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Predators That Eat Their Competitors: Mechanisms of Food Web Stability

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Predators That Eat Their Competitors: Mechanisms of Food Web Stability

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by

Clara Allison Woodie

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Dedication

I dedicate this dissertation to my family, who has supported me unconditionally in pursuing all my passions in life; and especially my late grandfather, a lover of nature, who passed away in the Sierra Nevada mountains in 2016. He instilled an unwavering love for ecology in me since before I could say the word ecology.

ABSTRACT OF THE DISSERTATION

Predators That Eat Their Competitors: Mechanisms of Food Web Stability

by

Clara Allison Woodie

Doctor of Philosophy, Graduate Program in Evolution, Ecology and Organismal Biology
University of California, Riverside, September 2024
Dr. Kurt E. Anderson, Chairperson

Nature is replete with a form of omnivory called intraguild predation (IGP), wherein an IG predator competes with its IG prey for a shared resource. Original theory predicted limited regions of coexistence, dependent on a tradeoff between competition and predation that occurs only at intermediate levels of resource productivity. However, evidence shows that natural food webs contain intraguild predation with frequencies up to 87%, creating a discrepancy between original IGP theory and empirical evidence in nature. Much theory has been developed to mend this discrepancy, altering key assumptions and investigating stabilizing mechanisms of IGP. This theory, however, has largely gone untested, resulting in a stark disconnect between theory and empiricism. In this dissertation, I bridge IGP theory and empiricism by developing and explicitly testing theory regarding stabilizing mechanisms of IGP dynamics. In the following chapters, I explore three theoretically-investigated stabilizing mechanisms: adaptive foraging, cannibalism, and spatial resource heterogeneity. First, I use mathematical modeling, including Lotka Volterra and Rosenweig-MacArthur models adapted to IGP systems, to develop new theory. Second, I use protist microcosm experiments, which allow for explicit integration of theory and empiricism, to test new and existing theory. I find that adaptive foraging, cannibalism, and spatial resource heterogeneity are all significant mechanisms that stabilize IGP dynamics, enhancing stable coexistence of IG predator and IG prey across a range of environmental conditions. First, adaptive foraging in the IG predator allows IG prey to rebound from densities close to zero, preventing IG prey exclusion. Second, preferential cannibalism in the IG predator serves as an important density-dependent population regulation factor, preventing both overexploitation and competitive exclusion of the IG prey when the IG predator is a strong resource competitor. Third, spatial resource heterogeneity promotes rescue effects that greatly enhance both regional and local coexistence in habitats that are otherwise suboptimal to the IG predator and/or IG prey. This dissertation fills an important gap in the literature that is the disconnect between theory and empiricism of one of the most ubiquitous species interactions, intraguild predation. These studies collectively reveal the biological importance of key generalizable mechanisms that stabilize this interaction.

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Introduction

Ecologists have historically studied competition and predation as distinct interactions that sometimes affect one another (Chase et al. 2002; Chesson and Kuang 2008), but one of the most ubiquitous species interactions in nature involves both predation and competition. Intraguild predation (IGP), the simplest form of omnivory, occurs when the intraguild (IG) predator competes with its IG prey for a shared resource. Original theoretical analyses suggested general criteria for coexistence being that the IG prey is a superior resource competitor, and the IG predator should gain significantly from consumption of the IG prey (Holt and Polis 1997). This tradeoff between predation and competition gives rise to a pattern of coexistence and exclusion across a resource productivity gradient. At low resource productivity, the IG prey outcompetes the IG predator and maintains too low of an abundance to support the IG predator via predation alone. Conversely, at high productivity, the IG predator is released of competitive pressure, reaching high enough abundances to overexploit the IG prey. Only at intermediate productivity is the competition-predation tradeoff balanced in such a way that coexistence is maintained.

Contrary to the predictions of limited coexistence from original theory, empirical evidence shows that nature is replete with intraguild predation (Polis et al. 1989; Polis and Holt 1992; Rosenheim et al. 1995), with this interaction occurring in natural food webs with up to 87% frequency (Arim and Marquet 2004). Because of this, theory has developed rapidly to mend the discrepancy between original IGP theory and the evidence of IGP's ubiquity in nature. Theoretical investigations incorporating various stabilizing mechanisms of IGP are manifold: alternative resources (Daugherty et al. 2007; Holt and Huxel 2007); prey defense (Urbani and Ramos-Jiliberto 2010; Ikegawa et al. 2015; Ingeman and Novak 2022); adaptive foraging in the IG predator (Krivan 2000; Krivan and Diehl 2005; Wu and Okuyama 2012; Wang et al. 2018); cannibalism in the IG predator (Rudolf 2007; Toscano et al. 2017; Hin and de Roos 2019; Bassar et al. 2023); life history IGP (Hin et al. 2011); Type II functional responses (Abrams and Fung 2010); and spatial factors such as spatial heterogeneity (Amarasekare 2006; Okuyama 2008; Nguyen and Nguyen-Ngoc 2015). Such stabilizing mechanisms often involve population regulation in the IG predator and/or refuges or defenses in the IG prey. This is because evidence of IG prey persistence, as opposed to exclusion, at high productivity in particular is common (Borer et al. 2003; Amarasekare 2007; Novak 2013).

Despite the abundance of theory, IGP theory has been largely disconnected from empiricism, with theory progressing far past empirical tests of the theory. Most empirical work with regard to IGP are not sufficient tests of theory, including short-term experiments (Gismervick and Anderson 1997; Davey et al. 2013; Jaworski et al. 2013; Novak 2013; Granados et al. 2017; Michalko and Pekar 2017), often using empirically-derived interaction strengths, predator preferences or behavioral changes to infer long-term outcomes (e.g. coexistence vs. exclusion). However, short-term dynamics cannot be extrapolated to long-term equilibria, which have important implications such as coexistence vs. exclusion (Briggs and Borer 2005). Other empirical studies are observational and lack causality (Novak 2013), lack a productivity gradient for testing productivity-abundance predictions (Reichstein et al. 2013; Goldberg et al. 2022), or are geared towards specific biocontrol implications rather than explicit integration of theory and empiricism (Provost et al. 2006; Jaworski et al. 2013; Michalko and Pekar 2017; Fernandez et al. 2020).

This dissertation aims to bridge the gap between IGP theory and empiricism by developing and testing IGP theory with protist microcosm experiments. Protist microcosm experiments have historically been the first empirical tests of theory and have been instrumental in the advancement of population ecology specifically (Gause 1934; Huffaker 1958; Luckinbill and Fenton 1978). This is due to their ability to fulfill the requirements of testing theory. First, protists' short generation times facilitate rapid accumulation of long-term population data necessary for comparison to the equilibrium predictions of theory (Briggs and Borer 2005). Multi-generational data also allow examination of complex dynamical behavior common in IGP systems, such as alternative stable states (Verdy and Amarasekare 2010), high-amplitude oscillations (Sen et al. 2018), and chaos (Namba et al. 2008). Second, protist microcosm experiments allow for precise control and manipulation of variables of interest, high replicability, and ease of reproducibility (Holyoak and Lawler 2005; Altermatt et al. 2015), which is necessary for establishing causality and elucidating mechanisms. With such precision, microcosm experiments adhere to model assumptions well while still maintaining the complexity of biological systems.

Protist microcosm experiments have provided some of the first support for certain core elements of IGP theory, such as the productivity-abundance relationship, while challenging other elements, such as IG prey exclusion at high productivity levels (Diehl and Feissel 2000, 2001; Morin 1999). These initial tests of the theory ignited meta-analyses (Arim and Marquet 2004), field studies (Amarasekare 2000; Borer et al. 2003), and further advancement of the theory (Krivan 2000; Krivan and Diehl 2005; Amarasekare 2006; Holt and Huxel 2007). Initial tests of the theory via microcosm studies thus stimulate both field studies and improved models (Holyoak and Lawler 2005; Benton et al. 2007). When they support theory, microcosm studies provide biological basis to theory and guide field studies towards which theoretical predictions and hypotheses to focus on. When microcosm experiments fail to support the theory, they provide guidance to theoreticians on how to refine the theory. However, tests of theory have fallen far behind advancement of the theory, leaving the literature rich with theory regarding stabilizing mechanisms of IGP but scant with empirical support for such theory.

