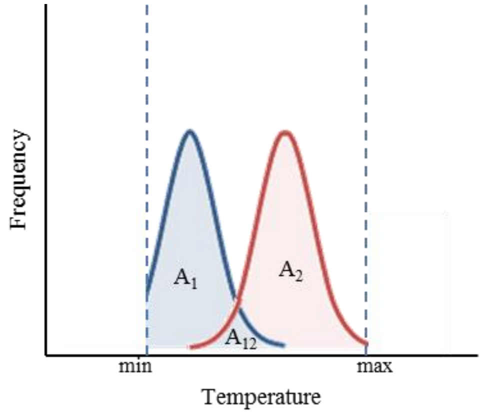


Figure A.5.6. Hypothetical thermal distributions for two species in lake X. Blue species is a cold-water tolerant species found at lower depths than red species, while red species has a higher thermal optimum and inhabits the epilimnion. The probability that a blue species encounters a red species is then A_{12}/A_1, and the probability that a red species encounters a blue species is then A_{12}/A_2. The dashed lines represent the minimum and maximum temperature for lake X.

We assembled species-specific thermal optima from literature (Wismer & Christie 1987; Coker *et al.* 2001; Hasnain *et al.* 2010). A complete list of species and thermal optima with the literature sources can be seen in Table S5.

Table A.5.5. A list of thermal optima (TO; °C) and references for all species sampled in the gill net surveys.

Common Name	**Latin Name**	**TO**	**Reference**
Alewife	*Alosa pseudoharengus*	19.70	Wismer and Christie 1987
Banded Killifish	*Fundulus diaphanus*	21.15	Wismer and Christie 1987
Black Bullhead	*Ameiurus melas*	23.50	Hill 1970
Black Crappie	*Pomoxis nigromaculatus*	20.96	Wismer and Christie 1987
Blackchin Shiner	*Notropis heterodon*	16.50	Wismer and Christie 1987
Blacknose Dace	*Rhinichthys atratulus*	24.63	Cincotta and Stauffer 1984
Blacknose Shiner	*Notropis heterolepis*	18.30	Roberts et al. 2006
Bluegill	*Lepomis macrochirus*	28.91	Wismer and Christie 1987
Bluntnose Minnow	*Pimephales notatus*	23.86	Wismer and Christie 1987
Bowfin	*Amia calva*	30.50	Wismer and Christie 1987
Bridle Shiner	*Notropis bifrenatus*	17.00	Hanson II 2013

Brook Silverside	*Labidesthes sicculus*	24.50	Wismer and Christie 1987
Brook Stickleback	*Culaea inconstans*	21.30	Coker et al. 2001
Brook Trout	*Salvelinus fontinalis*	17.47	Hasnain et al. 2010
Brown Bullhead	*Ameiurus nebulosus*	23.04	Wismer and Christie 1987
Burbot	*Lota lota*	13.62	Wismer and Christie 1987
Central Mudminnow	*Umbra limi*	13.00	Scott and Crossman 1973
Channel Catfish	*Ictalurus punctatus*	26.01	Hasnain et al. 2010
Chinook Salmon	*Oncorhynchus tshawytscha*	14.00	Wismer and Christie 1987
Cisco	*Coregonus artedi*	11.44	Wismer and Christie 1987
Common Carp	*Cyprinus carpio*	28.31	Wismer and Christie 1987
Common Shiner	*Luxilus cornutus*	21.90	Coker et al. 2001
Creek Chub	*Semotilus atromaculatus*	20.80	Coker et al. 2001
Deepwater Sculpin	*Myoxocephalus quadricornis*	5.00	Wismer and Christie 1987
Emerald Shiner	*Notropis atherinoides*	17.15	Wismer and Christie 1987
Fallfish	*Semotilus corporalis*	22.00	Hasnain et al. 2010
Fathead Minnow	*Pimephales promelas*	24.62	Wismer and Christie 1987
Finescale Dace	*Chrosomus neogaeus*	24.10	Hasnain et al. 2010
Fourhorn Sculpin	*Myoxocephalus quadricornis*	5.00	Hasnain et al. 2010
Freshwater Drum	*Aplodinotus grunniens*	24.41	Wismer and Christie 1987
Gizzard Shad	*Dorosoma cepedianum*	18.85	Wismer and Christie 1987
Golden Redhorse	*Moxostoma erythrurum*	26.00	Yoder and Emery 2003
Golden Shiner	*Notemigonus crysoleucas*	22.04	Wismer and Christie 1987

Goldeye	*Hiodon alosoides*	29.00	Coker et al. 2001
Grass Pickerel	*Esox americanus*	25.70	Wismer and Christie 1987
Greater Redhorse	*Moxostoma valenciennesi*	18.90	Jenkins 1970
Green Sunfish	*Lepomis cyanellus*	26.01	Wismer and Christie 1987
Iowa Darter	*Nocomis biguttatus*	25.00	Wismer and Christie 1987
Johnny Darter	*Etheostoma nigrum*	24.50	Wismer and Christie 1987
Lake Chub	*Couesius plumbeus*	19.00	Darveau et al. 2012
Lake Sturgeon	*Acipenser fulvescens*	13.50	Coker et al. 2001
Lake Trout	*Salvelinus namaycush*	11.61	Wismer and Christie 1987
Lake Whitefish	*Coregonus clupeaformis*	11.25	Wismer and Christie 1987
Largemouth Bass	*Micropterus salmoides*	29.18	Wismer and Christie 1987
Logperch	*Percina caprodes*	16.96	Wismer and Christie 1987
Longear Sunfish	*Lepomis megalotis*	22.86	Jennings 1991
Longnose Dace	*Rhinichthys cataractae*	13.22	Wismer and Christie 1987
Longnose Gar	*Lepisosteus osseus*	28.66	Wismer and Christie 1987
Longnose Sucker	*Catostomus catostomus*	10.85	Wismer and Christie 1987
Margined Madtom	*Noturus insignis*	25.10	Reutter and Herdendorf 1976
Mimic Shiner	*Notropis volucellus*	23.86	Lyons 1987
Mooneye	*Hiodon tergisus*	25.00	Wismer and Christie 1987
Mottled Sculpin	*Cottus bairdii*	16.47	Wismer and Christie 1987
Muskellunge	*Esox masquinongy*	23.34	Wismer and Christie 1987
Ninespine Stickleback	*Pungitius pungitius*	14.00	Wismer and Christie 1987
Northern Pike	*Esox Lucius*	18.20	Wismer and Christie 1987

Northern Redbelly Dace	*Chrosomus eos*	25.30	Wismer and Christie 1987
Pearl Dace	*Margariscus margarita*	16.20	Coker et al. 2001
Pumpkinseed	*Lepomis gibbosus*	27.93	Wismer and Christie 1987
Quillback	*Carpiodes cyprinus*	21.37	Wismer and Christie 1987
Rainbow Smelt	*Osmerus mordax*	12.01	Wismer and Christie 1987
Rainbow Trout	*Oncorhynchus mykiss*	16.75	Wismer and Christie 1987
River Redhorse	*Moxostoma carinatum*	23.30	Becker 1983
Rock Bass	*Ambloplites rupestris*	24.59	Wismer and Christie 1987
Rosyface Shiner	*Notropis rubellus*	23.55	Wismer and Christie 1987
Round Goby	*Neogobius melanostomus*	16.00	Young et al. 2010
Round Whitefish	*Prosopium cylindraceum*	8.26	Wismer and Christie 1987
Sand Shiner	*Notropis stramineus*	32.00	Platania and Altenbach 1998
Sauger	*Sander Canadensis*	19.68	Wismer and Christie 1987
Shorthead Redhorse	*Moxostoma macrolepidotum*	26.75	Wismer and Christie 1987
Silver Redhorse	*Moxostoma anisurum*	24.00	Coutant 1977
Slimy Sculpin	*Cottus cognatus*	9.35	Wismer and Christie 1987
Smallmouth Bass	*Micropterus dolomieu*	25.20	Wismer and Christie 1987
Splake	*Salvelinus fontinalis x Salvelinus namaycush*	13.97	Goddard and Tait 1976
Spoonhead Sculpin	*Cottus ricei*	6.00	Hasnain et al. 2010
Spotfin Shiner	*Cyprinella spiloptera*	27.79	Wismer and Christie 1987
Spottail Shiner	*Notropis hudsonius*	21.14	Wismer and Christie 1987

Striped Shiner	*Luxilus chrysocephalus*	27.90	Yoder and Emery 2003
Threespine Stickleback	*Gasterosteus aculeatus*	11.96	Wismer and Christie 1987
Trout-perch	*Percopsis omiscomaycus*	13.40	Wismer and Christie 1987
Walleye	*Sander vitreus*	19.84	Wismer and Christie 1987
White Bass	*Morone chrysops*	23.90	Wismer and Christie 1987
White Sucker	*Catostomus commersonii*	21.08	Wismer and Christie 1987
Yellow Bullhead	*Ameiurus natalis*	28.00	Yoder and Emery 2003
Yellow Perch	*Perca flavescens*	19.06	Wismer and Christie 1987

Morphology:

Body size has been shown to be very important in structuring interaction networks across terrestrial and aquatic systems (Eklöf *et al.* 2013). This is true in aquatic systems in particular because gape size is highly correlated to body size and freshwater fish are predominantly gape limited (e.g., Woodward et al. 2005). As such, the likelihood of interaction between a predator and prey should reflect the relationship between observed prey size and the optimal prey size range based on predator gape size. Thus, we predict that predators have a high probability of interaction with prey inside their optimal prey size range.

Scott and Crossman (1973) was used to determine the relationship between gape width and total length for all species in our networks. Species-specific gape widths (see Table S6) were then used to estimate optimal prey width for each predator using the conversion factor suggested by Gill (2003) (conversion factor = 0.6).

Table A.5.6. The coefficients for the relationship between gape width and total length of predator for all species from the stomach content survey**.** All relationships are of the form:

gape width = *a* · total length, where *a* is either the coefficient minimum, or maximum, optimal prey length.

Species	Minimum	Maximum
Black Crappie	0.065	0.078
Bluegill	0.039	0.051
Brook Trout	0.049	0.089
Brown Bullhead	0.072	0.090
Burbot	0.046	0.058
Channel Catfish	0.042	0.073
Cisco	0.044	0.056
Goldeye	0.058	0.074
Lake Whitefish	0.026	0.039
Lake Chub	0.030	0.053
Lake Sturgeon	0.021	0.054
Lake Trout	0.048	0.094
Largemouth Bass	0.073	0.103
Longnose Sucker	0.023	0.029
Mooneye	0.053	0.060
Muskellunge	0.066	0.081
Northern Pike	0.072	0.104
Pumpkinseed	0.043	0.068

Rainbow Trout	0.043	0.071
Rock Bass	0.061	0.094
Sauger	0.049	0.090
Smallmouth Bass	0.400	0.463
Splake	0.057	0.064
Walleye	0.059	0.103
White Sucker	0.021	0.030
Yellow Perch	0.043	0.087

Probability of interaction at a lake specific level between predator and prey species were then calculated by determining the proportion of overlap of the quadrilateral bounded by the size range of predator individuals sampled in the stomach content surveys of the lake, the maximum size of that prey species found in the lake ($\max_{prey}$), and the upper and lower limits of the total length to optimal prey size relationship (see Fig. S5.7 & S5.8).

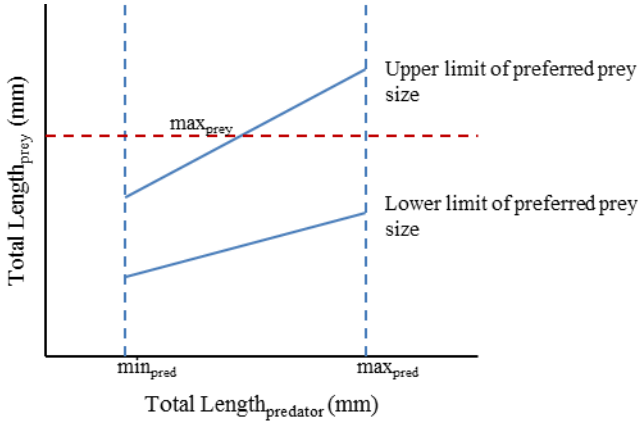


Figure A.5.7. The hypothetical relationship between a predator species and a prey species within a lake. The predator size range was obtained from the stomach content surveys, while the $\max_{prey}$ measurement was obtained from the fish surveys. Species-specific gape widths can be found in Table S5.

Here it was assumed that a predator could conceivably encounter any size prey between zero and $\max_{prey}$, but would prefer one within the optimal prey size range. Because of this, it was assumed that encountering a prey of size greater than $\max_{prey}$ was impossible, and consuming a prey item that was smaller than the lower limit was possible, but occurred with a probability evenly decaying from 1 to 0 (see Fig. S8).

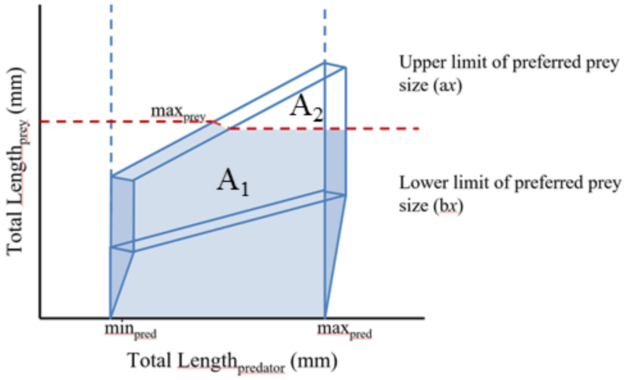


Figure S8. The hypothetical relationship between a predator species and a prey species within a lake. Here the z-axis is the probability of consumption, where $z_{max} = 1$.

The calculations for the total area are as follows:

TOTAL:

$$\text{A1} = \iint_{bx}^{ax} 1 \; dy\, dx$$

$$= \int_{minPred}^{maxPred} (a-b)x \;\, dx$$

$$= \frac{(a-b)}{2} x^2 \text{ (from minPred to maxPred)}$$

$$= \frac{(a-b)}{2} (maxPred^2 - minPred^2)$$

A$_2$ $= \iint_0^{bx} \frac{1}{bx} y \; dy \, dx$

$= \int_{minPred}^{maxPred} \frac{1}{2bx} y^2 dx$ (from 0 to bx)

$= \int_{minPred}^{maxPred} \frac{1}{2} bx \; dx$

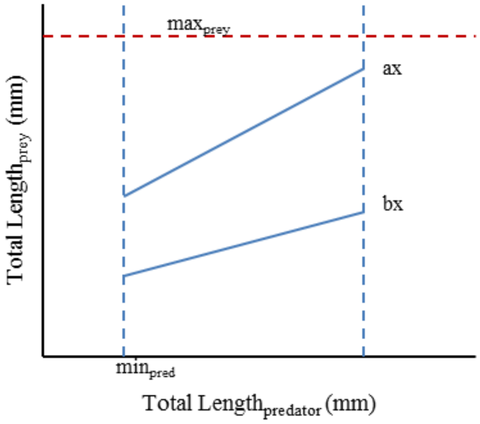
$= \frac{1}{4} bx^2$ (from minPred to maxPred)

$$= \frac{1}{4} b((maxPred)^2 - (minPred)^2)$$

$$Total = A_1 + A_2$$

As probability of interactions were calculated at lake specific levels between predator and prey species from the proportion of overlap of the quadrilateral bounded by the size range of individual predators and the maximum size of specific prey species, six different scenarios result from this approach: (1) when the maximum prey size is greater than the upper limit of preferred prey size across the range of predator species sizes, (2) when the maximum prey size is less than the lower limit of preferred prey size across the range of predator species sizes, (3) when the maximum prey size is less than the upper limit of preferred prey size across the range of predator species sizes, but intersects the lower limit of preferred prey sizes at some point during the range of predator species sizes, (4) when the maximum prey size is greater than the lower limit of preferred prey size across the range of predator sizes, but intersects the upper limit of preferred prey sizes at some point during the range of predator species sizes, (5) when the maximum prey size intersects both the lower limit of preferred prey sizes and the upper limit of preferred prey sizes at some point during the range of predator species sizes, and (6) when the maximum prey size is greater than the lower limit of preferred prey sizes across the range of predator species sizes, and is less than the upper limit of preferred prey sizes across the range of predator species sizes.

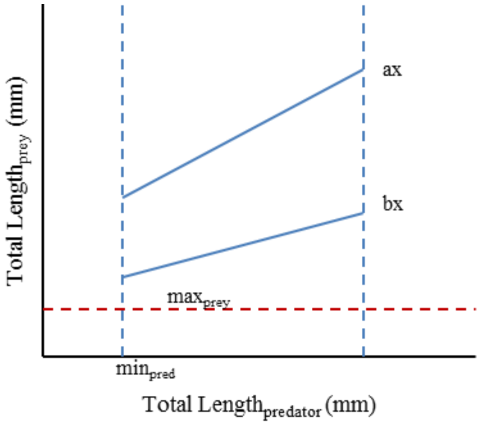
CASE 1.