In the following chapters, I combine mathematical modeling and protist microcosm experiments to uncover biologically-sound, generalizable mechanisms of IGP stability. In Chapter 1, I explore one of the simplest solutions to what stabilizes IGP dynamics, adaptive foraging in the IG predator. I develop an adaptive foraging IGP model and generate predictions relative to a nonadaptive IGP model to reproduce the common stabilizing result seen in the literature. To test these predictions with protist microcosm experiments, I use two functionally, behaviorally, and morphologically distinct protozoan omnivores. I found that systems in which the omnivore is equipped with adaptive foraging ability, including cannibalism, are the only systems that lead to long-term coexistence. Experimental results strongly supported model predictions. In

Chapter 2, I explore the effect of cannibalism and adaptive foraging via inducible trophic polymorphisms in more depth theoretically using modified Lotka-Volterra and Rosenzweig-MacArthur models. I focused on the interaction between IG predator foraging preference (for conspecifics vs. heterospecific IG prey) and competitive ability, two traits that heavily affect IGP stability and are potentially interrelated. I found that preferential cannibalism greatly enhances coexistence when the IG predator and IG prey are similar competitors for the shared resource. These two traits have been widely documented empirically—and are likely to be common in systems with trophic polymorphic IG predators—but have yet to be connected theoretically. Lastly, in Chapter 3, I zoom out to mechanisms on the landscape scale, testing spatial IGP theory regarding spatial resource heterogeneity (SRH, the variable spatial distribution of resources). Using explicit spatial microcosm experiments that manipulate resource productivity level and distribution among interconnected patches, I found that SRH significantly enhances persistence and coexistence of IG predators and IG prey both regionally and locally in their most suboptimal habitats through rescue effects.

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Chapter 1

Adaptive foraging stabilizes intraguild predation: Experimental support for model predictions

Abstract

One of the most theoretically-investigated stabilizing mechanisms of intraguild predation (IGP; the consumption of one's competitor) is adaptive foraging in the IG predator, yet theory has progressed far past empirical support for theoretical predictions. Here, we provide the first test of adaptive foraging IGP theory to our knowledge. We first build an IGP model that integrates adaptive preference dynamics, including cannibalism, in the IG predator. To explore the stabilizing potential of adaptive foraging, we compare simulated dynamics to a nonadaptive IGP model under conditions of varying interaction strengths. We then test model predictions using protist microcosm experiments with functionally and morphologically distinct protist species. One protozoan predator, *Blepharisma*, possesses an inducible trophic polymorphism (ITP) that allows it to forage adaptively via morphological plasticity on the shared resource of bacteria, heterospecific IG prey, and conspecific prey. The other protozoan predator, *Euplotes, has* a fixed morphology and consistent preference for protist prey. The two prey species include *Tetrahymena*, a small protist easily consumed by the predators, and *Colpidium*, a larger protist capable of evading predation more often. In a modified 3x3 factorial design, we crossed the predator and prey species including single-species controls and quantified population dynamics for 55 predator generations and 80 prey generations. We also measured distinct *Blepharisma* morphotypes, number of heterospecific and conspecific prey in *Blepharisma* vacuoles, and predator size. Empirical results strongly support model predictions: adaptive foraging, including cannibalism, enables long-term IGP coexistence across a range of IG predation rates. While *Euplotes* drove *Tetrahymena* extinct due to strong predation, and *Colpidium* outcompeted *Euplotes* due to weak predation, *Blepharisma* coexisted with both prey due to trait-mediated adaptive foraging. Notably, *Blepharisma* drove *Tetrahymena* to lower densities than *Colpidium*, but adaptive foraging and cannibalism prevented *Tetrahymena* extinction. The model was able to recapture not just changes in species' densities but also *Blepharisma's* density-dependent preference dynamics, which promoted *Tetrahymena* recovery from low densities. *Blepharisma* cannibals themselves foraged adaptively, with cannibals behaving as generalists when paired with *Colpidium*, which maintained high densities, and specialists when paired with *Tetrahymena*, which suffered lower densities. Our results point to the importance of trait-mediated adaptive foraging, including cannibalism, for long-term IGP coexistence, providing the first empirical test of model predictions to our knowledge.

Introduction

Intraguild predation (hereafter IGP) is the consumption of one's competitor for a shared resource, and what stabilizes this system has been an active area of research for several decades now. Original theory predicts limited regions of coexistence between intraguild (IG) predators and IG prey (Holt and Polis 1997), suggesting that IGP should be uncommon in nature unless under specific and limited conditions (e.g., unproductive resources, IG prey competitive superiority, and weak omnivory). Given the criteria that the IG prey is a superior competitor for the shared resource, the system should only coexist at intermediate resource productivity levels, because the IG predator is outcompeted at low productivity and the IG prey is overexploited at high productivity (Holt and Polis 1997). However, ample empirical evidence shows that IGP is ubiquitous in natural food webs (Polis et al. 1989; Arim and Marquet et al. 2004), creating a stark discrepancy between theory and evidence from nature. This has been deemed the paradox of intraguild predation (Polis et al. 1989) and has prompted rigorous, mostly theoretical, exploration of stabilizing mechanisms.

Adaptive foraging, the flexible feeding of a consumer as a function of changes in prey density, has been shown to stabilize food webs in general (Loeuille 2010; Valdovinos et al. 2010) and is one of the most theoretically-investigated stabilizing mechanisms of intraguild predation. Adaptive foraging behavior in the IG predator is one of the most theoretically-studied mechanisms to explain IGP’s persistence in nature (Gismervik and Andersen 1997; Krivan 2000; Okuyama and Ruyle 2003; Krivan and Diehl 2005; Faria and Costa 2009, 2010; Abrams and Fung 2010; Orlando et al. 2011; Visser et al. 2012; Wu and Okuyama 2012; Pal et al. 2014; Wang et al. 2018). When consumers switch between prey species as a function of their densities, they decrease foraging effort on scarce resources and allow resources to recover when rare (Uchida et al. 2007). Adaptive foraging can therefore prevent IG prey overexploitation/exclusion at high resource productivity in particular, where IG prey have been documented to coexist with IG predators in nature (Borer et al. 2003; Amarasekare 2007; Novak 2013).

One mechanism that allows species to forage adaptively is inducible trophic polymorphisms (hereafter ITP), flexible changes in morphology, physiology or behavior that allow a consumer to alter the trophic level on which it feeds (Banerji and Morin 2009). Also referred to as resource polyphenisms (Smith and Skúlason 1996), ITPs occur in a wide variety of taxa (i.e., protists, Giese 1973; insects, Greene 1989; gastropods, Padilla 2001; amphibians, Levis et al. 2015; fish, Amundsen 2016; birds, Afik and Karasov 1995), and are instrumental in an individual's adaptive response to changes in resource densities in their environment. When morphological, ITPs often involve increases in body size and/or alteration of mouthparts, relaxing gape limitation and allowing predators to consume larger prey species. Such trait-mediated interactions can be especially effective in adaptive foraging, enabling IG predator morphotypes to specialize in acquisition of both IG prey and the shared resource.

Size-dependent interactions, like those driven by morphological ITPs, often facilitate cannibalism, the consumption of conspecifics (Polis 1981; Baras and Jobling 2002; Claessen et al. 2004). As the simplest form of IGP, cannibalism is widespread in natural IGP systems (Polis 1981; Polis et al. 1989; Woodward and Hildrew 2002). Cannibal polyphenisms, typically involving rearranged mouth parts, body size, and/or growth rates, often appear in the same IG predators with ITPs (e.g., ciliates, Banerji and Morin 2009; insects, Vijendravarma et al. 2013; arachnids, Moreira et al. 2022; amphibians, Michimae and Wakahara 2002; fish, Persson et al. 2003), and cannibal morphs are often induced by the consumption of heterospecific IG prey (e.g., amphibians, Michimae and Wakahara 2001). Similar to adaptive foraging, cannibalism is a stabilizing mechanism of IGP systems by serving as a source of predator population regulation, shown both theoretically (Rudolf 2007; Toscano et al. 2017; Bassar et al. 2023) and empirically (reviewed in Rosenheim and Schrieber 2022). Additionally, cannibalism itself can be considered a form of adaptive foraging, as cannibalism by predatory morphs often increases when heterospecific IG prey decreases (e.g., in isopods, Leonardsson 1991; true bugs, Laycock et al. 2006; spiders, Wise 2006). Thus, cannibalism, ITPs, and adaptive foraging are likely inextricable mechanisms driving IGP dynamics, but their effects on long-term equilibrium outcomes (e.g., coexistence vs. exclusion) have yet to be elucidated.

Despite the overwhelming theoretical evidence that adaptive foraging and cannibalism stabilize IGP systems, empirical tests of the theory are nearly nonexistent. Empirical studies are largely disconnected from the theory, with experiments taking place on short time frames (Gismervick and Anderson 1997; Davey et al. 2013; Jaworski et al. 2013; Novak 2013; Granados et al. 2017; Michalko and Pekar 2017), often using empirically-derived interaction strengths, predator preferences or behavioral changes to infer multi-generational dynamics as predicted by theory. However, short-term behavioral or trait changes do not extrapolate to long-term equilibrium dynamics (Briggs and Borer 2005). Additionally, many empirical studies are also focused on specific application purposes such as biological control (Provost et al. 2006; Jaworski et al. 2013; Michalko and Pekar 2017; Fernandez et al. 2020) rather than the explicit integration of theory and empiricism. Even though adaptive foraging is one of the most plausible solutions to the paradox of IGP, we still lack appropriate tests of the theory, which is an important first step to uncovering generalizable stabilizing mechanisms of natural IGP systems.

Protist microcosm experiments enable tests of theory through direct manipulation and control of variables of interest, abundant replication, and quantification of multi-generational population dynamics (Holyoak and Lawler 2005). Protists often adhere well to model assumptions while still capturing the biological complexity of natural systems. They often provide the first biological support for model predictions (Desharnais 2005), or lack thereof, providing focus for comparative field studies and/or refinement of theory. Several original theoretical studies of adaptive IGP call for the use of protist microcosm experiments to test these predictions, particularly protists that have morphological mechanisms of prey switching and use mutually exclusive foraging modalities (Krivan 2000; Krivan and Diehl 2005). Despite this call for research, after nearly two decades, no study has employed a trait-based approach with protists to test predictions from adaptive foraging IGP theory.

Here we provide the first study to explicitly link theory and experiment with regard to the stabilizing potential of adaptive foraging in IGP systems. We define stability as the long-term persistence of all interacting species with populations sufficiently bounded from zero (Kondoh 2003; Kratina et al. 2012). We first build and parameterize two models, one with adaptive foraging including cannibalism and one without, to generate predictions about adaptive foraging. We then employ protist microcosm experiments including an adaptive foraging and cannibalistic omnivore with an ITP, *Blepharisma*, and one with fixed morphology, *Euplotes*. We pair the omnivores with two prey species of different sizes and interaction strengths to test the robustness of the adaptive foraging stabilizing potential. Our results are consistent across model and experiment: while the non-adaptive system precludes coexistence through either the exclusion of IG predator or IG prey, adaptive foraging (including cannibalism) stabilizes IGP dynamics and promotes long-term persistence of all species across a range of interaction strengths. Our model is further able to recapture adaptive preference dynamics and long-term IG prey densities as a function of different interaction strengths in the empirical system.

Methods

Study System

To study the effect of adaptive foraging on IGP coexistence, we chose two omnivore species that are functionally, morphologically, and behaviorally distinct. The ciliate, *Euplotes eurystomus* (mean size = 0.0103 mm^2), is a predatory protozoan with a fixed morphology that feeds primarily on smaller protist prey. It can feed on bacteria but does so inefficiently (i.e., a weak omnivore), often unable to sustain a population on bacteria long-term (C.W., personal observation; Holyoak and Sachdev 1998; Green et al. 2023). Weak omnivory refers to feeding primarily on one food source and using the other only as a supplement, whereas strong omnivory refers to feeding relatively equally and/or efficiently on both resource types (McCann and Hastings 1997). Thus, the strength of omnivory is highest when the IG predator is an effective adaptive forager, feeding efficiently on both the IG prey and the resource in proportion to their availability (Kratina et al. 2012).

The ciliate, *Blepharisma americanum* (hereafter *Blepharisma*), is a predatory protozoan that feeds efficiently on both smaller protist prey and the shared resource of bacteria (i.e., a strong omnivore). *Blepharisma* forages adaptively via an inducible trophic polymorphism (hereafter ITP), which involve changes in behavior, physiology or morphology to feed on different trophic levels (Giese 1973; Banerji and Morin 2009). *Blepharisma* has two discrete morphotypes, and switching between them is induced by changes in prey availability. The microstome morphotype is small (mean size = 0.0108 mm^2) and specialized on bacteria with densely-packed cilia that function to efficiently sweep up bacterial cells into their buccal cavity. Macrostome morphotypes are larger (mean size = 0.0357 mm^2) and induced by the capture and consumption of protist prey. By initial consumption of protist prey, macrostomes undergo morphological changes leading to larger, rearranged buccal cavities and longer cilia for effective capture of protist cells. Macrostomes include cannibals, which feed on conspecific microstomes. Macrostomes transform back into microstomes via cell division.

The two prey species we chose differ in size and therefore affect interaction strengths with predators (DeLong et al. 2015). Both are bacterivores, meaning they forage primarily on bacteria. *Tetrahymena pyriformis* (hereafter *Tetrahymena*) is a relatively small (mean size = 0.0017 mm^2) protozoan that is readily consumed by the predators in this study. *Colpidium colpoda* (hereafter *Colpidium*) is considerably larger (mean size = 0.0048 mm^2) and more prone to evading predation.

Mathematical Model

To demonstrate the stabilizing effect of adaptive foraging in IGP, we implement models that reproduce the common stabilizing result found consistently in the literature. First, the classic Holt and Polis (1997) model without adaptive foraging or cannibalism, deemed the “non-adaptive model,” is represented by three ordinary differential equations,

$$\frac{dR}{dt} = gR(1 - \frac{R}{K}) - c_{NR}NR - c_{PR}PR$$

$$\frac{dN}{dt} = e_{NR}c_{NR}NR - c_{PN}PN - d_N N$$

$$\frac{dP}{dt} = e_{PR}c_{PR}PR + e_{PN}c_{PN}PN - d_P P \qquad \text{(eq. 1)}$$

where *R* is the shared basal resource, *N* is the IG prey, and *P* is the IG predator. Parameters are defined in Table 1.1. We assume the resource is self-limited by logistic growth, consumers forage with a Type I functional response, and consumers suffer constant density-independent mortality.

Next, we implement an “adaptive model” which builds upon the non-adaptive model by 1) including cannibalism and 2) including three additional state variables corresponding to dynamic IG predator preferences over time: q_R, the dynamic preference for the resource; q_N, dynamic preference for IG prey; q_P, dynamic preference for conspecifics. The adaptive model therefore consists of six ordinary differential equations,

$$\frac{dR}{dt} = gR(1 - \frac{R}{K}) - c_{NR}NR - c_{PR}q_R PR$$

$$\frac{dN}{dt} = e_{NR}c_{NR}NR - c_{PN}q_N PN - d_N N$$

$$\frac{dP}{dt} = e_{PR}c_{PR}q_R PR + e_{PN}c_{PN}q_N PN + e_{PP}c_{PP}q_P PP - c_{PP}q_P PP - d_P P$$

$$\frac{dq_R}{dt} = vq_R[e_{PR}c_{PR}R - (e_{PR}c_{PR}q_RR + e_{PN}c_{PN}q_NN + e_{PP}c_{PP}q_PP)]$$

$$\frac{dq_N}{dt} = vq_N[e_{PN}c_{PN}N - (e_{PR}c_{PR}q_RR + e_{PN}c_{PN}q_NN + e_{PP}c_{PP}q_PP)]$$

$$\frac{dq_P}{dt} = vq_P[e_{PP}c_{PP}P - (e_{PR}c_{PR}q_RR + e_{PN}c_{PN}q_NN + e_{PP}c_{PP}q_PP)] \qquad \text{(eq. 2)}$$

where *v* is a rate constant that determines the timescale of changes in foraging effort. We incorporated adaptive foraging strategies similar to Fahimipour and Anderson (2015) with dynamic variables, q_x, which are based on replicator equations (Kondoh 2003). These represent the density-dependent foraging energy that the IG predator allocates to either of its three prey species (Kondoh 2003; Abrams and Fung 2010). The IG predator increases its foraging effort towards resource *x* if a change in q_x provides an increase in biomass production.

To make predictions with respect to our empirical system, we use the non-adaptive model to describe systems with *Euplotes* as the predator and the adaptive model to describe systems with *Blepharisma* as the predator. Model parameters are defined in Table 1.1. We kept the majority of parameters constant and manipulated only three parameters of interest: IG predator consumption rate on the IG prey, IG predator consumption rate on conspecifics, and IG predator conversion efficiency on the shared resource. Though we did not parameterize the model by fitting it to empirical data, we chose parameters relative to one another which reflect our empirical treatments and are broadly consistent with previous laboratory observations. For the non-adaptive system without cannibalism, we set IG predation rates relatively low (c_{PN}=0.01) to represent the *Euplotes-Colpidium* system (hereafter "EC"), and relatively high (c_{PN}=2) to represent the

Euplotes-Tetrahymena system (hereafter “ET”). For both EC and ET scenarios, we set the IG predator’s conversion efficiency on the resource low (e_{PR}=0.1) to represent weak omnivory and cannibal consumption rate to zero (c_{PP}=0) to reflect *Euplotes’* inability to cannibalize. For the adaptive system with cannibalism, we set IG predation and cannibalism rates equal (c_{PP}=0.1), set the IG predator’s conversion efficiency on the resource relatively high (e_{PR}=0.5) to represent stronger omnivory, and altered IG predation rates according to the following. To represent the *Blepharisma-Colpidium* system (hereafter “BC”), we set IG predation rates low (c_{PN}=0.1) to reflect low IG predation strength as a function of *Colpidium’s* large size and ability to evade capture attempts. To represent the *Blepharisma-Tetrahymena* system (hereafter “BT”), we set IG predation rates higher than BC (c_{PN}=0.5) to reflect *Blepharisma’s* ease of capture and consumption of *Tetrahymena* as a function of its smaller size.