A_1 = Total

p = 1

CASE 2.



$$A_2 = \iint_0^{maxPrey} \frac{1}{bx} y \ dy\, dx$$

$= \int_{minPred}^{maxPred} \frac{1}{2bx} y^2 \ dx$ (from 0 to maxPrey)

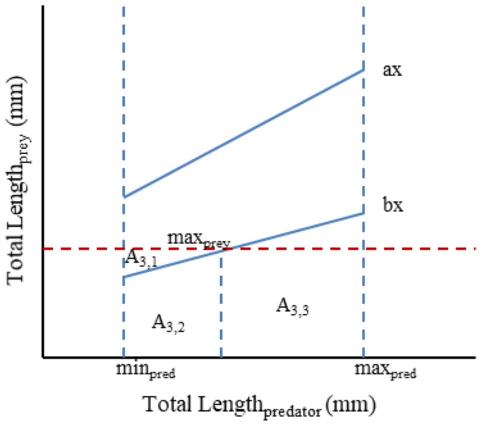
$$= \int_{minPred}^{maxPred} \frac{(maxPrey)^2}{2bx}\ dx$$

$= \frac{(maxP)^2}{2b} \cdot \ln x$ (from minPred to maxPred)

$$= \frac{(maxP)^2}{2b} \cdot (\ln maxPred - \ln minPred)$$

$$p = \frac{A_2}{Total}$$

CASE 3.



$A_{3,1} = \iint_{bx}^{maxPrey} 1\ dy\, dx$

$= \int_{minPred}^{maxPrey/b} maxPrey - bx\ \ dx$ here, max_{Prey}/b is the y-component of the point where max_{prey}

intersects bx.

$= maxPrey \cdot x - \frac{b}{2}x^2$ (from minPred to maxPrey/b)

$$= maxPrey\left(\frac{maxPrey}{b}\right) - \frac{b}{2}\left(\frac{maxPrey}{b}\right)^2 - maxPrey \cdot minPred + \frac{b}{2}(minPred)^2$$

$A_{3,2}\ = \iint_0^{bx} \frac{1}{bx} y\ \ dy\, dx$

$= \int_{minPred}^{maxPrey/b} \frac{1}{2bx} y^2 dx$ (from 0 to bx)

$= \int_{minPred}^{maxPrey/b} \frac{1}{2} bx \; dx$

$= \frac{1}{4} bx^2$ (from minPred to maxPrey/b)

$$= \frac{1}{4} b \left(\frac{maxPrey}{b}\right)^2 - \frac{1}{4} b(minPred)^2$$

A$_{3,3}$ $= \iint_0^{maxPrey} \frac{1}{bx} y \; dy\, dx$

$= \int_{maxPrey/b}^{maxPred} \frac{1}{2bx} y^2 \; dx$ (from 0 to maxPrey)

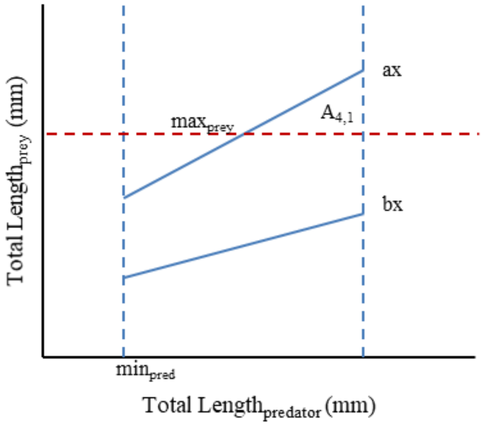
$$= \int_{maxPrey/b}^{maxPred} \frac{(maxPrey)^2}{2bx} \; dx$$

$= \frac{(maxPrey)^2}{2b} \cdot \ln x$ (from maxPred to maxPrey/b)

$$= \frac{(maxPrey)^2}{2b} \cdot \left(\ln maxPred - \ln\left(\frac{maxPrey}{b}\right)\right)$$

$$p = \frac{A_{3,1} + A_{3,2} + A_{3,3}}{Total}$$

CASE 4.



A$_{4,1}$ $= \iint_{maxPrey}^{ax} 1 \; dy\, dx$

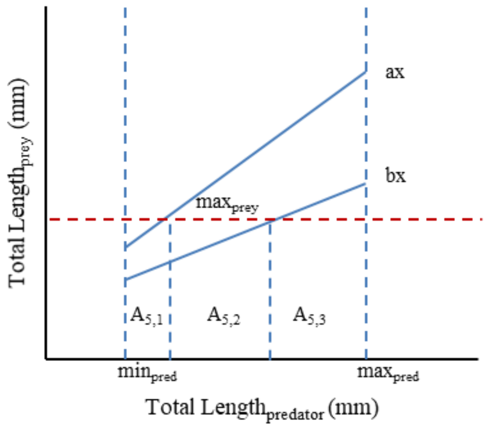
$$= \int_{maxPrey/a}^{maxPred} ax - maxPrey\,dx$$

$= \frac{a}{2}x^2 - maxPrey \cdot x$ (from maxPrey/a to maxPred)

$$= \frac{a}{2}(maxPred)^2 - maxPrey \cdot maxPred - \frac{a}{2}\left(\frac{maxPrey}{a}\right)^2 + maxPrey \cdot \left(\frac{maxPrey}{a}\right)$$

$$p = \frac{Total - A_{4,1}}{Total}$$

CASE 5.



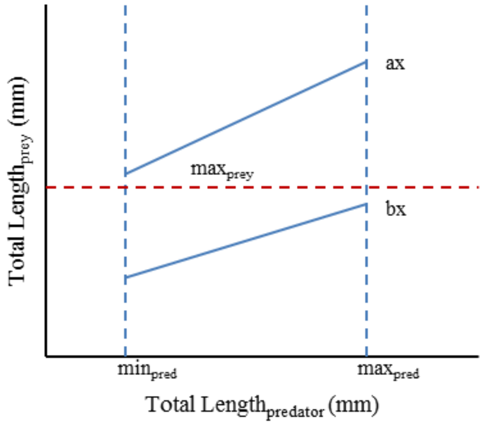
$A_{5,1} = \left(\frac{a-b}{2}\right)\left(\left(\frac{maxPred}{a}\right)^2 - (minPred)^2\right)$ (Same method as calculating Total, but x-limits are minPred and maxPrey/a)

$A_{5,2} = maxPred \cdot \left(\frac{maxPrey}{b}\right) - \frac{b}{2}\left(\frac{maxPrey}{b}\right)^2 - maxPred \cdot \left(\frac{maxPrey}{a}\right) + \frac{b}{2}\left(\frac{maxPrey}{a}\right)^2 + \frac{1}{4}b\left(\frac{maxPrey}{b}\right)^2 - \frac{1}{4}b\left(\frac{maxPrey}{b}\right)^2$ (Same as $A_{3,1}$ and $A_{3,2}$ but with maxPrey/a and maxPrey/b as the limits for x)

$A_{5,3} = \frac{(maxPrey)^2}{2b} \cdot \left(\ln maxPred - \ln\left(\frac{maxPrey}{b}\right)\right)$

$$p = \frac{A_{5,1} + A_{5,2} + A_{5,3}}{Total}$$

CASE 6.



$A_6 = maxPred \cdot (maxPred) - \frac{b}{2}(maxPred)^2 - maxPred \cdot (minPred) + \frac{b}{2}(minPred)^2 + \frac{1}{4}b(maxPred)^2 - \frac{1}{4}b(minPred)^2$ (Same as $A_{3,1}$ and $A_{3,2}$ but with minPred and maxPred as the limits for x)

$$p = \frac{A_6}{Total}$$

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APPENDIX B

Appendices for Chapter 3: The multiple meanings of omnivory influence empirical, modular theory, and whole food web stability relationships

Appendix B.1 Null model descriptions and results from the comparison of omnivory in empirical food webs to these null models

In this appendix we outline the null model descriptions for the empirical food web section of the main text and then we present the results from the analysis of the expression of both specific omnivory modules and specific omnivore-resource interactions in empirical food webs as compared to the four different null model reconstructions.

The *local rewiring algorithm* (e.g. Gale 1957; Roberts & Stone 1990; Milo 2002) maintains the degree (or number of interactions) of each species but randomizes which species are interacting by randomly selecting and rewiring pairs of links. For example, if A is observed to interact with B and C is observed to interact with D, the local rewiring algorithm would switch A to interacting with D and C to interact with B.

The *niche model* (Williams & Martinez 2000) assigns interactions maintaining the observed number of species and connectance in the real food web by randomly assigning a niche value, n_i, drawn uniformly from [0, 1]. Each species can then consume all species falling in a niche range, r_i, assigned using a beta function drawn from [0, 1] with an expected value of 2 C and multiplying that value by n_i to maintain observed connectance. This range is then centred on c_i which is drawn uniformly from [r_i/2, n_i].

The *nested hierarchy I* model is similar to the modified version of Cattin *et al.* (2004) presented in Bascompte & Melián (2005). In this version the generality (or number of prey) of each consumer is preserved. The niche model is used to assign a niche value and range to each species, and then starting with the smallest consumer's niche value trophic interactions are assigned from species with a niche value less than the upper limit of the niche range of the consumer (Note: this is a modification of the model presented in Bascompte & Melián (2005) to allow for cannibalism and mutual predation). If the chosen prey has other consumers then the next prey items will be chosen from the set of all of these consumers' prey. When the group of prey available becomes too small to choose from, then the remaining prey are randomly chosen from prey without consumers (that still have a niche value less than the upper limit of the niche range of the consumer). In this way groups of consumers are created.

The *nested hierarchy II* model is the same as the previous one, however, in this case when there are too few prey items available in the set of prey with shared consumers, the prey can be randomly selected from the set of consumers sharing at least one prey, instead of from remaining prey without consumers (see Bascompte & Melián (2005) for further details).

Results:

Table B.1.1. Number of observations of each type of omnivory module in six classic food webs (Benguela, Carribbean, Silwood, St Marks, Weddell and Ythan) and null model reconstructions of these food webs using three different null models (local rewiring algorithm, nested hierarchy I, and nested hierarchy II. Note for niche model results see Table 1). Here, sig. represents whether the number of modules observed in the empirical web was more extreme than 97.5 % of the null model generations (indicated by over), or less extreme than 2.5 % of the null model generations (indicated by under), with

NS indicating cases where there is no difference, and SD represents standard deviation. Finally, overall indicates the total number of omnivory modules observed irrespective of omnivory type.

		Local Rewiring Algorithm		Nested-hierarchy I		Nested-hierarchy II	
Food Web	Obs. No.	Mean (SD)	Sig.	Mean (SD)	Sig.	Mean (SD)	Sig.
Classic							
Silwood	209	5.55 (2.27)	Over	6.35 (3.64)	NS	12.3 (5.06)	NS
Weddell	290	47.97 (6.55)	Over	69.52 (18.34)	Over	67.47 (18.45)	Over
Benguela	10	9.99 (1.99)	Under	56.54 (25.45)	NS	41.87 (22.07)	NS
St Marks	65	18.07 (3.55)	Over	43.19 (18.31)	NS	37.8 (16.4)	NS
Ythan	47	46.36 (6.85)	Over	36.83 (11.83)	NS	45.25 (12.54)	NS
Caribbean	461	799.23 (32.98)	Under	1206.32 (181.54)	Under	250.8 (100.26)	Over
Mutual Predation							
Silwood	0	0.07 (0.26)	NS	0.12 (0.57)	NS	0.32 (0.91)	NS
Weddell	7	3.03 (2.62)	NS	2.98 (4.3)	NS	3.25 (4.54)	NS
Benguela	55	75.56 (13.09)	NS	38.56 (30.22)	NS	30.59 (25.92)	NS
St Marks	0	7.79 (5.09)	Under	10.09 (10.72)	NS	9.63 (10.17)	NS
Ythan	0	0.43 (0.93)	NS	1.38 (2.48)	NS	1.7 (2.64)	NS
Caribbean	73	150.05 (33.68)	NS	49.39 (45.22)	NS	271.07 (267.5)	NS
Trophic							
Silwood	136	6.56 (2.86)	Over	11.02 (6.59)	Over	62.76 (13.7)	Over
Weddell	62	116.17 (12.25)	Under	154.28 (37.75)	Under	228.9 (41.86)	Under
Benguela	444	526.49 (24.76)	Under	490.02 (51.94)	NS	522.2 (50.72)	NS
St Marks	173	183.94 (14.9)	Under	222.48 (39.45)	NS	256.41 (36.48)	NS
Ythan	11	29.83 (6.92)	Under	66.21 (22.23)	Under	117.85 (27.15)	Under
Caribbean	9628	4544.24 (102.23)	Over	4230.94 (374.88)	Over	10443.26 (537.85)	Under
Multi-Resource							
Silwood	120	273.56 (30.14)	Under	263.94 (45.9)	Under	45.9 (17.23)	NS
Weddell	5928	1374.22 (84.21)	Over	1452.72 (271.77)	Over	1182.91 (245.98)	Over
Benguela	2	12.45 (3.46)	Under	35.28 (18.02)	Under	26.54 (17.19)	NS
St Marks	175	80.22 (10.73)	Over	149.53 (58.96)	Over	117.47 (50.32)	Over
Ythan	1231	1238.73 (99.77)	Over	1017.47 (180.44)	NS	855.15 (160.46)	Over
Caribbean	1579	21896.12 (611.93)	Under	27532.78 (4205.9)	Under	703.68 (325.69)	Over
Cannibalism							
Silwood	11	3.01 (3.68)	Over	5.04 (5.39)	Over	27.54 (10.25)	NS
Weddell	29	30.46 (20.34)	NS	23.7 (17.05)	NS	40.2 (20.53)	Under
Benguela	86	101.7 (18.6)	NS	61.2 (23.42)	NS	68.54 (23.59)	NS

St Marks	10	33.31 (18.05)	NS	29.71 (18.11)	NS	41.26 (19.93)	NS
Ythan	41	7.65 (8.34)	NS	15.84 (11.94)	NS	38.39 (16.27)	NS
Caribbean	209	321.77 (103.99)	NS	151.11 (83.83)	NS	476.08 (192.43)	NS
Overall							
Silwood	476	288.76 (30.17)	Over	286.47 (45.63)	Over	148.81 (25.96)	Over
Weddell	6316	1571.85 (84.5)	Over	1703.21 (269.37)	Over	1522.74 (241.49)	Over
Benguela	597	726.18 (24.17)	Under	681.61 (38.24)	Under	689.74 (35.79)	Under
St Marks	423	323.32 (22.58)	Over	455.01 (68.12)	NS	462.58 (61.19)	NS
Ythan	1330	1322.99 (100.64)	NS	1137.74 (178.74)	NS	1058.34 (157.45)	NS
Caribbean	11950	27711.42 (629.74)	Under	33170.54 (4223.04)	Under	12144.88 (699.6)	NS

Table B.1.2. Number of observations of each type of omnivory-resource interaction in six classic food webs (Benguela, Carribbean, Silwood, St Marks, Weddell and Ythan) and null model reconstructions of these food webs using four different null models (local rewiring algorithm, nested hierarchy I, and nested hierarchy II. Note for niche model results see Table 1). Here over indicates that the number of modules observed in the empirical web is more extreme than 97.5 % of the null model generations, under indicates that the number of observed modules in the empirical web is less extreme than 2.5 % of the null model generations, and NS indicates no difference. Finally, overall indicates the total number of omnivory-resource interactions observed irrespective of omnivory type.

		Local Rewiring Algorithm		Nested-hierarchy I		Nested-hierarchy II	
Food Web	Obs. No.	Mean (SD)	Sig.	Mean (SD)	Sig.	Mean (SD)	Sig.
Classic							
Silwood	64	5.36 (2.16)	Over	6.04 (3.36)	Over	10.52 (4.05)	Over
Weddell	168	38.28 (4.81)	Over	49.6 (11.23)	Over	45.3 (10.27)	Over
Benguela	7	5.23 (1.02)	Over	14.53 (4.83)	NS	11.66 (4.54)	NS
St Marks	32	11.58 (2.03)	Over	20.66 (6.94)	NS	17.58 (5.84)	Over
Ythan	38	40.43 (5.48)	NS	30.71 (8.87)	NS	35.76 (8.55)	NS
Caribbean	125	319.73 (9.64)	Under	410.17 (46.66)	Under	46.72 (14.08)	Over
Mutual Predation							
Silwood	0	0.16 (0.58)	NS	0.29 (1.32)	NS	0.82 (2.14)	NS

Weddell	14	6.43 (5.39)	NS	6.12 (8.39)	NS	6.75 (8.83)	NS
Benguela	80	102.1 (12.59)	NS	57.58 (34.31)	NS	48.78 (33.17)	NS
St Marks	0	16.12 (10.03)	NS	18.72 (17.49)	NS	18.23 (17.03)	NS
Ythan	0	0.91 (1.9)	NS	2.95 (5.11)	NS	3.77 (5.45)	NS
Caribbean	109	285 (57.96)	Under	91.13 (74.7)	NS	382.99 (307.25)	NS
Trophic							
Silwood	65	6.4 (2.75)	Over	10.44 (5.97)	Over	56.53 (11.29)	NS
Weddell	50	94.19 (8.89)	Under	113.03 (23.05)	Under	150.47 (21.62)	Under
Benguela	128	153.02 (5.53)	Under	145.01 (8.64)	NS	148.75 (8.18)	Under
St Marks	95	108.23 (6.64)	NS	113.58 (13.59)	NS	123 (11.77)	Under
Ythan	11	26.68 (5.77)	Under	55.44 (16.47)	Under	90.8 (17.31)	Under
Caribbean	2157	1829.72 (24.75)	Over	1593.33 (92.33)	Over	2027.88 (60.44)	Over
Multi-Resource							
Silwood	13	78.6 (6.39)	Under	75.11 (9.61)	Under	19.11 (5.46)	NS
Weddell	341	140.44 (4.63)	Over	149 (18.83)	Over	116.25 (15.94)	Over
Benguela	1	6.06 (1.21)	Under	12.72 (5.09)	Under	9.59 (4.77)	NS
St Marks	35	20.31 (1.95)	Over	29.81 (8.36)	NS	22.78 (6.64)	NS
Ythan	218	184.49 (8.07)	Over	137.35 (16.26)	Over	110.1 (13.64)	Over
Caribbean	135	483.79 (3.38)	Under	630.96 (61.96)	Under	53.82 (16.04)	Over
Cannibalism							
Silwood	11	3.01 (3.68)	NS	5.04 (5.39)	NS	27.54 (10.25)	NS
Weddell	29	30.46 (20.34)	NS	23.7 (17.05)	NS	40.2 (20.53)	NS
Benguela	86	101.7 (18.6)	NS	61.2 (23.42)	NS	68.54 (23.59)	NS
St Marks	10	33.31 (18.05)	NS	29.71 (18.11)	NS	41.26 (19.93)	NS
Ythan	41	7.65 (8.34)	Over	15.84 (11.94)	NS	38.39 (16.27)	NS
Caribbean	209	321.77 (103.99)	NS	151.11 (83.83)	NS	476.08 (192.43)	NS
Overall							
Silwood	153	93.52 (8.34)	Over	96.91 (13.42)	Over	114.51 (18.88)	NS
Weddell	602	309.81 (24.48)	Over	341.45 (38.72)	Over	358.98 (38.75)	Over
Benguela	302	368.11 (19.21)	Under	291.04 (48.71)	NS	287.32 (45.11)	NS
St Marks	172	189.54 (19.65)	NS	212.48 (34.75)	NS	222.85 (33.11)	NS
Ythan	308	260.15 (13.73)	Over	242.28 (29.76)	Over	278.82 (30.79)	NS
Caribbean	2735	3240.01 (121.5)	Under	2876.7 (186.24)	NS	2987.48 (434.67)	NS

Appendix B.2 Species' biomass model parameterization

The species biomass model is parameterized as in previous studies (e.g. Brose, Williams, & Martinez, 2006; Stouffer & Bascompte, 2010; Williams, 2008), where the change in biomass density *B* of species *i* over time is represented by the following ordinary differential equation (ODE):

$$\frac{dB_i}{dt} = r_i G_i B_i - x_i B_i + x_i B_i \sum_{j=prey} y_i F_{ij} - \sum_{k=pred} \frac{x_k y_k B_k F_{ki}}{e_{ki}} \quad (1)$$

where r_i is the mass-specific maximum growth rate, G_i is the logistic net growth rate where $G_i = 1 - \frac{B_i}{K}$ and *K* is the carrying capacity, x_i is the mass-specific metabolic rate, y_i is a species' maximum consumption rate relative to its metabolic rate, F_{ij} is a type II functional response reflecting the consumption of prey *j* by predator *i*, and e_{ij} is the fraction of the biomass of species *j* lost due to consumption by species *i* that is actually metabolized. Note if species *i* is not a primary producer then $r_i G_i B_i = 0$.

The type II functional response is similar to that presented in Stouffer & Bascompte (2010) and is defined as

$$F_{ij} = \frac{w_{ij} B_j}{B_0 + \sum_{k=prey} w_{ik} B_k} \quad (2)$$

where w_{ij} is the relative inverse attack rate for predator *i* on prey *j*, and can be considered the consumer's prey preference (e.g. Bascompte, Melián, & Sala, 2005), in a type II functional response and B_0 is the half-saturation density. Comparing w_{ij} of one predator for different prey with similar biomass can provide some insight on the relative preference of that predator for each prey. To explore the influence of omnivore-resource interaction strength (w_{OR}) on module persistence, we randomly assigned w_{OR} a value between 0 to 1 from a uniform distribution for 5000 simulations. Here, the predator (*i*) and prey (*j*) of the interaction strength (w_{ij}) are special cases where the predator and prey is either an omnivore (O), a consumer (C), or a resource (R). In this way w_{OC} (or the interaction strength between the omnivore and consumer) was assigned the remainder (i.e., $w_{OC} = 1 - w_{OR}$), and we assume all other interaction strengths are equal ($w_{CR} = 1$, or the interaction strength between the consumer and the resource).

The time scale of the system is normalized to the mass-specific growth rate of the basal species by setting the mass-specific growth rate to 1. In this way

$$r_i = 1 \tag{3}$$

$$x_i = \frac{a_x}{a_r}\left(\frac{M_i}{M_b}\right)^{-1/4} \tag{4}$$

$$y_i = \frac{a_y}{a_x} \tag{5}$$

where a_x, a_r, and a_y are allometric constants, $\underline{M_i}$ is the body size of species *i*, and M_b is the body size of the basal species (see Brose *et al.* (2006b) for a more detailed description). We assigned body mass based on fixed predator-prey body-mass ratios, Z (e.g. (Brose *et al.* 2006b; Otto *et al.* 2007; Williams 2008). Specifically, $M_i = Z^T$ where *T* is the prey-averaged trophic position of species *i*, calculated here using the R package netindices, and Z = 42 and is the fixed predator-prey body-mass ratio (see Brose *et al.* 2006a). For all other parameters, we used the same values as Stouffer & Bascompte (2010). Namely, $e_{ij} = 0.85$, $K = 1$, $M_b = 1$, $a_r = 1$, $a_x = 0.2227$, and $a_y = 1.7816$.

At the start of each simulation species' biomass were initialized randomly from a uniform distribution in the range [0.05, 1]. Numerical integration of the ODEs was accomplished using the function lsode in the R package deSolve. We considered species as extinct when their biomass fell below 10^{-30}. Module simulations were run to 5000 time steps since most extinctions occur within the first 200 time steps, and transient dynamics of persistent populations settle by 1000 time steps (see Brose *et al.* 2006b; Williams 2008).

Appendix B.3 Modular theory results

In this appendix we present the persistence and stability of the omnivore-resource interaction strength for each omnivory module. Persistence is denoted by the solid red line and arrow and occurs when all species in the module maintain biomasses greater than 10^{-30} for the 5000 time steps. Stability is determined by the eigenvalues of the Jacobian where modules were homogeneously stable if the real parts of all eigenvalues were less than zero. They exhibited fixed point stability if the eigenvalues were real numbers, but had damped oscillatory dynamics, and otherwise, the module exhibits oscillatory or unstable dynamics. Different types of stability are denoted by different shades of blue.

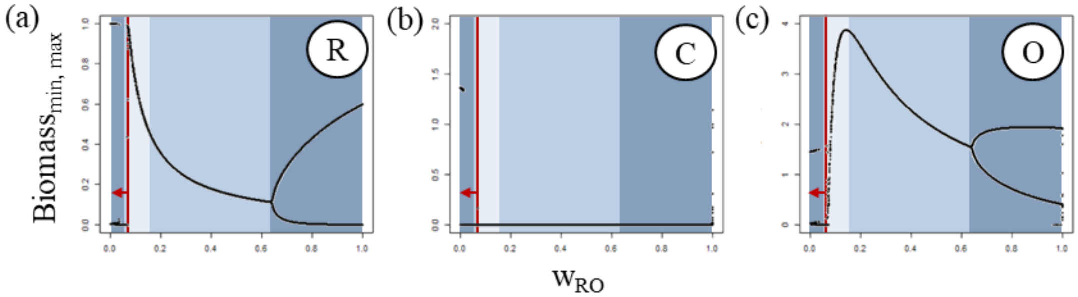

Figure B.3.1. Classic omnivory module persistence (a-c). Here, biomass minima and maxima are for the last 1000 time steps where the solid red line and arrow indicates the area of persistence, light blue shading indicates monotonic stability, the darker blue shading indicates damped oscillatory stability, and the dark blue indicates unstable oscillatory behaviour. The letter in the circle is the species being represented (resource (R), consumer (C), and omnivore (O), respectively) and w_{RO} represents the strength of the omnivore-resource interaction.

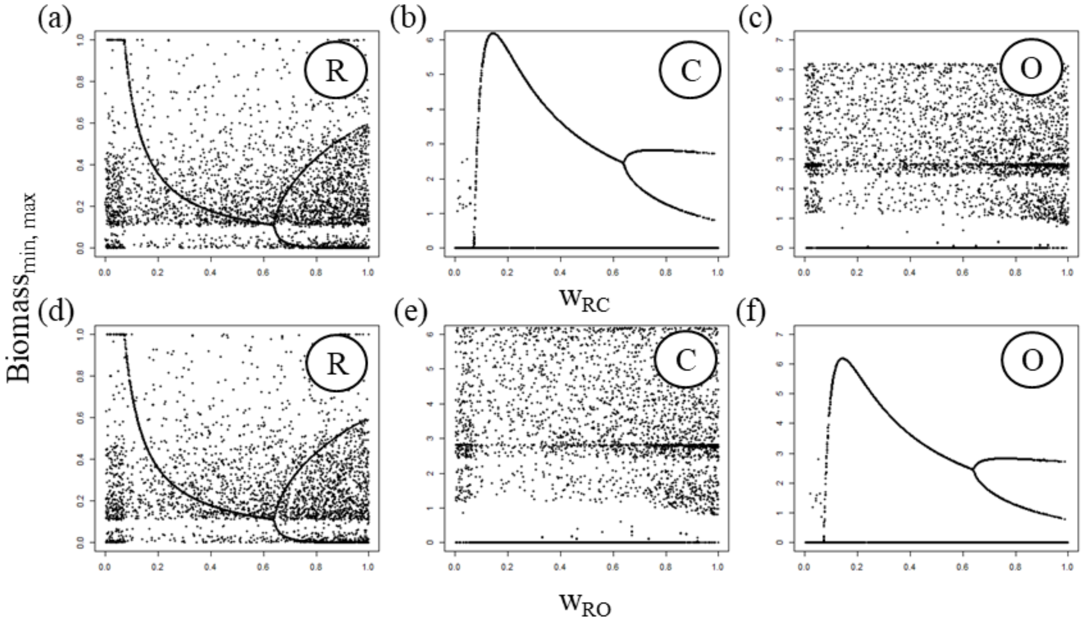

Figure B.3.2. Mutual predation module persistence. Here, biomass minima and maxima are for the last 1000 time steps, however, because two parameters were varying (w_{RC} and w_{RO}) model dynamics depend on both axes and thus feasibility (or persistence) and stability cannot be clearly demonstrated on the graph in the same manner as the other modules (see Table 2 for region of persistence and stability). The model dependence on two axes is also the reason for the cloud of points on the figures. The letter in the circle is the species being represented (resource (R), consumer (C), and omnivore (O), respectively) and w_{RO} or w_{RC} indicates the strength of the omnivore-resource, or resource-consumer interaction.

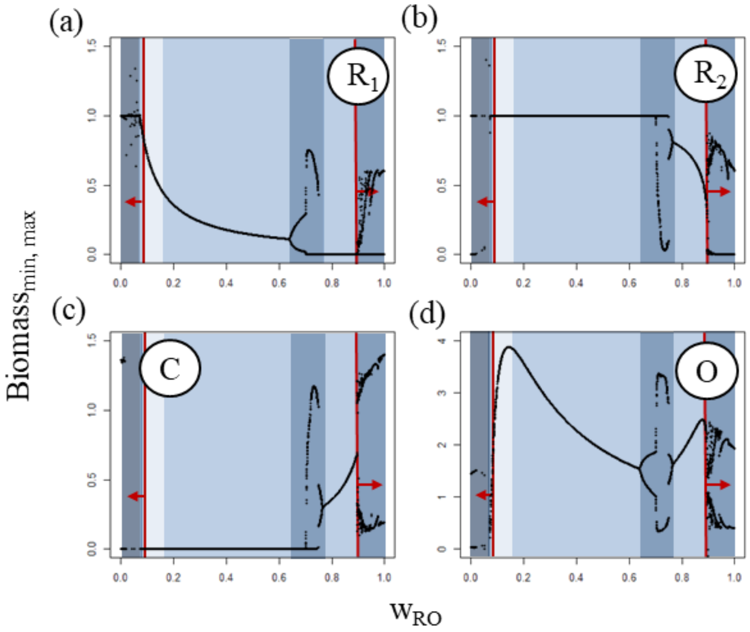

Figure B.3.3. Multi-resource omnivory module persistence. Here, biomass minima and maxima are for the last 1000 time steps where the solid red line and arrow indicates the area of persistence, light blue shading indicates monotonic stability, the darker blue shading indicates damped oscillatory stability, the dark blue indicates oscillatory behaviour, and the darkest blue/grey indicates unstable behaviour. The letter in the circle is the species being represented (resource one and two (R_1 and R_2), consumer (C), and omnivore (O), respectively) and w_{RO} represents the strength of the omnivore-resource interaction.

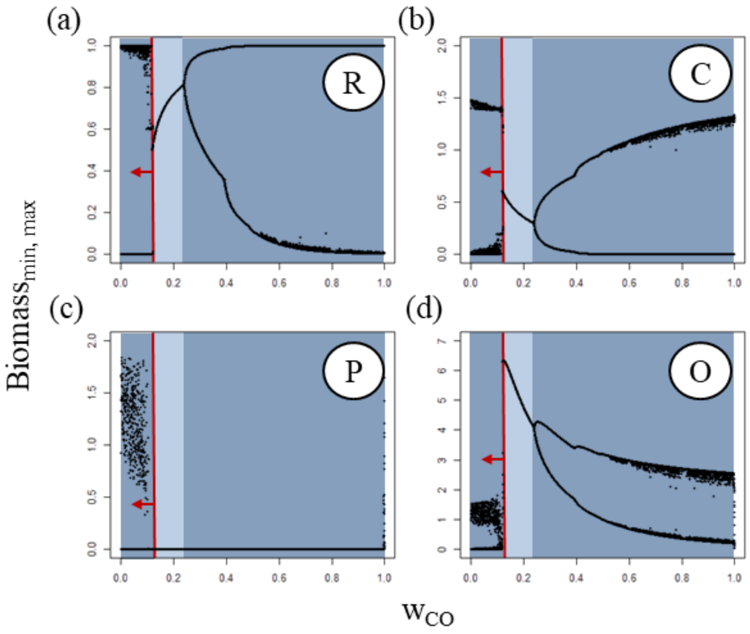

Figure B.3.4. Trophic omnivory module persistence. Here, biomass minima and maxima are for the last 1000 time steps where the solid red line and arrow indicates the area of persistence, light blue shading indicates damped oscillatory stability, and the dark blue indicates oscillatory behaviour. The letter in the circle is the species being represented (resource (R), consumer (C), predator (P), and omnivore (O), respectively) and w_{RO} represents the strength of the omnivore-resource interaction.