Additionally, the IG prey’s consumption rate and conversion efficiency on the resource are high (c_{NR}=e_{NR}=1) in all cases to reflect the IG prey’s competitive superiority over the resource, a general criterion of IGP theory (Holt and Polis 1997). To explore the condition of interest in IGP studies in which the IG prey is prone to extinction, we set K=5, which is on the mid to high end of carrying capacities used in previous adaptive foraging IGP models (Faria and Costa 2009; Abrams and Fung 2010; Orlando et al. 2011; Visser et al. 2012; Wang et al. 2018).

Dynamics were simulated numerically in R (R Core Team 2023) using the package deSolve. We simulated dynamics for 100 time steps at which point they had begun to settle on a stable equilibrium. We explored stability in our models using linear stability analysis (Gurney and Nisbet 1998; Murdoch et al. 2003). To summarize, we linearized equations 1 and 2 around their interior equilibrium and then assessed the stability of these systems against minor disturbances. We began by determining the equilibrium where all species maintain positive, non-zero abundances through Mathematica's “Solve” function (Wolfram Research, Inc., Mathematica, Version 12.0, Champaign, IL, 2019). Next, we evaluated the Jacobian matrix at this equilibrium and used the “Eigenvalues” function to numerically derive the eigenvalues, focusing on the eigenvalue with a negative real part which indicates stability.

Experimental Design and Sampling

To test model predictions, we employed a protist microcosm experiment consisting of the two protozoan omnivore species, the two protozoan prey species, and a shared resource of bacteria (Figure 1.1). We crossed omnivores and prey, including single-species controls, in a modified 3x3 factorial design (excluding the condition of no predator, no prey). The bacteria resource consisted of a standard mixture of three species: *Bacillus cereus*, *Bacillus subtilis*, *Serratia marcescens* (Morin 1999; Altermatt et al. 2015; Chang and Cardinale 2020). Microcosm communities were assembled in isolated 175mL polypropylene Nalgene bottles filled with 50 mL medium. Bacteria productivity level was determined by the amount of Protozoan Pellets (Carolina Biological Supply Co.) used to create the medium (Altermatt et al. 2015). We chose a productivity level that is relatively high (1.4 g/L) compared to other IGP microcosm studies (Diehl and Feissel 2000, 2001; Banerji and Morin 2009), but not too high such that larger cells (e.g. *Blepharisma* macrostomes) would suffer alkaline stress (Woodie and Anderson, unpublished manuscript; Morin 1999). Medium was created by mixing 1.4 g of Protozoan Pellets per 1 L of deionized water, autoclaving to sterilize it, and inoculating once cool with equal parts of each bacteria species. We gave the bacteria five days to grow before initializing the experiment to ensure growth to carrying capacity. Each bottle contained one autoclaved wheat seed for a slow release of nutrients throughout the experiment (Morin 1999; Diehl and Feissel 2000, 2001). Each treatment was replicated 10 times.

We quantified protist population dynamics, including distinct *Blepharisma* morphotypes, three days a week (Monday, Wednesday, Friday) for 40 days, encompassing approximately 80 predator generations and 160 prey generations. We did not quantify bacteria levels and assumed changes in bacteria levels were negligible, as we have shown previously (Green et al. 2023). On day 0, we added 500 individuals of prey (*Tetrahymena* or *Colpidium*) and let them grow until day 3, in which we added 100 predator individuals (*Blepharisma* or *Euplotes*). Sampling followed standard microcosm protocol (Altermatt et al. 2015). To sample, we thoroughly mixed the medium in a bottle, pipetted 10 drops of 20 microliters onto a tared petri dish, identified and counted protist individuals in each drop using a compound light microscope (Leica DME Binocular Microscope), and calculated density. All removed medium was discarded to avoid microcosm contamination.

In our quantification of population dynamics, we differentiated between *Blepharisma* microstomes, macrostomes and cannibals. Although cannibals are a form of macrostome (Giese 1973), they are easily distinguished from macrostomes due to the presence of dark red vacuoles, which indicates the recent consumption of a conspecific microstome. Conversely, white vacuoles indicate the recent consumption of a heterospecific IG prey individual (*Tetrahymena* or *Colpidium*). Thus, when a *Blepharisma* macrostome or cannibal was identified, we quantified the number of vacuoles and identified the type of prey inside each vacuole (i.e., heterospecific IG prey or conspecific microstome). These data were used to calculate preference dynamics over time, where "heterospecific preference" refers to preference for heterospecific IG prey and "conspecific preference" refers to preference for conspecific microstome prey.

Finally, we recorded videos to measure predator size changes over time to link size changes to adaptive foraging. Following daily sampling, we transferred 1 mL of medium from each microcosm containing predators to a Wildco Gridded Sedgewick Rafter counting chamber. We recorded approximately 10 seconds each of 12 evenly spaced spots along 4 columns and 3 rows of the cell. Videos were recorded using the Leica DFC295 digital color camera c-mount and SwiftCam Microscope Digital Camera. Following video processing, we used ImageJ to measure the length, width, and area of predator individuals that were horizontal and in focus, up to a maximum of 15 individuals per video.

Starting on day 14, we replaced 12% of each bottle's medium once a week to remove waste and replenish nutrients to a limited extent. Because 3 mL was already removed each week for videos, and 0.6 mL removed for sampling, we therefore removed an additional 2 mL for a total of 5.6 mL and replaced it with 6 mL fresh, sterile medium. Given that lids must remain ajar to allow airflow (Altermatt et al. 2015), the extra 0.4 mL was to account for medium lost to natural evaporation in our specific laboratory setting, which was calculated from a pilot experiment. Previous experiments show that standard medium renewal does not strongly affect ciliate growth rates (Diehl and Feissel 2000, 2001).

Statistical Analysis

Statistical models were used to explore differences between empirical preference dynamics, prey and morphotype density dynamics, and vacuole data. Model selection was guided by characteristics of the response variable and its corresponding goodness-of-fit metrics. For preference data, which are constrained within the interval [0, 1], we implemented a generalized linear mixed effects model (GLMM) with a beta regression and logit link function using the glmmTMB package in R. Replicate ID was incorporated as a random effect to account for the repeated measures through time within each replicate. GLMMs handle nested, non-independent observations well (Bolker et al. 2009), such as those observed within a replicate microcosm times series. Among the suite of candidate models evaluated—including more complex generalized additive models and generalized additive mixed effects models—the GLMM was the most parsimonious model and demonstrated superior performance, as evidenced by analysis of the residuals.

We employed linear mixed effects models (LMMs) to analyze continuous response variables, including prey density, morphotype density, and vacuole data. In each instance, LMMs provided a better combination of fit and parsimony when compared to other candidate models, including nonlinear mixed effects models. Replicate ID was again indicated as a random effect. For post hoc analyses on all models, we calculated estimated marginal means (EMMs) for each treatment level using the emmeans package, and these pairwise comparisons were adjusted for multiple testing with Tukey's HSD (Honest Significant Difference) method. All statistical computing was done in R (R Core Team 2023).

Results

Our model predicts that the region of stable coexistence is considerably expanded with the addition of adaptive foraging in the model (Figure 2.2), reproducing the common stabilizing result in previous theory (Krivan 2000; Krivan and Diehl 2005; Faria and Costa 2009; Abrams and Fung 2010; Orlando et al. 2011; Pal et al. 2014). Without adaptive preferences, the IG predator largely drives the IG prey extinct across most of the range of IG predation rates, c_{PN}, and resource consumption rates, c_{PR} (Figure 2.2a). The IG predator, being the inferior competitor, is competitively excluded at considerably low values of IG predation rates, where the system behaves akin to an exploitative competition system. The whole system coexists only at sufficiently low values of IG predation rates on the resource, in which the system behaves similarly to a tri-trophic food chain. The addition of adaptive preferences to the model yields whole-system stable coexistence for the majority of IG predation and resource consumption rates (Figure 2.2b), with the IG prey again competitively excluding the IG predator only at very low values of IG predation rates.