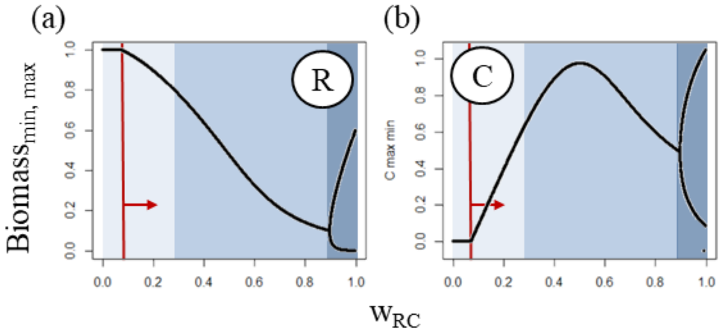

Figure B.3.5. Cannibalism module persistence (a, b). Here, biomass minima and maxima are for the last 1000 time steps where the solid red line and arrow indicates the area of persistence, light blue shading indicates monotonic stability, the darker blue shading indicates damped oscillatory stability, and the dark blue indicates oscillatory behaviour. The letter in the circle is the species being represented (resource (R) and consumer (C) respectively) and w_{RC} represents the strength of the resource-consumer interaction.

Appendix B.4 Additional Whole Food Web Results

In this appendix we present the statistical results from the analyses comparing whole food web persistence to both module frequency and omnivore-resource interaction frequency, and then further analyses controlling for the influence of omnivore-resource interaction strengths.

Modular theory suggests that it is the omnivore-resource interaction strength that stabilizes complex dynamics (e.g. McCann et al., 1998). Consequently, we quantified the number of each omnivore-resource interaction type and the average interaction strengths. We then used the presented linear regression models to determine the influence of each omnivore-resource interaction type on whole food web persistence both when accounting for average interaction strength and not (Table S3c).

Table B.4.3. Results from the analyses examining (a) the influence of module frequency on whole food web persistence when statistically controlling for the effects of other modules, (b) the influence of omnivore-resource interaction frequency on whole food web persistence when statistically controlling for the effects of other omnivore-resource interactions, and (c) the influence of omnivore-resource interaction frequency on whole food web persistence when statistically controlling for the effects of other omnivore-resource interactions and the change in average interaction strength of these interactions. A module's (or module's omnivore-resource interaction's) contribution to whole food web persistence is equal to the partial residuals of the model given by $persistence \sim \beta_0 + \sum_l c_l N_l$ where *l* indicates the different modules, c_l is the influence of the different modules, and N_l is the number of those modules in the given whole food web. Since apparent competition, exploitative competition, tri-trophic food chains and trophic and classic omnivory combined make up 95% of modules within food webs (Bascompte & Melián 2005) these additional modules were accounted for in (a). Finally, here correlation represents the Pearson correlation coefficient between partial residuals and persistence.

(a)

	Intercept	Slope (Standard Error)	p-Value	Correlation
Classic	$-3.01\text{x}10^{-3}$	$4.36\text{x}10^{-5}$ ($9.89\text{x}10^{-6}$)	< 0.05	0.025
Mutual Predation	$5.45\text{x}10^{-3}$	$-2.29\text{x}10^{-4}$ ($1.49\text{x}10^{-5}$)	< 0.05	-0.088
Multi-Resource	$-4.69\text{x}10^{-2}$	$1.01\text{x}10^{-4}$ ($1.16\text{x}10^{-6}$)	< 0.05	0.446
Trophic	$-2.62\text{x}10^{-2}$	$1.04\text{x}10^{-4}$ ($3.48\text{x}10^{-6}$)	< 0.05	0.169
Cannibalism	$-1.12\text{x}10^{-2}$	$1.67\text{x}10^{-4}$ ($1.69\text{x}10^{-6}$)	< 0.05	0.057

(b)

	Intercept	Slope (Standard Error)	p-Value	Correlation
Classic	$1.33\text{x}10^{-2}$	$-1.93\text{x}10^{-4}$ ($1.05\text{x}10^{-5}$)	< 0.05	-0.141
Mutual Predation	$-4.58\text{x}10^{-4}$	$1.93\text{x}10^{-5}$ ($1.58\text{x}10^{-5}$)	< 0.05	0.008
Multi-Resource	$-3.20\text{x}10^{-3}$	$6.85\text{x}10^{-5}$ ($1.23\text{x}10^{-6}$)	< 0.05	0.302
Trophic	$6.58\text{x}10^{-3}$	$-2.60\text{x}10^{-5}$ ($3.69\text{x}10^{-6}$)	< 0.05	-0.067
Cannibalism	$-3.03\text{x}10^{-2}$	$4.58\text{x}10^{-4}$ ($1.79\text{x}10^{-5}$)	< 0.05	0.032

(c)

	Intercept	Slope (Standard Error)	p-Value	Correlation
Classic	$3.51\text{x}10^{-3}$	$-5.09\text{x}10^{-5}$ ($1.15\text{x}10^{-5}$)	<0.05	-0.053
Mutual Predation	$-7.40\text{x}10^{-4}$	$3.04\text{x}10^{-5}$ ($1.69\text{x}10^{-5}$)	0.073	0.018
Multi-Resource	$-7.34\text{x}10^{-4}$	$1.60\text{x}10^{-6}$ ($1.48\text{x}10^{-6}$)	0.282	-0.045
Trophic	$-5.72\text{x}10^{-3}$	$2.27\text{x}10^{-5}$ ($4.02\text{x}10^{-6}$)	<0.05	-0.072
Cannibalism	$-6.50\text{x}10^{-3}$	$9.73\text{x}10^{-5}$ ($1.93\text{x}10^{-5}$)	< 0.05	-0.037

Appendix B.5 Whole food web model results for connectance 0.15 and 0.2

In this appendix we present the additional model results and corresponding analyses for whole food web models with connectance of 0.15 and 0.2.

Connectance 0.15:

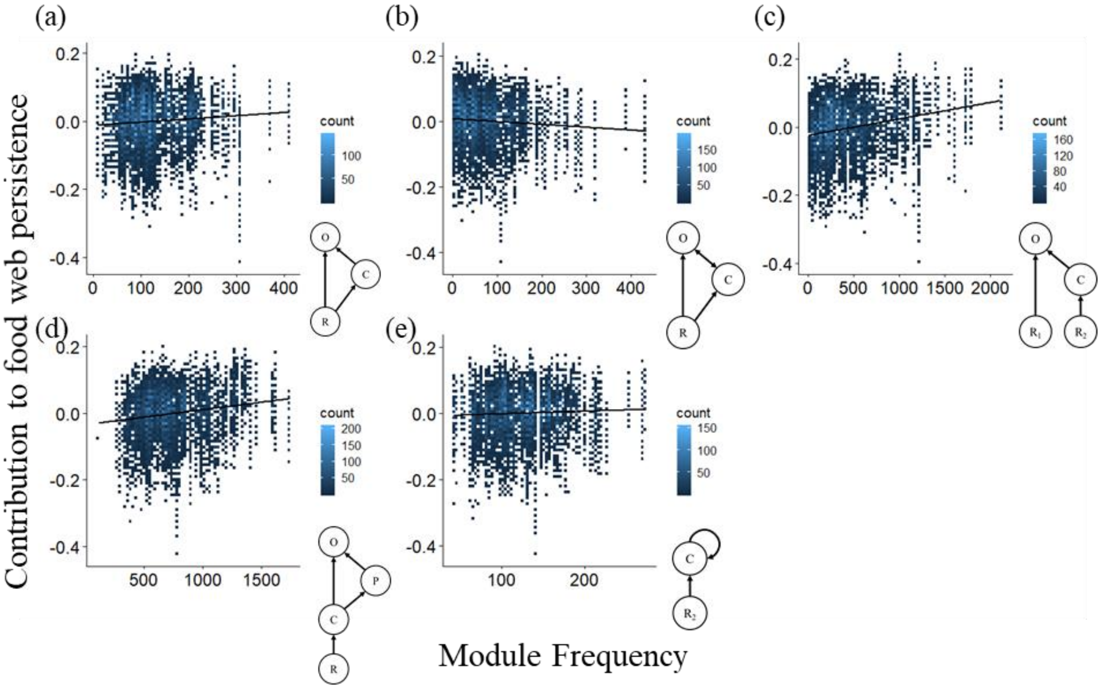

Figure B.5.6. Relationship between module frequency and whole food web persistence for a connectance of 0.15. (a) The classic omnivory, (b) the mutual predation, (c) the multi-resource omnivory, (d) the trophic omnivory, and (e) cannibalism modules. On the x-axes the frequency of each module type is shown, and on the y-axes the contribution to whole food web persistence when statistically controlling for the effects of the other modules. A module's contribution to whole food web persistence is equal to the partial residuals of the model given by $persistence \sim \beta_0 + \sum_l c_l N_l$ where l indicates the different modules, c_l is the influence of the different modules, and N_l is the number of those modules in the given whole food web.

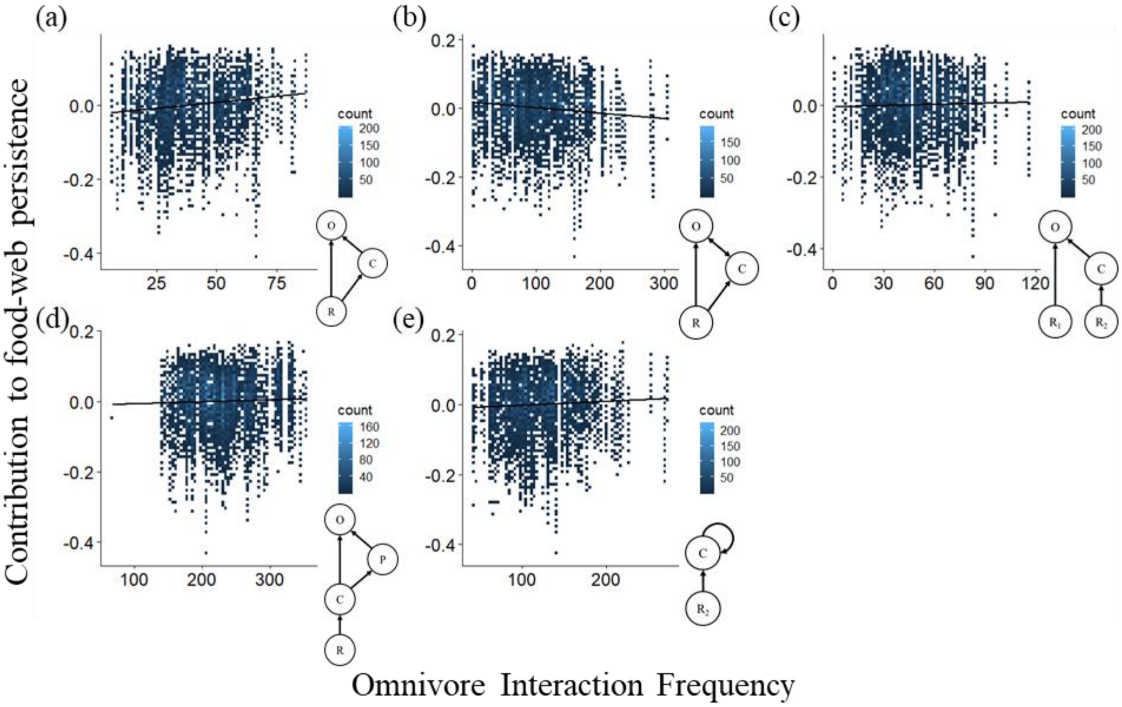

Figure B.5.7. Relationship between frequency of module specific omnivore-resource interactions and whole food web persistence for a connectance of 0.15. (a) The classic-omnivory, (b) the mutual predation, (c) the multi-resource omnivory, (d) the trophic omnivory, and (e) cannibalism modules. On the x-axes the frequency of each omnivore-resource interaction type is shown, and on the y-axes the contribution to whole food web persistence when statistically controlling for the effects of the other omnivore-resource interaction types. An omnivory interactions' contribution to whole food web persistence is equal to the partial residuals of the model given by $persistence \sim \beta_0 + \sum_l a_l N_l$ where *l* indicates the different omnivory interaction types, a_l is the influence of the different interaction types, and N_l is the number of those interaction types in the given whole food web.

Table B.5.4. Results from the analyses examining (a) the influence of module frequency on whole food web persistence when statistically controlling for the effects of other modules, (b) the influence of omnivore-resource interaction frequency on whole food web persistence when statistically controlling for the effects of other omnivore-resource interactions, and (c) the influence of omnivore-resource interaction frequency on whole food web persistence when statistically controlling for the effects of other omnivore-resource interactions and the change in average interaction strength of these interactions for a connectance of 0.15. A module's (or module's omnivore-resource interactions) contribution to whole food web persistence is equal to the partial residuals of the model given by $persistence \sim \beta_0 + \sum_l c_l N_l$ where l indicates the different modules, c_l is the influence of the different modules, and N_l is the number of those modules in the given whole food web. Since apparent competition, exploitative competition, tri-trophic food chains and trophic and classic omnivory combined make up 95% of modules within food webs (Bascompte & Melián 2005) these additional modules were accounted for in (a). Finally, here correlation represents the Pearson correlation coefficient between partial residuals and persistence.

(a)

	Intercept	Slope (Standard Error)	p-Value	Correlation
Classic	-1.21×10^{-2}	9.37×10^{-5} (5.77×10^{-6})	< 0.05	0.093
Mutual Predation	7.31×10^{-3}	-8.59×10^{-5} (5.58×10^{-6})	< 0.05	-0.088
Multi-Resource	-2.37×10^{-2}	4.82×10^{-5} (1.02×10^{-6})	< 0.05	0.262
Trophic	-3.45×10^{-2}	4.50×10^{-5} (1.37×10^{-6})	< 0.05	0.185
Cannibalism	-9.83×10^{-3}	7.88×10^{-5} (9.26×10^{-6})	< 0.05	0.049

(b)

	Intercept	Slope (Standard Error)	p-Value	Correlation
Classic	-1.50×10^{-2}	1.16×10^{-4} (6.17×10^{-6})	< 0.05	0.145
Mutual Predation	9.57×10^{-3}	-1.13×10^{-4} (5.94×10^{-6})	< 0.05	-0.127

Multi-Resource	3.94×10^{-4}	-8.00×10^{-7} (1.09×10^{-6})	< 0.05	0.031
Trophic	-8.98×10^{-3}	1.17×10^{-5} (1.46×10^{-6})	< 0.05	0.037
Cannibalism	-1.37×10^{-2}	1.10×10^{-4} (9.84×10^{-6})	< 0.05	0.001

(c)

	Intercept	Slope (Standard Error)	p-Value	Correlation
Classic	-1.07×10^{-2}	8.22×10^{-5} (6.15×10^{-6})	<0.05	0.070
Mutual Predation	3.08×10^{-3}	-3.64×10^{-5} (5.94×10^{-6})	0.073	-0.054
Multi-Resource	-2.61×10^{-3}	5.29×10^{-6} (1.07×10^{-6})	0.282	0.035
Trophic	-4.31×10^{-3}	5.63×10^{-6} (1.45×10^{-6})	<0.05	-0.003
Cannibalism	2.44×10^{-3}	-1.95×10^{-5} (9.80×10^{-6})	< 0.05	0.047

Connectance 0.2:

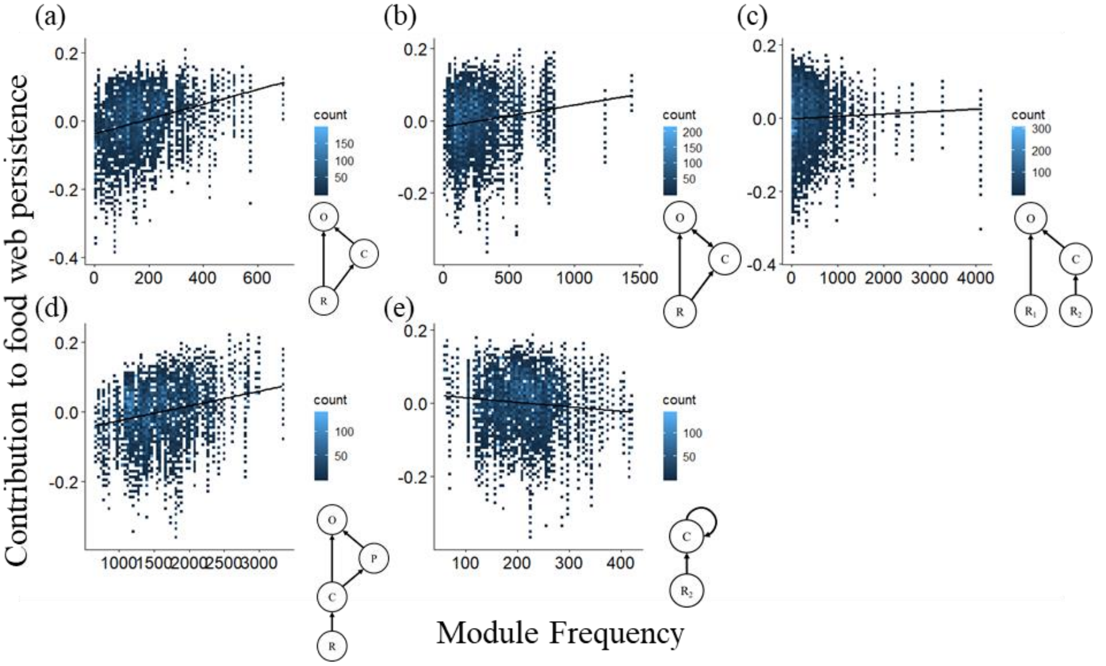

Figure B.5.8. Relationship between module frequency and whole food web persistence for a connectance 0.2. (a) The classic omnivory, (b) the mutual predation, (c) the multi-resource omnivory, (d) the trophic omnivory, and (e) cannibalism modules. On the x-axes the frequency of each module type is shown, and on the y-axes the contribution to whole food web persistence when statistically controlling for the effects of the other modules. A module's contribution to whole food web persistence is equal to the partial residuals of the model given by $persistence \sim \beta_0 + \sum_l c_l N_l$ where l indicates the different modules, c_l is the influence of the different modules, and N_l is the number of those modules in the given whole food web.