Our experimental results provide strong validation for the ubiquitous theoretical finding that adaptive foraging stabilizes IGP systems. Experimental results were broadly consistent with model predictions with respect to coexistence vs. exclusion across the four treatments (Figure 1.3). Generally, dynamics without adaptive foraging and cannibalism yielded extinction of either omnivore or prey (EC and ET scenarios; Figure 1.3a-d) while dynamics with adaptive foraging and cannibalism yielded coexistence (BC and BT scenarios; Figure 1.3e-h). In the ET scenario, characteristic of considerably high IG predation rates and no cannibalism, the IG predator overexploited the IG prey in both the model (Figure 1.3a) and all ten experimental replicates (Figure 1.3b). Empirically, after overexploiting *Tetrahymena*, *Euplotes* was on a slow walk to extinction given its inability to persist solely on bacteria long-term (Holyoak and Sachdev 1998; Green et al. 2023). The model was not able to recapture this. *Euplotes'* slow walk to extinction was also seen in the controls (Figure S1.1) where *Euplotes*, although initially able to establish a population, declined in abundance over time. In comparison, *Blepharisma* in the controls were able to maintain a steady density over time on bacteria alone due to the microstomes' morphological specialization on bacteria (Figure S1.1). Furthermore, in the EC scenario, characteristic of considerably low IG predation rates and no cannibalism, the IG predator was outcompeted and driven extinct in both the model (Figure 1.3c) and all ten experimental replicates (Figure 1.3d). Only a handful of observations were made across all sampling occurrences that revealed *Euplotes* having successfully captured and consumed a *Colpidium* individual (C.W., personal observation). The model was able to capture the short-term persistence of the IG predator, albeit at a relatively low density compared to the empirical dynamics. The model also predicted greater fluctuations of the IG prey population than *Colpidium* experienced.

In the BT scenario, characteristic of high IG predation rates and cannibalism, the system coexisted in both the model (Figure 1.3e) and all ten experimental replicates

(Figure 1.3f). Note that the model does not differentiate between different predator types, but the experiment included quantification of distinct *Blepharisma* morphotypes. Both empirically and theoretically, *Tetrahymena* density initially experienced a boom-bust cycle but eventually increased again, settling on an equilibrium in the model. Note the long period of low density the IG prey faces in the model, only recovering once IG predation eases (Figure 1.3e), which we began to see towards the end of the experiment duration (Figure 1.3f). Empirically, mean *Blepharisma* density increased but began to decrease in the experiment similarly to the model towards day 40 as a lag response to *Tetrahymena's* suppressed density. However, model simulations suggest the system could continue to coexist long-term following these transient fluctuations. Note that the mean *Blepharisma* density in BT (Figure 1.3f) reached similar values as *Euplotes* in ET (Figure 1.3b) without overexploiting *Tetrahymena* due to adaptive foraging. Strong IG predation by *Blepharisma* macrostomes initially depressed *Tetrahymena* density, at which point *Blepharisma* microstomes experienced an increase in density due to reduced competitive pressure for bacteria (Figure 1.3f). Cannibals subsequently appear and grow in abundance as a result of increased conspecific prey (microstome) density.

Lastly, in the BC scenario, characteristic of intermediate IG predation rates and cannibalism, the system also coexists in both the model (Figure 1.3g) and all ten experimental replicates (Figure 1.3h). Notably, *Colpidium* is not driven to abundances as low as those of *Tetrahymena* due to reduced interaction strength between *Blepharisma* and *Colpidium*, the much larger prey. We saw several dynamical effects of this. First, *Colpidium* density remained high and bounded from zero both empirically and theoretically. Closer to the end of the experiment, *Blepharisma* began decreasing as in BT following a gradual decrease in *Colpidium* density. Long-term simulations suggest an eventual rebound and coexistence of both IG predator and IG prey at densities bounded from zero. Second, although macrostomes maintained a similar density as in BT, microstomes maintained lower density due to increased competition from *Colpidium* for bacteria, and cannibals experienced subsequently lower density due to decreased prey (microstomes). Similarly to BT, cannibals appear in the time series in BC following macrostome induction and the increase in microstome density.

Our model was able to recapture the qualitative differences in the adaptive changes in *Blepharisma's* preferences as a function of prey density seen in the experiment (Figure 1.4). Preference dynamics were density-dependent with a lag response. In the case of intermediate IG predation rates (BC scenario; Figure 1.4a-c), preference for heterospecific IG prey stayed relatively high compared to preference for conspecific prey in both the model (Figure 1.4a) and the experiment (Figure 1.4b). This reflected the overall high *Colpidium* abundance relative to microstome abundance (Figure 1.4c). The slight decrease in heterospecific preference and increase in conspecific preference lag behind the slight decrease in *Colpidium* abundance and increase in microstome abundance. Furthermore, in the case of high IG predation rates (BT scenario; Figure 1.4d-f), preference for heterospecific IG prey started high but promptly decreased, associated with a sharp increase in conspecific preference in both the model (Figure 1.4d) and the experiment (Figure 1.4e). This was again associated with the considerable decrease in *Tetrahymena* density and considerable increase in microstome density (Figure

1.4f), in which the preferences lagged behind the density changes. We do not show model results for resource preference for two reasons. First, it remained low given the reduced profitability of consuming (and competing for) resources. Secondly, we do not have data for microstomes' consumption on bacteria for comparison.

Next, we compare long-term IG prey densities and adaptive preferences between simulated and empirical data (Figure 1.5) analyzed by mixed effects models. The different time scales (40 day experiment duration vs. 100 simulated time steps) are responsible for some of the quantitative differences, but qualitative differences remain consistent once past the absolute initial transients. Empirical heterospecific preference was significantly higher than conspecific preference in both treatments (con.BC-hetero.BC: est. = -2.52, 95% CI = -3.51 to -1.53; con.BT-hetero.BT: est. = -2.1, 95% CI = -3.02 to -1.17; Figure 1.5a; Table S1.1). Conspecific preference was higher–and heterospecific preference lower–in BT compared to BC (Figure 1.5a), though not significantly (Table S1.1). *Blepharisma* exploited *Tetrahymena* prey more readily than *Colpidium* prey, consequently driving higher conspecific preference once *Tetrahymena* was scarce and microstomes were abundant. Simulated dynamics were qualitatively similar to empirical ones, but the model predicted overall higher conspecific, and lower heterospecific, preferences in BT. This could be explained by the lag response of preference dynamics to density dynamics seen in the experiment, and further empirical data may have revealed more equal long-term preference dynamics in BT.

Long-term IG prey densities reflected the nature and strength of interaction with each predator (Figure 1.5b). All empirical long-term IG prey densities were significantly different from one another (Table S1.2). Explanations regarding different long-term IG prey densities are explained above. The purpose of this graph is to show that, despite transient dynamics differing between simulated and empirical data in Figure 1.3, long-term trends were consistent between model and experiment. Under the adaptive foraging condition, BC yielded significantly higher IG prey density than BT (BC-BT: est. = 4.82, 95% CI: 4.31 to 5.34), indicating higher stability of the two adaptive foraging systems.

Blepharisma morphotype density and feeding behavior varied across treatments (Figure 1.6). Notably, macrostomes and cannibals were absent from *Blepharisma* controls with the exception of a single cannibal seen across all replicate time series. Microstomes were thus significantly more abundant in Blepharisma controls than BC (B.micro-BC.micro: est. = 2.21, 95% CI: 1.65 to 2.78; Table S1.3) and BT (B.micro-BT.micro: est. = 0.70, 95% CI: 0.16 to 1.24; Table S1.3). Microstomes were significantly higher in BT than BC (BC.micro-BT.micro: est. = -1.51, 95% CI: -2.06 to -0.96). Macrostome density was about the same in BT as BC, and cannibal density is higher in BT than BC, although not significantly. Within BC and BT, microstomes were significantly more abundant than macrostomes, which were significantly more abundant than cannibals (Table S1.3).

Blepharisma cannibals themselves foraged adaptively. Although morphotype density was similar depending on whether *Blepharisma* is paired with *Tetrahymena* or *Colpidium*, the number of heterospecific IG prey consumed by macrostomes and cannibals (Figure 1.6b) and the number of conspecific prey consumed by cannibals (Figure 1.6c) varied considerably (Table S1.4). While the number of heterospecific IG prey consumed by macrostomes was about the same, cannibals in BC consumed significantly more heterospecific IG prey than the zero heterospecific IG prey consumed in BT (BC.cann.hetero-BT.cann.hetero: est. = 1.52, 95% CI: 1.16 to 1.87). Cannibals behaved as generalists in BC and specialists in BT (Figure 1.6b). This was corroborated by *Blepharisma's* size distribution across treatments (Figure S1.2), in which some *Blepharisma* individuals reached much larger sizes in BC than BT due to the large generalist cannibals. These generalist cannibals can get quite big (C.W., personal observation), because they consume two relatively large prey types. Additionally, the number of conspecific prey consumed by cannibals was significantly higher in BT than BC (BT.cann.consp-BC.cann.consp: est. = -0.46, 95% CI:- 0.82 to -0.10). The density dependence of cannibalism is evidenced not just by significantly higher microstome density in BT but also the higher rates of conspecific consumption in BT.

Discussion

Our integration of theory and empiricism reveals that adaptive foraging, including cannibalism, promotes long-term IGP coexistence. In our study, dynamical outcomes were a function of both predator traits (i.e., presence or absence of ITP in the IG predator) and prey traits (i.e., large vs. small IG prey body size). Consistent across theory and experiment, coexistence was achieved in the case of adaptive foraging by preventing IG prey extinction at high productivity. Coexistence occurred regardless of IG predation strength, a strong determinant of IGP stability (Holt and Polis 1997; McCann and Hastings 1997; Krivan and Diehl 2005). However, the system with weaker IG predation rates was most stable in that IG prey densities were bounded furthest from zero.

Conversely, the lack of adaptive foraging and cannibalism prevented coexistence via extinction of either the IG prey, when IG predation was considerably strong, or IG predator, when IG predation was considerably weak. These results highlight the potential for adaptive foraging to be a powerful stabilizing force, especially when foraging traits like ITPs mitigate gape limitation and promote a wide range of resource use, including cannibalism. Our results provide important empirical validation for the prevalent, yet under-tested, theoretical finding that adaptive foraging increases IGP stability (Gismervik and Andersen 1997; Krivan 2000; Okuyama and Ruyle 2003; Krivan and Diehl 2005; Faria and Costa 2009, 2010; Abrams and Fung 2010; Orlando et al. 2011; Visser et al. 2012; Wu and Okuyama 2012; Pal et al. 2014; Wang et al. 2018). Our results further provide empirical support for the predicted stabilizing mechanism of cannibalism in IGP systems (Rudolf 2007; Toscano et al. 2017; Bassar et al. 2023). Lastly, our experiment helps elucidate the functional significance of trait plasticity and trait-mediated interactions, an important area of research needing further empirical exploration (Kishida et al. 2010).

A common theoretical finding is that persistence is most likely when omnivory is weak and the system is more oriented towards a tri-trophic food chain (McCann and Hastings 1997; Mylius et al. 2001; Diehl 2003; Kuijper 2003). Within existing adaptive foraging IGP models, some studies find that adaptive foraging stabilizes IGP dynamics only under weak omnivory (e.g., IG predator cannot persist on the resource alone; Krivan 2000; Krivan and Diehl 2005; Abrams and Fung 2010) while others find that adaptive foraging mitigates the destabilizing effects of strong omnivory (Faria and Costa 2009; Pal et al. 2014). Our empirical results support the latter given that *Blepharisma* is a strong omnivore due to its ITP, effectively foraging on both the resource and IG prey in proportion to their availability (Kratina et al. 2012). Furthermore, McCann and Hastings (1997) found that with stronger omnivory, IG predation rates should be lower to maintain stability. This is precisely what we found within our adaptive foraging systems: *Blepharisma's* lower IG predation rates on *Colpidium* increased stability, by bounding *Colpidium* densities further from zero, compared to *Blepharisma's* higher IG predation rates on *Tetrahymena*, driving a boom-bust cycle. So while adaptive foraging stabilizes strong omnivory in general, our results within adaptive foraging systems support the common finding that weaker omnivory (i.e., less effective IG predation) is more stable. Our results highlight the importance of considering interacting functional traits, such as morphological (e.g., ITPs) and behavioral (e.g., adaptive foraging), in the study of IGP dynamics.

Mutually exclusive foraging modes often involve time lags and energetic costs associated with transitions between discrete states. Time lags associated with changes in foraging allocation can have significant impacts on system dynamics (Abrams 1992; Padilla and Adolph 1996). Quicker adaptive change is generally most stabilizing, effectively preventing IG prey overexploitation and mitigating other instabilities such as high-amplitude population cycles and chaos (Krivan and Diehl 2005; Faria and Costa 2010; Wang et al. 2018). We found adaptive preference changes lagged behind density changes in both BT and BC scenarios, which contributed to density fluctuations both empirically and theoretically. However, our results highlight the important interplay between IG predation strength and time lags: the fluctuations were higher in amplitude and reached densities dangerously close to zero when IG predation rates were strongest in the BT scenario. The time frame of *Blepharisma's* switching rate is generally on par with behavioral changes (Giese 1973), despite greater energetic costs associated with morphological change. Thus, *Blepahrisma's* relatively strong IG predation on *Tetrahymena* combined with its relatively short time lag likely aided in *Tetrahymena's* persistence despite short-term troughs in density. These results suggest that IG predation rates can be stronger if time lags are shorter, and weaker if time lags are longer, and still promote stability. Future studies should explore the effects of distinct adaptive foraging strategies, including different magnitudes of response times and/or energetic costs. Understanding what happens in the middle ground between *Euplotes*, a weak omnivore lacking effective adaptive foraging capabilities, and *Blepharisma*, a strong omnivore with highly specialized morphology and switching time lags, could yield more insight into how the various costs associated with adaptive foraging contribute to the results in the present study.

Blepharisma's mode of adaptive foraging (the ITP) facilitates cannibalism by driving body size heterogeneity and mitigating gape limitation, similar to other systems such as amphibians and fish (Michimae and Wakahara 2002; Persson et al. 2003; Amundsen 2016). Our results show that cannibalism largely only occurs when *Blepharisma* is paired with protist prey, likely due to the ease with which macrostomes can capture and consume microstomes compared to microstomes capturing other microstomes (Giese 1973). Such heterospecific IG prey-induced cannibal morphology is common (e.g., salamanders, Kishida et al. 2009; tadpoles, Levis et al. 2015). Hence, cannibalism and IGP are often found within the same system (reviewed in Polis 1981; Montserrat et al. 2006) and in conjunction with ITPs (Andersson et al. 2007). These three phenotypes may commonly evolve together because cannibalism in the IG predator enables stability despite higher IG predator resource exploitation rates relative to IG prey (Rudolf 2007; Toscano et al. 2017), which is a common characteristic of IG predators with ITPs (Woodie and Anderson 2024). Our results suggest the combination of cannibalism, ITPs, and adaptive foraging are especially beneficial in IGP systems because of the benefit to both IG prey (adaptive foraging and cannibalism prevent overexploitation) and IG predator (ITPs enable efficient consumption of multiple prey types).

The incorporation of cannibalism does not affect the overall high stability of our adaptive model (Figure 1.2), but cannibal behavior plays a notable role in the dynamics of our empirical systems. We have treated cannibalism as a form of adaptive foraging given that the cannibals themselves forage adaptively. *Blepharisma* alters its cannibal-specific feeding behavior as a function of IG prey type and density: cannibals forage as specialists in BT, where *Tetrahymena* is in low abundance, but as generalists in BC, where *Colpidium* is in high abundance. Both cannibal density and cannibalism consumption rates are higher in BT likely due to a combination of factors: 1) low *Tetrahymena* density causing *Blepharisma* to allocate less energy towards foraging for *Tetrahymena*, and 2) high microstome density due to reduced competition pressure from scarce *Tetrahymena*. This reduced predation pressure from macrostomes/cannibals combined with reduced competitive pressure from microstomes permitted *Tetrahymena* to recover from considerably low densities. Increased preference for conspecifics following decreased heterospecific IG prey density has been documented in many types of systems, such as in other protists (Grønlien et al. 2002), isopods (Leonardsson 1991), true bugs (Laycock et al. 2006; Takizawa and Snyder 2011), and spiders (Wise 2006). Additionally, cannibalism has been shown to increase predation pressure on heterospecific IG prey when readily available (Takatsu and Kishida 2015), which is what we see in BC with the generalist cannibals feeding heavily on both microstomes and *Colpidium*. Our study is unique in that it links these short-term behavioral outcomes to long-term coexistence. Future studies should parse out cannibalism from adaptive foraging given that cannibalism alone provides its own degree of stabilization (Rudolf 2007; Toscano et al. 2017; Bassar et al. 2023).