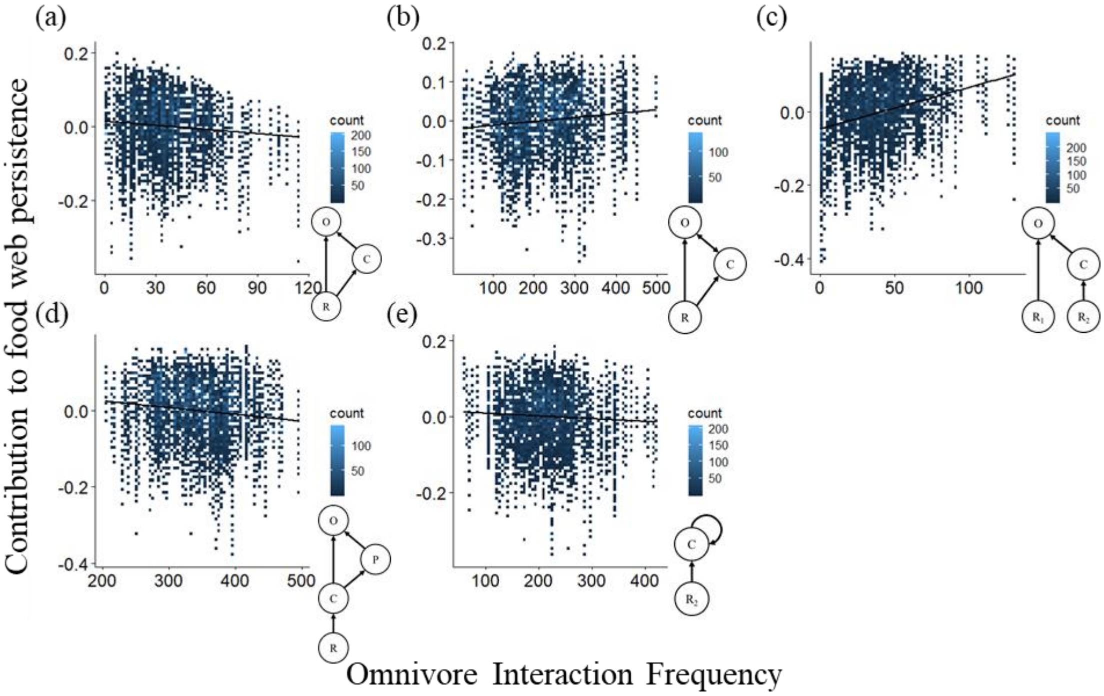

Figure B.5.9. Relationship between frequency of module specific omnivore-resource interactions and whole food web persistence for a connectance of 0.2. (a) The classic-omnivory, (b) the mutual predation, (c) the multi-resource omnivory, (d) the trophic omnivory, and (e) cannibalism modules. On the x-axes the frequency of each omnivore-resource interaction type is shown, and on the y-axes the contribution to whole food web persistence when statistically controlling for the effects of the other omnivore-resource interaction types. An omnivory interactions' contribution to whole food web persistence is equal to the partial residuals of the model given by $persistence \sim \beta_0 + \sum_l a_l N_l$ where l indicates the different omnivory interaction types, a_l is the influence of the different interaction types, and N_l is the number of those interaction types in the given whole food web.

Table B.5.5. Results from the analyses examining (a) the influence of module frequency on whole food web persistence when statistically controlling for the effects of other modules, (b) the influence of omnivore-resource interaction frequency on whole food web persistence when statistically controlling for the effects of other omnivore-resource interactions, and (c) the influence of omnivore-resource interaction frequency on whole food web persistence when statistically controlling for the effects of other omnivore-resource interactions and the change in average interaction strength of these interactions for a connectance of 0.2. A module's (or module's omnivore-resource interaction's) contribution to whole food web persistence is equal to the partial residuals of the model given by $persistence \sim \beta_0 + \sum_l c_l N_l$ where l indicates the different modules, c_l is the influence of the different modules, and N_l is the number of those modules in the given whole food web. Since apparent competition, exploitative competition, tri-trophic food chains and trophic and classic omnivory combined make up 95% of modules within food webs (Bascompte & Melián 2005) these additional modules were accounted for in (a). Finally, here correlation represents the Pearson correlation coefficient between partial residuals and persistence.

(a)

	Intercept	Slope (Standard Error)	p-Value	Correlation
Classic	-3.83×10^{-2}	2.17×10^{-4} (3.59×10^{-6})	< 0.05	0.325
Mutual Predation	-1.70×10^{-2}	6.05×10^{-5} (1.97×10^{-6})	< 0.05	0.171
Multi-Resource	-3.01×10^{-3}	6.63×10^{-6} (7.94×10^{-7})	< 0.05	0.047
Trophic	-6.80×10^{-2}	4.23×10^{-5} (8.62×10^{-7})	< 0.05	0.268
Cannibalism	2.65×10^{-2}	-1.24×10^{-4} (6.45×10^{-6})	< 0.05	-0.110

(b)

	Intercept	Slope (Standard Error)	p-Value	Correlation
Classic	$1.50x10^{-2}$	$-8.44x10^{-5}$ ($3.59x10^{-6}$)	< 0.05	-0.105
Mutual Predation	$-1.07x10^{-2}$	$3.82x10^{-5}$ ($1.99x10^{-6}$)	< 0.05	0.119
Multi-Resource	$-1.71x10^{-2}$	$3.76x10^{-5}$ ($8.25x10^{-7}$)	< 0.05	0.349
Trophic	$2.68x10^{-2}$	$-1.66x10^{-5}$ ($8.69x10^{-7}$)	< 0.05	-0.134
Cannibalism	$1.55x10^{-2}$	$-7.24x10^{-5}$ ($6.48x10^{-6}$)	< 0.05	0.001

(c)

	Intercept	Slope (Standard Error)	p-Value	Correlation
Classic	$2.81x10^{-3}$	$-1.61x10^{-5}$ ($3.64x10^{-6}$)	<0.05	-0.047
Mutual Predation	$5.35x10^{-4}$	$-1.88x10^{-6}$ ($1.97x10^{-6}$)	0.073	0.003
Multi-Resource	$3.17x10^{-3}$	$-7.02x10^{-6}$ ($7.87x10^{-7}$)	0.282	-0.054
Trophic	$1.95x10^{-3}$	$-1.21x10^{-6}$ ($8.47x10^{-7}$)	<0.05	0.009
Cannibalism	$3.02x10^{-3}$	$-1.41x10^{-5}$ ($6.37x10^{-6}$)	< 0.05	-0.045

References

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APPENDIX C

Appendix for Chapter 4: Multiscale analysis reveals incongruent relationships between network metrics and community, species, and interaction persistence in food webs

Appendix C.1 Additional results

Table C.1.1. Results from the community persistence analyses examining the influence of each network metric on community persistence. Here, C. Cent is closeness centrality, Mod is modularity, OD is out/in degree, and Av IS is the average interaction strength of the network at the beginning of the simulations.

	Intercept			Slope				
Metric	Estimate	SE	p-val.	Estimate	SE	p-val.	R^2	AIC
C. Cent	0.847	0.001	0	0.007	0.002	0.005	0	-204829
Mod.	0.853	0	0	-0.042	0.004	0	0.002	-204957
OD	0.812	0.001	0	0.005	0	0	0.028	-207431
MR	0.842	0	0	0.072	0.003	0	0.005	-205288
M6	0.901	0.001	0	-0.389	0.007	0	0.034	-207953
M12	0.846	0.001	0	0.017	0.006	0.004	0	-204829
M14	0.845	0	0	2.652	0.13	0	0.005	-205238
M36	0.992	0.002	0	-0.422	0.005	0	0.068	-211193
M38	0.816	0.001	0	0.213	0.004	0	0.025	-207107
M46	0.842	0	0	1.172	0.039	0	0.01	-205701
M74	0.839	0	0	0.797	0.024	0	0.013	-205961
M78	0.844	0	0	21.707	0.596	0	0.014	-206139
M98	0.85	0	0	-75.564	6.663	0	0.001	-204950
M102	0.846	0	0	16.407	0.7	0	0.006	-205369
M108	0.84	0	0	0.551	0.016	0	0.013	-206025
M110	0.844	0	0	3.814	0.123	0	0.011	-205781
M238	0.846	0	0	4.604	0.189	0	0.007	-205415
Av. IS	0.801	0.001	0	2.915	0.051	0	0.035	-208006

Table C.1.2. The correlation coefficients between the top 5 predictors of community persistence**.** Here OD stands for out/in degree, and Av IS stands for average interaction strength of the network.

	M36	M6	M38	OD
M6	0.142			
M38	-0.396	-0.351		
OD	-0.379	-0.278	0.707	
Av. IS	-0.473	-0.357	0.814	0.738

Table C.1.3. Results from the AIC model selection for community persistence. Note that because of the high correlation between interaction strength and the other metrics, interaction strength was omitted from this analyses. Here, OD stands for out/in degree, and Dev Expl deviance explained.

	AIC	Dev. Expl.	LogLik	Nag. R^2	ΔAIC	Aikaike weights
OD	-207431	2.84239	103718.3	0.028508	6101.887	0
M6	-207953	3.401175	103979.3	0.034112	5579.913	0
M36	-211193	6.798699	105599.4	0.06818	2339.713	0
OD+M6	-209359	4.893115	104683.6	0.049073	4173.323	0
OD+M36	-211746	7.36901	105877.1	0.073898	1786.255	0
M6+M36	-213373	9.019488	106690.6	0.090445	159.2798	2.59E-35
OD+M6+M36	-213532	9.181487	106771.2	0.092069	0	1
Intercept	-204823	0	102413.5	0	8709.401	0

Table C.1.4. Results from the species persistence analyses examining the influence of each network metric on species persistence. Here, Odds is log Odds, TL is trophic level of the species, ID_IS is the in degree interaction strength, OD_IS is the average interaction strength for out degree, Nag is nagelkerke's R^2, and p-val is p-value.

	Intercept			Slope				
Metric	Mean	SE	p-val.	Odds	Odds Ratio	SE	p-val.	Nag. R^2
S1	1.499	0.002	0	13.465	7.04x10^5	1.183	0	1.00x10^{-04}
S2	1.467	0.002	0	21.881	3.18x10^9	0.594	0	7.00x10^{-04}
S3	1.51	0.002	0	1.526	4.600	0.819	0.062	0
S4	1.49	0.002	0	12.691	3.25x10^5	0.569	0	3.00x10^{-04}
S5	1.491	0.002	0	11.825	1.37x10^5	0.676	0	2.00x10^{-04}
S6	1.518	0.002	0	-441.3	0.00	28.826	0	1.00x10^{-04}
S7	1.514	0.001	0	-176.0	0.00	21.795	0	0
S8	1.517	0.001	0	-397.7	0.00	21.725	0	2.00x10^{-04}
S9	1.452	0.003	0	12.74	3.41x10^5	0.487	0	4.00x10^{-04}
S10	1.489	0.002	0	8.936	7.6x10^3	0.307	0	5.00x10^{-04}
S11	1.553	0.002	0	-38.65	0	1.204	0	5.00x10^{-04}
S12	1.533	0.002	0	-17.67	0	0.933	0	2.00x10^{-04}
S13	1.517	0.002	0	-4.297	0.014	0.628	0	0
S14	1.521	0.002	0	-95.66	0	4.518	0	2.00x10^{-04}
S15	1.521	0.002	0	-211.8	0	11.443	0	2.00x10^{-04}
S16	1.532	0.002	0	-214.9	0	9.797	0	2.00x10^{-04}
S17	1.516	0.002	0	-38.62	0	3.843	0	1.00x10^{-04}
S18	1.514	0.001	0	-17.66	0	3.145	0	0
S19	1.516	0.001	0	-1204	0	56.847	0	2.00x10^{-04}
S20	1.513	0.001	0	-674.7	0	63.259	0	1.00x10^{-04}
S21	1.511	0.001	0	14767	Inf	1038.77	0	2.00x10^{-04}
S22	1.513	0.001	0	-825.6	0	102.422	0	0
S23	1.512	0.001	0	-85.53	0	104.546	0.413	0
S24	1.513	0.001	0	-849.8	0	90.999	0	0
S25	1.524	0.002	0	-111.2	0	6.9	0	1.00x10^{-04}
S26	1.516	0.002	0	-18.01	0	1.776	0	1.00x10^{-04}
S27	1.515	0.001	0	-316.6	0	28.905	0	1.00x10^{-04}

S28	1.518	0.001	0	-658.0	0	27.473	0	3.00x10^{-04}
S29	1.513	0.001	0	-112.8	0	18.989	0	0
S30	1.511	0.001	0	36.39	6.35x 10^{15}	20.773	0.08	0
R1	1.508	0.002	0	8.534	5.08x 10^{3}	0.83	0	1.00x10^{-04}
R2	1.508	0.001	0	8.587	5.36x 10^{3}	0.81	0	1.00x10^{-04}
C1	1.503	0.002	0	20.41	7.29x 10^{8}	1.139	0	2.00x10^{-04}
O	1.503	0.002	0	22.16	4.22x 10^{9}	0.888	0	4.00x10^{-04}
TL	1.636	0.004	0	-0.043	0.958	0.001	0	6.00x10^{-04}
Degree	1.655	0.003	0	-0.009	0.991	0	0	0.0015
ID_IS	1.51	0.003	0	0.021	1.021	0.019	0.283	0
OD_IS	1.497	0.002	0	0.088	1.092	0.006	0	1.00x10^{-04}

Table C.1.5. The correlation coefficients between the top 5 predictors of species persistence. Here, TL stands for trophic level.

	Degree	S2	S10	S11
S2	0.261			
S10	0.638	0.364		
S11	0.207	-0.178	-0.264	
TL	-0.003	-0.019	-0.018	-0.003

Table C.1.6. Results from the AIC model selection for species persistence. Note that because of the high correlation between S10 and the other metrics, S10 was omitted from this analyses. Here, TL stands for trophic level, Deg stands for degree, Nag stands for nagelkerke's, and Dev. Expl for deviance explained.

	AIC	Dev. Expl.	LogLik	Nag. R^2	ΔAIC	Aikaike weights
Deg	2975154	0.09938	-1487575	0.001535	3978.938	0
S2	2976730	0.046481	-1488363	0.000718	5554.308	0
S11	2977097	0.034141	-1488547	0.000528	5921.819	0
TL	2976937	0.03951	-1488467	0.000611	5761.927	0
Deg + S2	2972380	0.192622	-1486187	0.002975	1204.081	0
Deg + S11	2974694	0.114926	-1487344	0.001775	3517.947	0
Deg + TL	2973972	0.139158	-1486983	0.00215	2796.291	0
S2 + S11	2976069	0.068737	-1488032	0.001062	4893.497	0
S2 + TL	2975603	0.084373	-1487799	0.001304	4427.863	0
S11 + TL	2975918	0.073804	-1487956	0.00114	4742.604	0
Deg + S2 + S11	2972293	0.19559	-1486143	0.00302	1117.7	0
Deg + S2 + TL	2971265	0.230101	-1485629	0.003553	89.90041	0
Deg + S11 + TL	2973509	0.15476	-1486751	0.00239	2333.654	0
S2 + S11 + TL	2974933	0.106952	-1487462	0.001652	3757.439	0
Deg + S2 + S11 + TL	2971176	0.233187	-1485583	0.0036	0	1
Intercept	2978112	-1.31E-12	-1489055	0	6936.574	0

Table C.1.7. Results from the interaction persistence analyses examining the influence of each network metric on interaction persistence. Here, i. strength stands for interaction strength, bet stands for betweenness, p-val for p-value, and Nag stands for Nagelkerke's.