Though we find a strong stabilizing effect of adaptive foraging and cannibalism on IGP dynamics, there is not a 1:1 scaling relationship between the persistence of a food web module in isolation and its effect on larger food web stability (Stouffer and Bascompte 2010). It is still largely debated whether omnivory is generally stabilizing or destabilizing when embedded in larger food webs (McLeod and Leroux 2020). Possibly the nature of the omnivorous interaction matters. Our results show strong effects of different mechanisms and strengths of omnivorous interactions on persistence, and it is not unreasonable to speculate that these differences would play a role in the stability of larger food webs. For instance, evidence suggests cannibalism to be the particular form of omnivory module that is most stable, yet cannibalism can destabilize food webs as a whole (McLeod and Leroux 2020). So while our results show that adaptive foraging and cannibalism are strong stabilizing mechanisms of the IGP module, their function in larger food webs may be different. Because a common theoretical finding is that weak omnivory is stabilizing for whole food webs (Neutel et al. 2007; McCann 2000; Emmerson and Yearsley 2004; Gellner and McCann 2012), our ET and EC systems, while less stable in isolation, could potentially contribute greatly to the stability of larger food webs. How these modules interact with one another when assembled in a greater food web context is an active area of research needing more theoretical and empirical investigation.

Conclusion

We have shown that adaptive foraging, including cannibalism, plays a significant stabilizing role in IGP systems, supported by both theory and experimental tests of theory. The stabilizing effect is robust to variations in IG predation strength, a quality that determines IGP stability. This work provides empirical support for long-term model predictions regarding coexistence, generating greater connection between theory and empiricism, an important area in food web research that is often neglected (Kratina et al. 2012). Our study also contributes to the recent call to research for understanding the effects of morphological change on IGP systems (Pahl et al. 2020). Our results add to the growing body of knowledge that dynamic omnivory, and density-dependent preference in particular, is a potent stabilizing force in food web dynamics (Gutgesell et al. 2022). As humans continue to disturb the natural environment, a predator’s ability to flexibly respond to changes in prey availability may become increasingly important.

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Tables & Figures

Table 1.1. A description of the parameters and their values used in this study.

Parameter	Description (units)	Default Value
g	Resource, R, intrinsic growth rate (time^{-1})	5
K	Resource, R, carrying capacity (biomass)	5
d_N	Death rate of IG prey, N (time^{-1})	0.05
d_P	Death rate of IG predator, P (time^{-1})	0.05
c_{NR}	Consumption rate IG prey, N, on resource, R (time^{-1})	1
c_{PR}	Consumption rate IG predator, P, on resource, R (time^{-1})	0.5
c_{PN}	Consumption rate IG predator, P, on IG prey, N (time^{-1})	Varied: 0.01 (EC scenario); 0.1 (BC scenario); 0.5 (BT scenario); 2 (ET scenario)
c_{PP}	Consumption rate IG predator, P, on conspecifics, P (time^{-1})	Varied: 0 (EC and ET scenarios); 0.1 (BC and BT scenarios)
e_{NR}	Conversion efficiency of IG prey, N, on resource, R (biomass of N/unit R consumed)	1
e_{PR}	Conversion efficiency of IG predator, P, on resource, R (biomass of P/unit R consumed)	Varied: 0.1 (EC and ET scenarios); 0.5 (BC and BT scenarios)
e_{PN}	Conversion efficiency of IG predator, P, on IG prey, N (biomass of P/unit N consumed)	0.5
e_{PP}	Conversion efficiency of IG predator, P, on conspecifics, P (biomass of P/unit P consumed)	0.5

v	Rate of change of timescale of foraging effort (unitless)	0.5

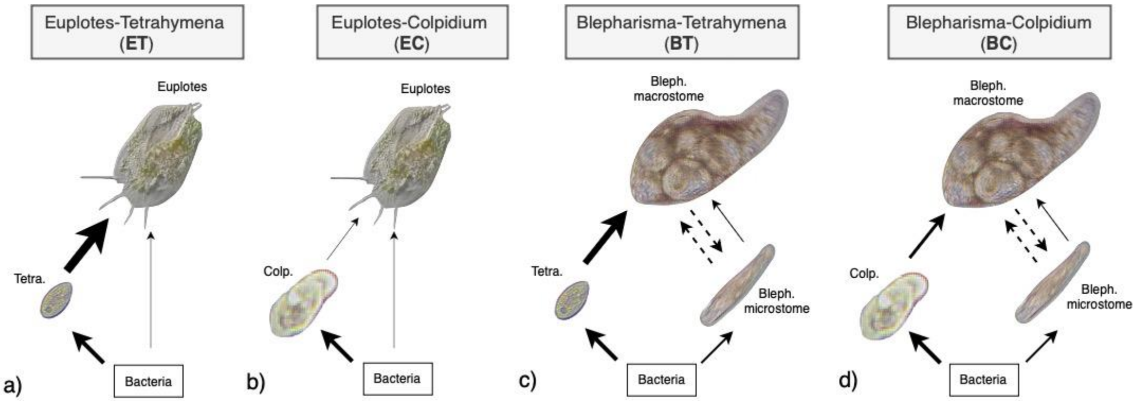


Figure 1.1. The major food web modules assembled in the experiment (excluding single species controls) with associated interaction strengths. Solid arrows signify feeding relationships while broken arrows signify bidirectional switching between *Blepharisma* morphs. Thickness of the arrows correspond to relative interaction strengths, and protists are scaled approximately to size relative to one another. Each treatment consisted of 10 replicate microcosms. ET is characteristic of the strongest IG predation rates and very weak resource consumption rates (a). EC is characteristic of very weak IG predation rates and very weak resource consumption rates (b). BT is characteristic of somewhat strong IG predation rates, intermediate resource consumption rates, and cannibalism (c). BC is characteristic of intermediate IG predation rates, intermediate resource consumption rates, and cannibalism (d). Although Blepharisma microstomes are effective resource consumers, they are inferior in competition to IG prey.

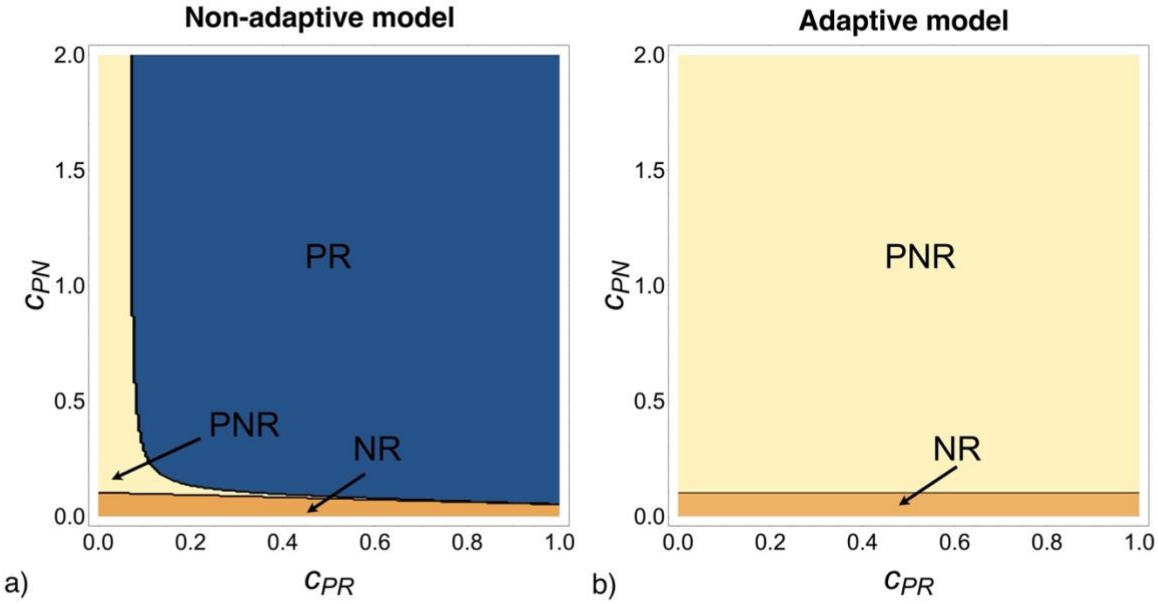


Figure 1.2. Equilibrium outcomes as a function of the IG predator's consumption rate on the resource, c_{PR}, and IG prey, c_{PN} for the a) non-adaptive model, and the b) adaptive model. Here the adaptive model does not include cannibalism ($c_{PP} = 0$) but results do not change with non-zero values of c_{PP}. Other parameters are listed in Table 1.1. Blue regions denote stable *PR* equilibrium where just the IG predator and resource persist, orange regions denote stable *NR* equilibrium where just the IG prey and resource persist, and yellow regions denote stable *PNR* equilibrium (coexistence between IG predator, IG prey and resource).