	Intercept			Slope				
Metric	Mean	SE	p-val.	logOdds	Odds Ratio	SE	p-val.	Nag. R^2
E1	1.492	0.001	0	240.183	2.04x10^{104}	0.916	0	0.015
E2	1.49	0.001	0	291.755	5.10x10^{126}	1.051	0	0.017
E3	1.572	0.001	0	161.035	8.64x10^{69}	0.787	0	0.009
E4	1.667	0.001	0	1988.151	Inf	25.281	0	0.002
E5	1.668	0.001	0	847.792	Inf	12.422	0	0.001
E6	1.406	0.001	0	144.472	5.54x10^{62}	0.459	0	0.022
E7	1.468	0.001	0	537.061	1.75x10^{233}	1.557	0	0.03
E8	1.444	0.001	0	602.28	3.69x10^{261}	1.644	0	0.034
E9	1.54	0.001	0	349.82	8.41x10^{151}	1.246	0	0.02
E10	1.664	0.001	0	417.767	2.72x10^{181}	4.619	0	0.002
E11	1.628	0.001	0	1783.648	Inf	9.56	0	0.01
E12	1.633	0.001	0	1374.037	Inf	8.256	0	0.007
E13	1.663	0.001	0	184.611	1.49x10^{80}	2.151	0	0.002
E14	1.671	0.001	0	2061.402	Inf	36.468	0	0.001
E15	1.675	0.001	0	838.372	Inf	199.23	0	0
E16	1.674	0.001	0	1816.242	Inf	69.818	0	0
E17	1.674	0.001	0	2417.594	Inf	84.791	0	0
E18	1.673	0.001	0	1472.221	Inf	45.066	0	0
E19	1.578	0.001	0	1361.829	Inf	5.216	0	0.018
E20	1.659	0.001	0	199.625	4.97x10^{86}	1.899	0	0.003
E21	1.669	0.001	0	2145.297	Inf	30.454	0	0.001
E22	1.667	0.001	0	1249.012	Inf	16.822	0	0.001
E23	1.666	0.001	0	1470.44	Inf	18.293	0	0.002
E24	1.66	0.001	0	2284.807	Inf	21.44	0	0.004
E25	1.721	0.001	0	-241.658	0	1.076	0	0.008
E26	1.729	0.001	0	-284.002	0	1.247	0	0.008
E27	1.709	0.001	0	-162.404	0	1.162	0	0.003
I. Strength	1.673	0.001	0	0.018	1.018	0.006	0	0
Bet.	1.737	0.001	0	-0.013	0.987	0	0	0.003

Table C.1.7. The correlation coefficients between the top 5 predictors of interaction persistence.

	E8	E7	E6	E9
E7	0.002			
E6	0.547	0.114		
E9	0.127	0.127	0.221	
E19	0.127	0.152	0.3	0.163

Table C.1.8. Results from the AIC model selection for interaction persistence. Note that because of the high correlation between E6 and the other metrics, E6 was omitted from this analyses. Here, Dev Expl stands for deviance explained and Nag stands for nagelkerke's.

	AIC	Dev. Expl.	LogLik	Nag. R^2	ΔAIC	Aikaike weights
E8	8649542	2.314701	-4324769	0.034	247635.8	0
E7	8673620	2.04277	-4336808	0.030	271713.9	0
E9	8736608	1.331405	-4368302	0.012	334701.7	0
E19	8746491	1.219779	-4373244	0.018	344585.6	0
E8 + E7	8480792	4.220535	-4240393	0.062	78885.94	0
E8 + E9	8568353	3.231646	-4284173	0.048	166447	0
E8 + E19	8576083	3.144344	-4288039	0.046	174177.2	0
E8 + E7 + E19	8437525	4.709197	-4218759	0.069	35619.36	0
E8 + E7 + E9	8432254	4.768726	-4216123	0.070	30348.36	0
E8 + E9 + E19	8516117	3.821606	-4258054	0.056	114211	0
E8 + E9 + E19 + E7	8401906	5.111494	-4200948	0.075	0	1
E7 + E9	8592021	2.964341	-4296008	0.044	190115.5	0
E7 + E19	8599777	2.876755	-4299885	0.043	197871.1	0
E7 + E9 + E19	8539545	3.557021	-4269768	0.052	137638.7	0
E9 + E19	8657995	2.219254	-4328995	0.033	256089.2	0
Intercept	8854495	3.93E-12	-4427246	0	452588.9	0

APPENDIX D

Appendix for Chapter 5: Incorporating abiotic controls on animal movements in metacommunities

Appendix D.1 Additional results

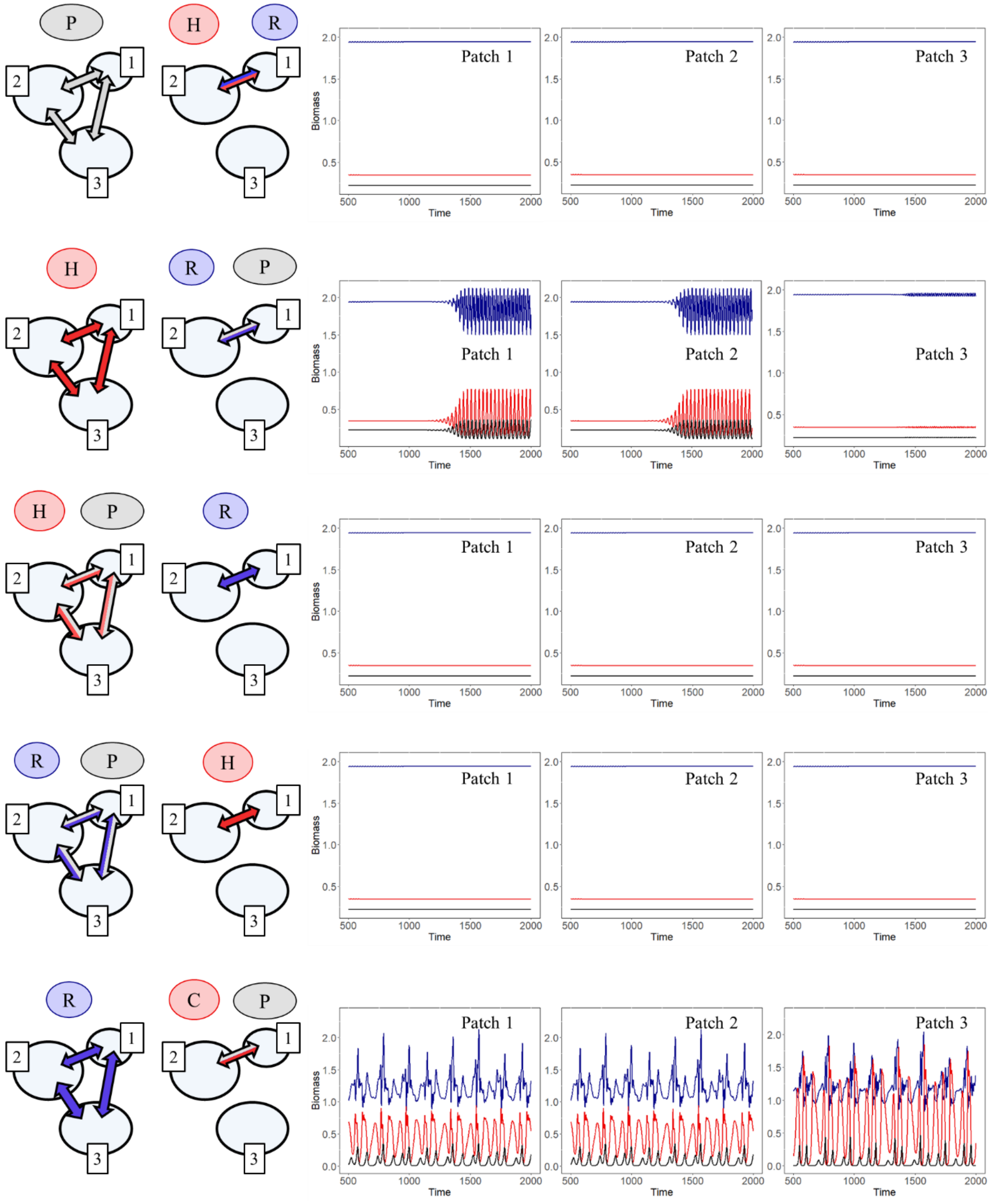

Figure D.1.1. Assuming a three patch system and a tri-trophic food chain we can contrast biomass dynamics depending on all combinations of species-specific connectivity from Figure 3. Here, the resource (R) is in blue, the herbivore (H) is in red, and the predator (P) is in black (Parameters are the same as in McCann et al. (2005): $K = 2.75$, $a_R = 2.5$, $a_H = 8.75$, $h_R = 0.4$, $h_H = 1.15$, $e_H = 0.8$, $e_P = 0.8$, $d_H = 1$, $d_P = 0.4$, $r = 1$ and spatial parameters are $m_R = 3.5$, $m_H = 0.01$, and $m_P = 0.1$).

Appendix D.2 Model Proof

In this Appendix we present the full proof with annotations presented in Jansen and Lloyd (2000), followed by our proof for the species-specific connectivity version following the same format.

Universal Connectivity Matrix (Original):

$$\begin{pmatrix} \dot{x}_{1,j} \\ \vdots \\ \dot{x}_{k,1} \end{pmatrix} = \begin{pmatrix} f_1\left(x_j\right) \\ \vdots \\ f_k\left(x_j\right) \end{pmatrix} \tag{1}$$

Represents the local patch dynamics of *j* in the absence of migration where

- $\dot{x}$ represents differentiation with respect to time
- $\dot{x} = (x_{1,j}, \dots, x_{k,j})^T$ is the vector which holds the densities of all species in patch *j*
- $\dot{x} = f(x_j)$ where $f = \mathbb{R}^k \rightarrow \mathbb{R}^k$

Note that the Jacobian of *f* is

$$D\left(f\left(x_j\right)\right) = \begin{pmatrix} \frac{\partial f_1}{\partial x_{1j}} & \cdots & \frac{\partial f_1}{\partial x_{kj}} \\ \vdots & \ddots & \vdots \\ \frac{\partial f_k}{\partial x_{1j}} & \cdots & \frac{\partial f_k}{\partial x_{kj}} \end{pmatrix} \tag{2}$$

Thus, the population dynamics of the spatial system are combinations of local dynamics and dispersal, and can be combined according to the following equation:

$$\dot{x}_j = f\left(x_j\right) + \sum_{i=1}^{n} c_{ij} M x_i \tag{3}$$

Where

- M = k x k diagonal matrix where m_h describes migration of each species h
- C = n x n matrix such that $C = c_{ij}$ where the density of species h in patch j changes through migration from patch i to j at rate $m_j c_{ij}$
- And, $c_{ii} < 0$ because the diagonals are the rate at which the species leaves the patch.

Example:

In this example we have a simple tri-trophic food chain ($k = 3$) where each species is represented as R for resource, C for consumer, or P for predator. Each species (h) moves at a species' specific rate m_h, and it is a simple two patch system. Thus,

$$M = \begin{pmatrix} m_r & 0 & 0 \\ 0 & m_c & 0 \\ 0 & 0 & m_p \end{pmatrix} \tag{4}$$

And

$$C = \begin{pmatrix} c_{11} & c_{12} \\ c_{21} & c_{22} \end{pmatrix} \tag{5}$$

Then, if we use equation (3) we can describe differentiation in patch 1 with respect to time as

$$\begin{aligned}\begin{pmatrix}\dot{R}_1\\ \dot{C}_1\\ \dot{P}_1\end{pmatrix} &= f\begin{pmatrix}R_1\\ C_1\\ P_1\end{pmatrix} + c_{11}\begin{pmatrix}m_r & 0 & 0\\ 0 & m_c & 0\\ 0 & 0 & m_p\end{pmatrix}\begin{pmatrix}R_1\\ C_1\\ P_1\end{pmatrix} + c_{21}\begin{pmatrix}m_r & 0 & 0\\ 0 & m_c & 0\\ 0 & 0 & m_p\end{pmatrix}\begin{pmatrix}R_2\\ C_2\\ P_2\end{pmatrix}\\ &= \begin{pmatrix}f(R_1)\\ f(C_1)\\ f(P_1)\end{pmatrix} + \begin{pmatrix}c_{11}m_r & 0 & 0\\ 0 & c_{11}m_c & 0\\ 0 & 0 & c_{11}m_p\end{pmatrix}\begin{pmatrix}R_1\\ C_1\\ P_1\end{pmatrix} + \begin{pmatrix}c_{21}m_r & 0 & 0\\ 0 & c_{21}m_c & 0\\ 0 & 0 & c_{21}m_p\end{pmatrix}\begin{pmatrix}R_2\\ C_2\\ P_2\end{pmatrix}\\ &= \begin{pmatrix}f(R_1)\\ f(C_1)\\ f(P_1)\end{pmatrix} + \begin{pmatrix}c_{11}m_rR_1\\ c_{11}m_cC_1\\ c_{11}m_pP_1\end{pmatrix} + \begin{pmatrix}c_{21}m_rR_2\\ c_{21}m_cC_2\\ c_{21}m_pP_2\end{pmatrix}\end{aligned}$$

Note: $c_{11} < 0$.

It is obvious that equation (3) accurately describes the population dynamics of the spatial system.

Definition*:* A solution is <u>spatially homogeneous</u> (or <u>flat</u>) when the densities in all patches are identical, i.e. when $x_j(t) = s(t)$ for all *t* and for all $j = 1, \ldots, n$ with *s* taking values in $\mathbb{R}^k$.

Note: if $\sum_{i=1}^{n} C_{ij} = 0$ (or all columns sum to 0), then matrix *C* should have a flat solution.

Theorem: Let *M* be a *k x k* matrix, and *C* a *n x n* matrix with *n* linearly independent eigenvectors, one of which is the left eigenvector (1,…,1) with associated eigenvalue 0. Let $f = \mathbb{R}^k \to \mathbb{R}^k$ be a vector function which is at least once continuously differentiable and let *s(t)* be a solution of $\dot{x} = f(x_j)$ and S_{flat} the corresponding flat solution of $\dot{x} = f(x_j) + \sum_{i=1}^{n} c_{ij} M x_i$.

The linearization of the system 3 around $S_{flat}(t)$ can be transformed by a imilarity transformation into *n* decoupled systems of the form:

$$\dot{x} = \left(Df\left(s\left(t\right)\right) + \lambda_i M\right) x \qquad (6)$$

for $i = 1, \ldots, n$, where λ_i is an eigenvalue of C and $x(t) \epsilon \mathbb{C}^k$

Proof: Let

$$X = (x_1, \ldots, x_n) = \begin{pmatrix} x_{1,1} & \ldots & x_{1,n} \\ \vdots & \ddots & \vdots \\ x_{k,1} & \ldots & x_{k_n} \end{pmatrix} \quad (7)$$

Recall that $x_j = (x_{1,j}, \ldots, x_{k,j})$ where k is the number of species, n is the number of patches and X is a k x n matrix. Then,

$$F(X) = (f(x_1), \ldots, f(x_n)) \quad (8)$$

Where F(X) are the local interactions between species in their patches (in the absene of movement).

Then, migration can be expressed by post-multiplication of *X* by the matrix *C*.

Different species migrate at different rates which can be expressed as a pre-mulitplication of *X* by *M*.

Thus, *M X C* represents the dispersal process and

$$\dot{X} = F(X) + MXC \quad (9)$$

Describes the dynamis of a continuous time spatial system.

Example: Let

$$X = \begin{pmatrix} R_1 & R_2 \\ C_1 & C_2 \\ P_1 & P_2 \end{pmatrix}$$ then:

$$\dot{X} = F(X) + MXC$$

$$\begin{aligned}
\begin{pmatrix} \dot{R}_1 & \dot{R}_2 \\ \dot{C}_1 & \dot{C}_2 \\ \dot{P}_1 & \dot{P}_2 \end{pmatrix} &= \begin{pmatrix} f(R_1) & f(R_2) \\ f(C_1) & f(C_2) \\ f(P_1) & f(P_2) \end{pmatrix} + \begin{pmatrix} m_R & 0 & 0 \\ 0 & m_C & 0 \\ 0 & 0 & m_p \end{pmatrix} \begin{pmatrix} R_1 & R_2 \\ C_1 & C_2 \\ P_1 & P_2 \end{pmatrix} \begin{pmatrix} c_{11} & c_{12} \\ c_{21} & c_{22} \end{pmatrix} \\
&= \begin{pmatrix} f(R_1) & f(R_2) \\ f(C_1) & f(C_2) \\ f(P_1) & f(P_2) \end{pmatrix} + \begin{pmatrix} m_R R_1 & m_R R_2 \\ m_C C_1 & m_C C_2 \\ m_P P_1 & m_P P_2 \end{pmatrix} \begin{pmatrix} c_{11} & c_{12} \\ c_{21} & c_{22} \end{pmatrix} \\
&= \begin{pmatrix} f(R_1) & f(R_2) \\ f(C_1) & f(C_2) \\ f(P_1) & f(P_2) \end{pmatrix} + \begin{pmatrix} c_{11} m_R R_1 + c_{21} m_R R_2 & c_{12} m_R R_1 + c_{22} m_R R_2 \\ c_{11} m_C C_1 + c_{21} m_C C_2 & c_{12} m_C C_1 + c_{22} m_C C_2 \\ c_{11} m_P P_1 + c_{21} m_P P_2 & c_{12} m_P P_1 + c_{22} m_P P_2 \end{pmatrix} \\
&= \begin{pmatrix} f(R_1) + c_{11} m_R R_1 + c_{21} m_R R_2 & f(R_2) + c_{12} m_R R_1 + c_{22} m_R R_2 \\ f(C_1) + c_{11} m_C C_1 + c_{21} m_C C_2 & f(C_2) + c_{12} m_C C_1 + c_{22} m_C C_2 \\ f(P_1) + c_{11} m_P P_1 + c_{21} m_P P_2 & f(P_2) + c_{12} m_P P_1 + c_{22} m_P P_2 \end{pmatrix}
\end{aligned}$$

Note: $c_{11}, c_{22} < 0$.

Proof Continued:

Consider the time evolution of a solution, *X*, which arises by making a small perturbation to the flat solution then:

$$\dot{X} - \dot{S}_{flat} = F(X) - F(S_{flat}) + M(X - S_{flat})C \quad (10)$$

We can linearize around S_{flat} where $X = S_{flat} + \epsilon Y + h.o.t.$ Thus we have

$$F(X) = F(S_{flat} + \epsilon Y + h.o.t.) \quad (11)$$

Which can be expanded using the Taylor series to:

$$F\left(X\right)=F\left(S_{flat}\right)+\epsilon D\left(f\left(s\left(t\right)\right)\right)Y+h.o.t. \quad (12)$$

Substituting this into (10) we get:

$$\dot{Y}=D\left(f\left(s\left(t\right)\right)\right)Y+MYC \quad (13)$$

Because C is invertible (because of the requirements of the structure of C), there exists a matrix A such that $A^{-1}CA = \Lambda$ and if A is constructed from the right eigenvectors of C ($Cw_i = \lambda_i w_i$) then A^{-1} are the left eigenvectors and Λ is a diagonal matrix where the diagonal elements are the eigenvalues, λ_i, of C.

We can now left multiply equation (13) by A and factor using $\Psi = Y\,A$. In this equation (13) now becomes:

$$\dot{Y}A=D\left(f\left(s\left(t\right)\right)\right)YA+MYCA \quad (14)$$

Then, knowing that $AA^{-1} = I$, or the identity matrix, which is the equivalent for matrix multiplication as multiplying by 1, and knowing that $A^{-1}CA = \Lambda$ equation (14) becomes:

$$\begin{aligned}\Psi&=D\left(f\left(s\left(t\right)\right)\right)\Psi+MYA^{-1}CA\\&=D\left(f\left(s\left(t\right)\right)\right)\Psi+M\Psi\Lambda\end{aligned} \quad (15)$$

Here, Y is k x n matrix, A is an n x n matrix, which makes Ψ a k x n matrix.

Species' Independent Connectivity:

Consider a spatial system of *n* patches in which *k* species interact. It is assumed that, from the perspective of the species, all patches are identical environments, and therefore, in the absence of migration the local dynamics of each patch is defined by

$$\begin{pmatrix} \dot{x}_{1,j} & 0 & \dots & 0 \\ 0 & \dot{x}_{2,j} & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & \dot{x}_{k,j} \end{pmatrix} = \begin{pmatrix} f_1(x_j) & 0 & \dots & 0 \\ 0 & f_2(x_j) & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & f_k(x_j) \end{pmatrix} \quad (16)$$

Where $\dot{x}$ indicates differentiation of x with respect to time, and x_j holds the densities of all species in a patch j on its diagonal.

Note: $\begin{pmatrix} \dot{x}_{1,j} & 0 & \dots & 0 \\ 0 & \dot{x}_{2,j} & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & \dot{x}_{k,j} \end{pmatrix} \begin{pmatrix} 1 \\ \vdots \\ 1 \end{pmatrix} = \begin{pmatrix} x_{1,j} \\ \vdots \\ x_{k_j} \end{pmatrix}$

Thus, $\dot{x} = f(x)$ and the Jacobian of $f(x_j)$ is:

$$D(f(x_j)) = \begin{pmatrix} \frac{\partial f_1}{\partial x_{1,j}} & \dots & \frac{\partial f_1}{\partial x_{k,j}} \\ \vdots & \ddots & \vdots \\ \frac{\partial f_k}{\partial x_{1,j}} & \dots & \frac{\partial f_k}{\partial x_{k,j}} \end{pmatrix} \quad (17)$$

Note: despite the weird form of f this is easy to see since it can be vectorized as demonstrated above.

Now, we have species' specific connectivity, so we need species' specific connectivity matrices:

$$C_1 = \begin{pmatrix} c_{11,1} & \dots & c_{1n,1} \\ \vdots & \ddots & \vdots \\ c_{n1,1} & \dots & c_{nn,1} \end{pmatrix} \quad \dots \quad C_k = \begin{pmatrix} c_{11,k} & \dots & c_{1n,k} \\ \vdots & \ddots & \vdots \\ c_{n1,k} & \dots & c_{nn,k} \end{pmatrix} \tag{18}$$

So, we can then describe the population dynamcis of the spatial system as a combination of local dynamics and dispersal such that:

$$\dot{x}_j = f\left(x_j\right) + \sum_{i=1}^{n} \begin{pmatrix} c_{ij,1} & 0 & \dots & 0 \\ 0 & c_{ij,2} & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & c_{ij_k} \end{pmatrix} M x_i \tag{19}$$

Where *M* is a *k x k* diagonal matrix with species' specific movement rates on the diagonal, x_j is a *k x k* matrix with species' densities on the diagonal and the rules for the species' specific connectivity matrices are the same as the rules for the universal connectivity matrix.

Example: Let *k = 3, n = 2,*

$$M = \begin{pmatrix} m_R & 0 & 0 \\ 0 & m_C & 0 \\ 0 & 0 & m_P \end{pmatrix} \text{ and } C_{sp} = \begin{pmatrix} c_{11,sp} & c_{12,sp} \\ c_{21,sp} & c_{22,sp} \end{pmatrix}$$

Then, equation (19) becomes:

$$\dot{x}_1 = \begin{pmatrix} f\left(R_1\right) & 0 & 0 \\ 0 & f\left(C_1\right) & 0 \\ 0 & 0 & f\left(P_1\right) \end{pmatrix} + \begin{pmatrix} c_{11,R} & 0 & 0 \\ 0 & c_{11,C} & 0 \\ 0 & 0 & c_{11,P} \end{pmatrix} \begin{pmatrix} m_R & 0 & 0 \\ 0 & m_C & 0 \\ 0 & 0 & m_P \end{pmatrix} \begin{pmatrix} R_1 & 0 & 0 \\ 0 & C_1 & 0 \\ 0 & 0 & P_1 \end{pmatrix}$$
$$+ \begin{pmatrix} c_{12,R} & 0 & 0 \\ 0 & c_{12,C} & 0 \\ 0 & 0 & c_{12,P} \end{pmatrix} \begin{pmatrix} m_R & 0 & 0 \\ 0 & m_C & 0 \\ 0 & 0 & m_P \end{pmatrix} \begin{pmatrix} R_2 & 0 & 0 \\ 0 & C_2 & 0 \\ 0 & 0 & P_2 \end{pmatrix}$$

$$\dot{x}_1 = \begin{pmatrix} f\left(R_1\right) & 0 & 0 \\ 0 & f\left(C_1\right) & 0 \\ 0 & 0 & f\left(P_1\right) \end{pmatrix} + \begin{pmatrix} m_R c_{11,R} R_1 & 0 & 0 \\ 0 & m_C c_{11,C} C_1 & 0 \\ 0 & 0 & m_P c_{11,P} P_1 \end{pmatrix}$$
$$+ \begin{pmatrix} m_R c_{12,R} R_2 & 0 & 0 \\ 0 & m_C c_{12,C} C_2 & 0 \\ 0 & 0 & m_P c_{12,P} P_2 \end{pmatrix}$$

Theorem: Let *M* be a *k* x *k* matrix and C_1, … , C_k be *n* x *n* matrices for species' *i*, each with *n* linearly independent eigenvectors, one of which (for each species) is the left eigenvector (1, …, 1) with associated eigenvalues 0. Let *f* be a function which is at least once differentiable and let *s (t)* be a solution of $x_j = f(x_j)$ and S_{flat} the corresponding at solution for equation 19.

Then, the linearization of the above system around $S_{flat}(t)$ can be transformed by a similarity transformation into *n* decoupled systems of the form

$$\dot{x} = \left[D\left(f\left(s\left(t\right)\right)\right) + \begin{pmatrix} \lambda_{1,i} \\ \vdots \\ \lambda_{k,i} \end{pmatrix} M \right] x \qquad i = 1, \ldots, n \tag{20}$$

Proof:

Let

$$X=(x_1,\dots,x_n)=\begin{pmatrix} x_{1,1} & 0 & \dots & 0 & & x_{1,n} & 0 & \dots & 0 \\ 0 & x_{2,1} & \dots & 0 & & 0 & x_{2,n} & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots & \dots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & x_{k,1} & & 0 & 0 & \dots & x_{k,n} \end{pmatrix} \quad (21)$$

Now X is a k x kn matrix.

$$F(X)=(f(x_1),\dots,f(x_n))=\begin{pmatrix} f(x_{1,1}) & \dots & 0 & & f(x_{1,n}) & \dots & 0 \\ \vdots & \ddots & \vdots & \dots & \vdots & \ddots & \vdots \\ 0 & \dots & f(x_{k,1}) & & 0 & \dots & f(x_{k,n}) \end{pmatrix} \quad (22)$$

and we construct C as a kn x kn matrix:

$$C=\begin{pmatrix} c_{11,1} & \dots & 0 & & c_{1n,1} & \dots & 0 \\ \vdots & \ddots & \vdots & \dots & \vdots & \ddots & \vdots \\ 0 & \dots & c_{11,k} & & 0 & \dots & c_{1n,k} \\ & \vdots & & & & \vdots & \\ c_{n1,1} & \dots & 0 & & c_{nn,1} & \dots & 0 \\ \vdots & \ddots & \vdots & \dots & \vdots & \ddots & \vdots \\ 0 & \dots & c_{n1,k} & & 0 & \dots & c_{nn,k} \end{pmatrix} \quad (23)$$

where $c_{ij,k}$ comes from the ij^{th} entry of C_k.

Then, we can describe the dispersal portion of $M\,X\,C$ and thus,

$$\dot{X}=F(X)+MXC \quad (24)$$

Describes the dynamics of a continuous time spatial system (and can be vectorized).

Example: Let

$$X = \begin{pmatrix} R_1 & 0 & 0 & R_2 & 0 & 0 \\ 0 & C_1 & 0 & 0 & C_2 & 0 \\ 0 & 0 & P_1 & 0 & 0 & P_2 \end{pmatrix} \quad M = \begin{pmatrix} m_R & 0 & 0 \\ 0 & m_C & 0 \\ 0 & 0 & m_P \end{pmatrix}$$

And

$$C_R = \begin{pmatrix} c_{11,R} & c_{12,R} \\ c_{21,R} & c_{22,R} \end{pmatrix} \quad C_C = \begin{pmatrix} c_{11,C} & c_{12,C} \\ c_{21,C} & c_{22,C} \end{pmatrix} \quad C_P = \begin{pmatrix} c_{11,P} & c_{12,P} \\ c_{21,P} & c_{22,P} \end{pmatrix}$$

Then

$$C = \begin{pmatrix} c_{11,R} & 0 & 0 & c_{12,R} & 0 & 0 \\ 0 & c_{11,C} & 0 & 0 & c_{12,C} & 0 \\ 0 & 0 & c_{11,P} & 0 & 0 & c_{12,P} \\ c_{21,R} & 0 & 0 & c_{22,R} & 0 & 0 \\ 0 & c_{21,C} & 0 & 0 & c_{22,C} & 0 \\ 0 & 0 & c_{21,P} & 0 & 0 & c_{22,P} \end{pmatrix}$$

Substituting these into equation (24) we get:

$$\dot{X} = \begin{pmatrix} f\left(R_1\right) & 0 & 0 & f\left(R_2\right) & 0 & 0 \\ 0 & f\left(C_1\right) & 0 & 0 & f\left(C_2\right) & 0 \\ 0 & 0 & f\left(P_1\right) & 0 & 0 & f\left(P_2\right) \end{pmatrix} + \begin{pmatrix} m_R & 0 & 0 \\ 0 & m_C & 0 \\ 0 & 0 & m_P \end{pmatrix} \begin{pmatrix} R_1 & 0 & 0 & R_2 & 0 & 0 \\ 0 & C_1 & 0 & 0 & C_2 & 0 \\ 0 & 0 & P_1 & 0 & 0 & P_2 \end{pmatrix} C$$

$$= \begin{pmatrix} f\left(R_1\right) & 0 & 0 & f\left(R_2\right) & 0 & 0 \\ 0 & f\left(C_1\right) & 0 & 0 & f\left(C_2\right) & 0 \\ 0 & 0 & f\left(P_1\right) & 0 & 0 & f\left(P_2\right) \end{pmatrix} + \begin{pmatrix} m_R R_1 & 0 & 0 & m_R R_2 & 0 & 0 \\ 0 & m_C C_1 & 0 & 0 & m_C C_2 & 0 \\ 0 & 0 & m_P P_1 & 0 & 0 & m_P P_2 \end{pmatrix} C$$

$$= \begin{pmatrix} f\left(R_1\right) & 0 & 0 & f\left(R_2\right) & 0 & 0 \\ 0 & f\left(C_1\right) & 0 & 0 & f\left(C_2\right) & 0 \\ 0 & 0 & f\left(P_1\right) & 0 & 0 & f\left(P_2\right) \end{pmatrix} + \begin{pmatrix} c_{11,R} m_R R_1 + c_{21,R} m_R R_2 & 0 & 0 & c_{12,R} m_R R_1 + c_{22,R} m_R R_2 & 0 & 0 \\ 0 & c_{11,C} m_C C_1 + c_{21,C} m_C C_2 & 0 & 0 & c_{12,C} m_C C_1 + c_{22,C} m_C C_2 & 0 \\ 0 & 0 & c_{11,P} m_P P_1 + c_{21,P} m_P P_2 & 0 & 0 & c_{12,P} m_P P_1 + c_{22,P} m_P P_2 \end{pmatrix}$$

Proof Continued:

Because equation (24) works, by the same logic as before we can take and transform this equation into:

$$\dot{\Psi} = D\left(f\left(s\left(t\right)\right)\right)\Psi + M\Psi\Lambda \qquad (25)$$

Where $\Psi = Y\ A$. Recall that $Y = X - S_{flat}$ so it is a k x kn matrix. A is made up of the eigenvectors of C so A is a kn x kn matrix which means that Ψ is a k x kn matrix.

Note: In this case Ψ is still a k x kn matrix, however, it can be transformed into the same format as in previous case (which is more important to demonstrate that when using the equation provided in the theorem – that is

$$\dot{x} = \left[D\left(f\left(s\left(t\right)\right)\right) + \begin{pmatrix} \lambda_{1,i} \\ \vdots \\ \lambda_{k,i} \end{pmatrix} M \right] x \qquad i = 1, \ldots, n \tag{26}$$

x is of vector form). This transformation matrix (T) is a kn x n matrix made up of k x 1 blocks of 1s.

$$T = \begin{pmatrix} 1 & 0 & \ldots & 0 \\ \vdots & \vdots & \ldots & \vdots \\ 1 & 0 & \ldots & 0 \\ 0 & 1 & \ldots & 0 \\ \vdots & \vdots & \ldots & \vdots \\ 0 & 1 & \ldots & 0 \\ 0 & 0 & \ldots & 1 \\ \vdots & \vdots & \ldots & \vdots \\ 0 & 0 & \ldots & 1 \end{pmatrix} \tag{27}$$

Worked example:

Here we demonstrate how the *Species' Specific Connectivity* approach has the same answer when a universal connectivity matrix is used.

First, we solve using the *Universal Connectivity Approach*, and then apply the proposed approach to demonstrate that the answers are equivalent.

For this example we use three species and 2 patches that are bidirectional (i.e. both patches are connected to each other). In this way we have the following matrices:

$$X = \begin{pmatrix} R_1 & R_2 \\ C_1 & C_2 \\ P_1 & P_2 \end{pmatrix} \quad M = \begin{pmatrix} m_R & 0 & 0 \\ 0 & m_C & 0 \\ 0 & 0 & m_P \end{pmatrix} \quad C = \begin{pmatrix} -1/2 & 1/2 \\ 1/2 & -1/2 \end{pmatrix}$$

Which means that matrix A such that $A^{-1}CA = \Lambda$, Λ and the Jacobian *(D(f(s(t))))* of *f* are:

$$A = \begin{pmatrix} -1 & 1 \\ 1 & 1 \end{pmatrix} \quad \Lambda = \begin{pmatrix} -1 & 0 \\ 0 & 0 \end{pmatrix} \quad D\left(f\left(s\left(t\right)\right)\right) = \begin{pmatrix} j_{11} & j_{12} & j_{13} \\ j_{21} & j_{22} & j_{23} \\ j_{31} & j_{32} & j_{33} \end{pmatrix}$$

We want to evaluate around $Y = X - S_{flat}$, which is

$$Y = \begin{pmatrix} R_1 - S_{R_1} & R_2 - S_{R_2} \\ C_1 - S_{C_1} & C_2 - S_{C_2} \\ P_1 - S_{P_1} & P_2 - S_{P_2} \end{pmatrix}$$

Then,

$$\begin{aligned} \Psi = YA &= \begin{pmatrix} R_1 - S_{R_1} & R_2 - S_{R_2} \\ C_1 - S_{C_1} & C_2 - S_{C_2} \\ P_1 - S_{P_1} & P_2 - S_{P_2} \end{pmatrix} \begin{pmatrix} -1 & 1 \\ 1 & 1 \end{pmatrix} \\ &= \begin{pmatrix} -\left(R_1 - S_{R_1}\right) + R_2 - S_{R_2} & R_1 - S_{R_1} + R_2 - S_{R_2} \\ -\left(C_1 - S_{C_1}\right) + C_2 - S_{C_2} & C_1 - S_{C_1} + C_2 - S_{C_2} \\ -\left(P_1 - S_{P_1}\right) + P_2 - S_{P_2} & P_1 - S_{P_1} + P_2 - S_{P_2} \end{pmatrix} = \begin{pmatrix} \Psi_{11} & \Psi_{12} \\ \Psi_{21} & \Psi_{22} \\ \Psi_{31} & \Psi_{32} \end{pmatrix} \end{aligned}$$

Now, recal that:

$$\dot{\Psi} = D\left(f\left(s\left(t\right)\right)\right)\Psi + M\Psi\Lambda$$

Then the first part of the right hand side of the equation becomes:

$$\begin{aligned}
D\left(f\left(s\left(t\right)\right)\right)\Psi &= \begin{pmatrix} j_{11} & j_{12} & j_{13} \\ j_{21} & j_{22} & j_{23} \\ j_{31} & j_{32} & j_{33} \end{pmatrix} \begin{pmatrix} \Psi_{11} & \Psi_{12} \\ \Psi_{21} & \Psi_{22} \\ \Psi_{31} & \Psi_{32} \end{pmatrix} \\
&= \begin{pmatrix} j_{11}\Psi_{11} + j_{12}\Psi_{21} + j_{13}\Psi_{31} & j_{11}\Psi_{12} + j_{12}\Psi_{22} + j_{13}\Psi_{32} \\ j_{21}\Psi_{11} + j_{22}\Psi_{21} + j_{23}\Psi_{31} & j_{21}\Psi_{12} + j_{22}\Psi_{22} + j_{23}\Psi_{32} \\ j_{11}\Psi_{11} + j_{12}\Psi_{21} + j_{13}\Psi_{31} & j_{31}\Psi_{12} + j_{32}\Psi_{22} + j_{33}\Psi_{32} \end{pmatrix}
\end{aligned}$$

Then the second part of the right hand side of the equation becomes:

$$\begin{aligned}
M\Psi\Lambda &= \begin{pmatrix} m_R & 0 & 0 \\ 0 & m_C & 0 \\ 0 & 0 & m_P \end{pmatrix} \begin{pmatrix} \Psi_{11} & \Psi_{12} \\ \Psi_{21} & \Psi_{22} \\ \Psi_{31} & \Psi_{32} \end{pmatrix} \begin{pmatrix} -1 & 0 \\ 0 & 0 \end{pmatrix} \\
&= \begin{pmatrix} m_R\Psi_{11} & m_R\Psi_{12} \\ m_C\Psi_{21} & m_C\Psi_{22} \\ m_P\Psi_{31} & m_P\Psi_{32} \end{pmatrix} \begin{pmatrix} -1 & 0 \\ 0 & 0 \end{pmatrix} \\
&= \begin{pmatrix} -m_R\Psi_{11} & 0 \\ -m_C\Psi_{21} & 0 \\ -m_P\Psi_{31} & 0 \end{pmatrix}
\end{aligned}$$

Together, this means that the previous equation equals:

$$\begin{aligned}
\begin{pmatrix} \dot{\Psi}_{11} & \dot{\Psi}_{12} \\ \dot{\Psi}_{21} & \dot{\Psi}_{22} \\ \dot{\Psi}_{31} & \dot{\Psi}_{32} \end{pmatrix} &= \begin{pmatrix} j_{11}\Psi_{11} + j_{12}\Psi_{21} + j_{13}\Psi_{31} & j_{11}\Psi_{12} + j_{12}\Psi_{22} + j_{13}\Psi_{32} \\ j_{21}\Psi_{11} + j_{22}\Psi_{21} + j_{23}\Psi_{31} & j_{21}\Psi_{12} + j_{22}\Psi_{22} + j_{23}\Psi_{32} \\ j_{11}\Psi_{11} + j_{12}\Psi_{21} + j_{13}\Psi_{31} & j_{31}\Psi_{12} + j_{32}\Psi_{22} + j_{33}\Psi_{32} \end{pmatrix} + \begin{pmatrix} -m_R\Psi_{11} & 0 \\ -m_C\Psi_{21} & 0 \\ -m_P\Psi_{31} & 0 \end{pmatrix} \\
&= \begin{pmatrix} j_{11}\Psi_{11} + j_{12}\Psi_{21} + j_{13}\Psi_{31} - m_R\Psi_{11} & j_{11}\Psi_{12} + j_{12}\Psi_{22} + j_{13}\Psi_{32} \\ j_{21}\Psi_{11} + j_{22}\Psi_{21} + j_{23}\Psi_{31} - m_C\Psi_{21} & j_{21}\Psi_{12} + j_{22}\Psi_{22} + j_{23}\Psi_{32} \\ j_{11}\Psi_{11} + j_{12}\Psi_{21} + j_{13}\Psi_{31} - m_P\Psi_{31} & j_{31}\Psi_{12} + j_{32}\Psi_{22} + j_{33}\Psi_{32} \end{pmatrix}
\end{aligned}$$

Now, using the *Species' Specific Connectivity approach*:

In this case, we have the following matrices:

$$X = \begin{pmatrix} R_1 & 0 & 0R_2 & 0 & 0 & \\ 0 & C_1 & 0 & 0 & C_2 & 0 \\ 0 & 0 & P_1 & 0 & 0 & P_2 \end{pmatrix} \quad M = \begin{pmatrix} m_R & 0 & 0 \\ 0 & m_C & 0 \\ 0 & 0 & m_P \end{pmatrix} \quad C_{sp} = \begin{pmatrix} -1/2 & 1/2 \\ 1/2 & -1/2 \end{pmatrix}$$

Because all of the species' have the same connectivity the C_{sp} is identical for all species for the purpose of comparing to the previous example. However, despite this, we still have the new Connectivity Matrix:

$$C = \begin{pmatrix} -1/2 & 0 & 0 & 1/2 & 0 & 0 \\ 0 & -1/2 & 0 & 0 & 1/2 & 0 \\ 0 & 0 & -1/2 & 0 & 0 & 1/2 \\ 1/2 & 0 & 0 & -1/2 & 0 & 0 \\ 0 & 1/2 & 0 & 0 & -1/2 & 0 \\ 0 & 0 & 1/2 & 0 & 0 & -1/2 \end{pmatrix}$$

But, because the underlying C_{sp} is the same for all species we have a similar Λ matrix, but a slightly different A matrix. These now look like:

$$\Lambda = \begin{pmatrix} -1 & 0 & 0 & 0 & 0 & 0 \\ 0 & -1 & 0 & 0 & 0 & 0 \\ 0 & 0 & -1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix} \quad A = \begin{pmatrix} 0 & 0 & -1 & 0 & 0 & 1 \\ 0 & -1 & 0 & 0 & 1 & 0 \\ -1 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 1 \\ 0 & 1 & 0 & 0 & 1 & 0 \\ 1 & 0 & 0 & 1 & 0 & 0 \end{pmatrix}$$

Becaucse the local processes are the same the Jacobian is the same as before:

$$D\left(f\left(s\left(t\right)\right)\right) = \begin{pmatrix} j_{11} & j_{12} & j_{13} \\ j_{21} & j_{22} & j_{23} \\ j_{31} & j_{32} & j_{33} \end{pmatrix}$$

We want to evaluate around $Y = X - S_{flat}$ which is:

$$Y = \begin{pmatrix} R_1 - S_{R_1} & 0 & 0 & R_2 - S_{R_2} & 0 & 0 \\ 0 & C_1 - S_{C_1} & 0 & 0 & C_2 - S_{C_2} & 0 \\ 0 & 0 & P_1 - S_{P_1} & 0 & 0 & P_2 - S_{P_2} \end{pmatrix}$$

Then,

$$\Psi = YA = \begin{pmatrix} R_1 - S_{R_1} & 0 & 0 & R_2 - S_{R_2} & 0 & 0 \\ 0 & C_1 - S_{C_1} & 0 & 0 & C_2 - S_{C_2} & 0 \\ 0 & 0 & P_1 - S_{P_1} & 0 & 0 & P_2 - S_{P_2} \end{pmatrix} \begin{pmatrix} 0 & 0 & -1 & 0 & 0 & 1 \\ 0 & -1 & 0 & 0 & 1 & 0 \\ -1 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 1 \\ 0 & 1 & 0 & 0 & 1 & 0 \\ 1 & 0 & 0 & 1 & 0 & 0 \end{pmatrix}$$

$$= \begin{pmatrix} 0 & 0 & -\left(R_1 - S_{R_1}\right) + R_2 - S_{R_2} & 0 & 0 & R_1 - S_{R_1} + R_2 - S_{R_2} \\ 0 & -\left(C_1 - S_{C_1}\right) + C_2 - S_{C_2} & 0 & 0 & C_1 - S_{C_1} + C_2 - S_{C_2} & 0 \\ -\left(P_1 - S_{P_1}\right) + P_2 - S_{P_2} & 0 & 0 & P_1 - S_{P_1} + P_2 - S_{P_2} & 0 & 0 \end{pmatrix}$$

But, in fact, the entries of Ψ are the same as the entries in *Universal Connectivity Apprach* Ψ matrix, so we will keep this consistent. In this way we get:

$$\Psi = \begin{pmatrix} 0 & 0 & \Psi_{11} & 0 & 0 & \Psi_{12} \\ 0 & \Psi_{21} & 0 & 0 & \Psi_{22} & 0 \\ \Psi_{31} & 0 & 0 & \Psi_{32} & 0 & 0 \end{pmatrix}$$

Now recall that we again have the equation:

$$\dot{\Psi} = D\left(f\left(s\left(t\right)\right)\right)\Psi + M\Psi\Lambda$$

Working through it in the same way as the previous example, the first part of the right hand side of the equation becomes:

$$D\left(f\left(s\left(t\right)\right)\right)\Psi = \begin{pmatrix} j_{11} & j_{12} & j_{13} \\ j_{21} & j_{22} & j_{23} \\ j_{31} & j_{32} & j_{33} \end{pmatrix} \begin{pmatrix} 0 & 0 & \Psi_{11} & 0 & 0 & \Psi_{12} \\ 0 & \Psi_{21} & 0 & 0 & \Psi_{22} & 0 \\ \Psi_{31} & 0 & 0 & \Psi_{32} & 0 & 0 \end{pmatrix}$$

$$= \begin{pmatrix} j_{13}\Psi_{31} & j_{12}\Psi_{21} & j_{11}\Psi_{11} & j_{13}\Psi_{32} & j_{12}\Psi_{22} & j_{11}\Psi_{12} \\ j_{23}\Psi_{31} & j_{22}\Psi_{21} & j_{21}\Psi_{11} & j_{23}\Psi_{32} & j_{22}\Psi_{22} & j_{21}\Psi_{12} \\ j_{33}\Psi_{31} & j_{32}\Psi_{21} & j_{31}\Psi_{11} & j_{33}\Psi_{32} & j_{32}\Psi_{22} & j_{31}\Psi_{12} \end{pmatrix}$$

Then, the second part of the right hand side of the equation becomes:

$$M\Psi\Lambda = \begin{pmatrix} m_R & 0 & 0 \\ 0 & m_C & 0 \\ 0 & 0 & m_P \end{pmatrix} \begin{pmatrix} 0 & 0 & \Psi_{11} & 0 & 0 & \Psi_{12} \\ 0 & \Psi_{21} & 0 & 0 & \Psi_{22} & 0 \\ \Psi_{31} & 0 & 0 & \Psi_{32} & 0 & 0 \end{pmatrix} \begin{pmatrix} -1 & 0 & 0 & 0 & 0 & 0 \\ 0 & -1 & 0 & 0 & 0 & 0 \\ 0 & 0 & -1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}$$

$$= \begin{pmatrix} 0 & 0 & m_R\Psi_{11} & 0 & 0 & m_R\Psi_{12} \\ 0 & m_C\Psi_{21} & 0 & 0 & m_C\Psi_{22} & 0 \\ m_P\Psi_{31} & 0 & 0 & m_P\Psi_{32} & 0 & 0 \end{pmatrix} \begin{pmatrix} -1 & 0 & 0 & 0 & 0 & 0 \\ 0 & -1 & 0 & 0 & 0 & 0 \\ 0 & 0 & -1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}$$

$$= \begin{pmatrix} 0 & 0 & -m_R\Psi_{11} & 0 & 0 & 0 \\ 0 & -m_C\Psi_{21} & 0 & 0 & 0 & 0 \\ -m_P\Psi_{31} & 0 & 0 & 0 & 0 & 0 \end{pmatrix}$$

Together, this means the previous equation equals:

$$\begin{pmatrix} \dot{R}_1 & 0 & 0\dot{R}_2 & 0 & 0 & \\ 0 & \dot{C}_1 & 0 & 0 & \dot{C}_2 & 0 \\ 0 & 0 & \dot{P}_1 & 0 & 0 & \dot{P}_2 \end{pmatrix} = \begin{pmatrix} j_{13}\Psi_{31} & j_{12}\Psi_{21} & j_{11}\Psi_{11} - m_R\Psi_{11} & j_{13}\Psi_{32} & j_{12}\Psi_{22} & j_{11}\Psi_{12} \\ j_{23}\Psi_{31} & j_{22}\Psi_{21} - m_C\Psi_{21} & j_{21}\Psi_{11} & j_{23}\Psi_{32} & j_{22}\Psi_{22} & j_{21}\Psi_{12} \\ j_{33}\Psi_{31} - m_P\Psi_{31} & j_{32}\Psi_{21} & j_{31}\Psi_{11} & j_{33}\Psi_{32} & j_{32}\Psi_{22} & j_{31}\Psi_{12} \end{pmatrix}$$

We can then transform both sides into *k* x *n* matrices by right multiplying both sides by a transformation matrix *T* where *T* is:

$$T = \begin{pmatrix} 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \\ 0 & 1 \end{pmatrix}$$

Multiplying both sides by *T* then gives us:

$$\begin{pmatrix} \dot{\Psi}_{11} & \dot{\Psi}_{12} \\ \dot{\Psi}_{21} & \dot{\Psi}_{22} \\ \dot{\Psi}_{31} & \dot{\Psi}_{32} \end{pmatrix} = \begin{pmatrix} j_{11}\Psi_{11} + j_{12}\Psi_{21} + j_{13}\Psi_{31} - m_R\Psi_{11} & j_{11}\Psi_{12} + j_{12}\Psi_{22} + j_{13}\Psi_{32} \\ j_{21}\Psi_{11} + j_{22}\Psi_{21} + j_{23}\Psi_{31} - m_C\Psi_{21} & j_{21}\Psi_{12} + j_{22}\Psi_{22} + j_{23}\Psi_{32} \\ j_{11}\Psi_{11} + j_{12}\Psi_{21} + j_{13}\Psi_{31} - m_P\Psi_{31} & j_{31}\Psi_{12} + j_{32}\Psi_{22} + j_{33}\Psi_{32} \end{pmatrix}$$

Which is the same as the previous solution.