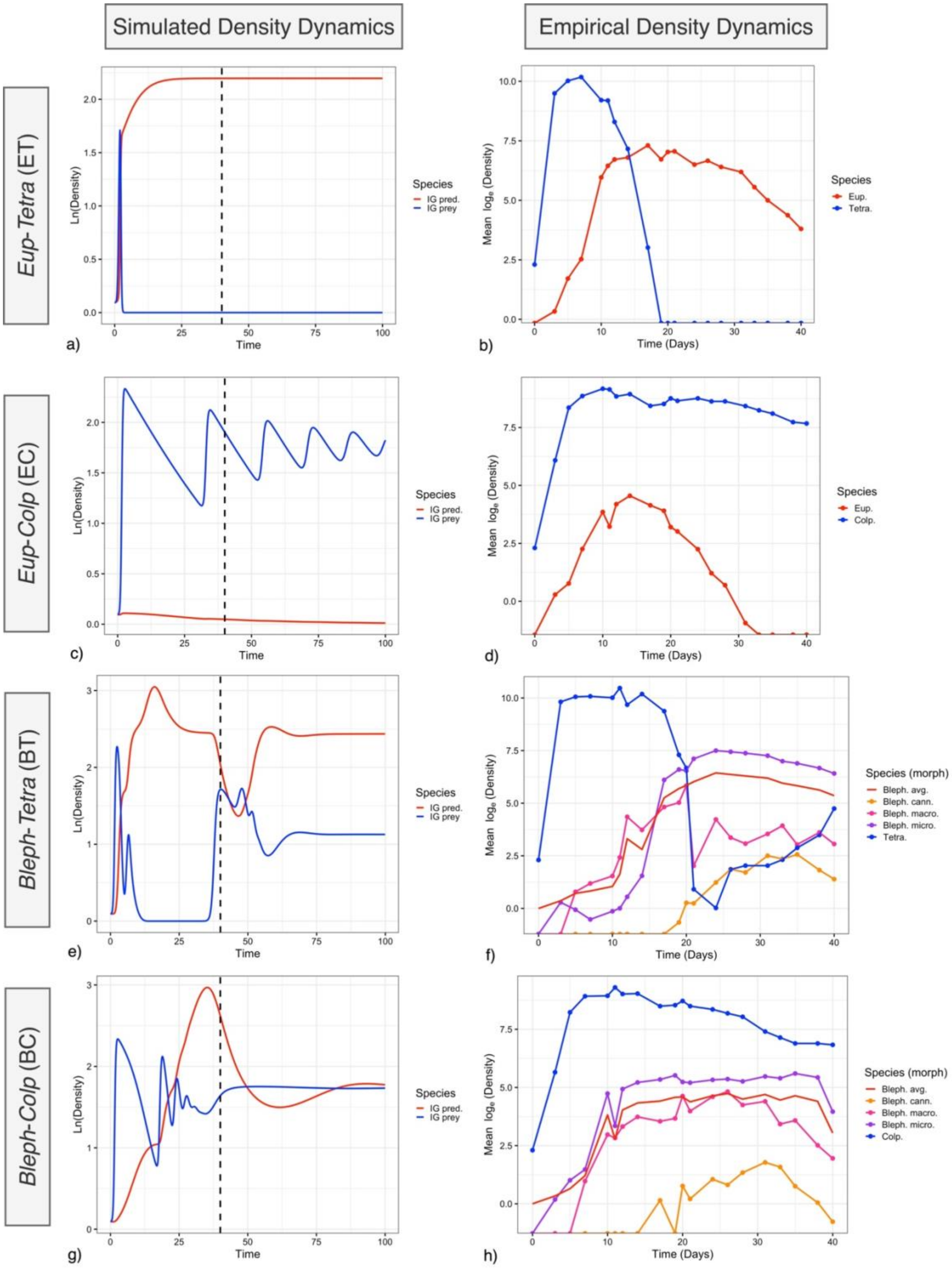

Simulated Density Dynamics
Empirical Density Dynamics
Eup-Tetra (ET)
Eup-Colp (EC)
Bleph-Tetra (BT)
Bleph-Colp (BC)
Ln(Density)
Time
Mean log$_e$ (Density)
Time (Days)
Species
IG pred.
IG prey
Eup.
Tetra.
Colp.
Species (morph)
Bleph. avg.
Bleph. cann.
Bleph. macro.
Bleph. micro.
a)
b)
c)
d)
e)
f)
g)
h)

Figure 1.3. Simulated (a, c, e, g) and empirical (b, d, f, h) density dynamics in the ET treatment (a, b), EC treatment (c, d), BT treatment (e, f), and BC treatment (g, h). *Blepharisma* morphotypes were quantified separately in the experiment, whereas the model did not include separate IG predator state variables. Average *Blepharisma* density refers to the average of all morphotype densities shown. Note that the duration of the experiment is shown (40 days), but 100 time steps of the simulated data are included to show the long-term dynamics once they begin to settle at an equilibrium. The dashed line in the simulation subgraphs indicates the 40 day cutoff for ease of comparison to the experimental time scale. Parameters for the simulations are listed in Table 1.1.

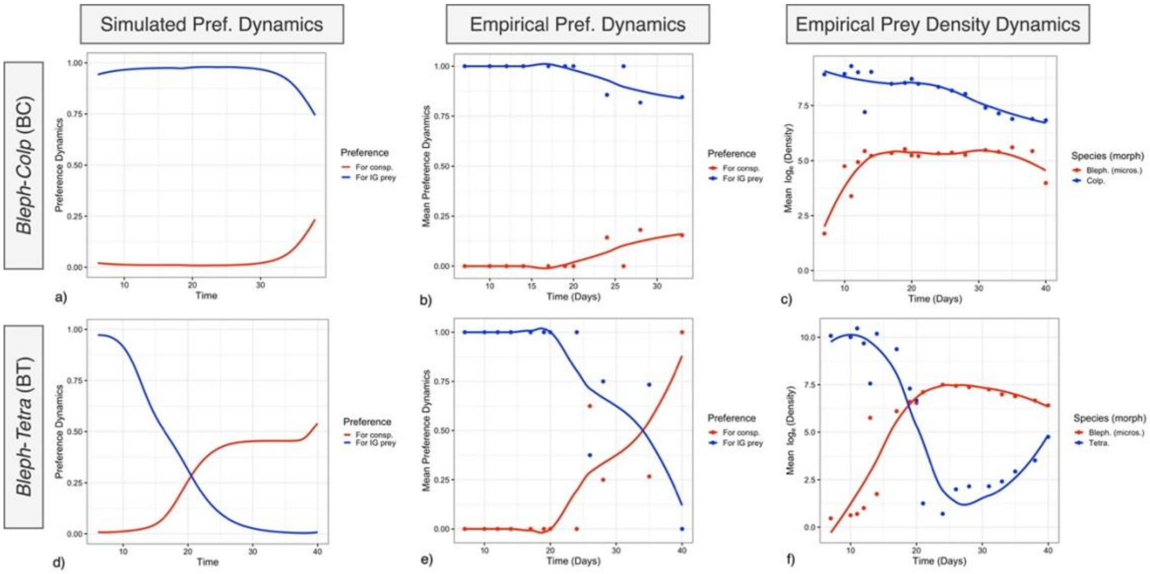
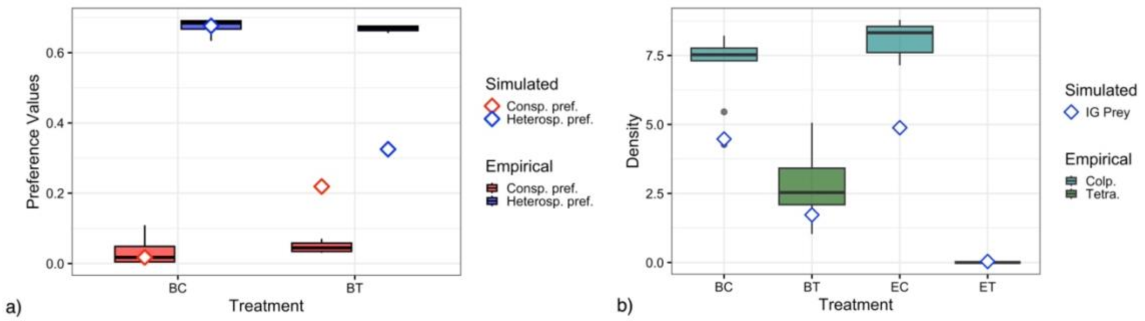
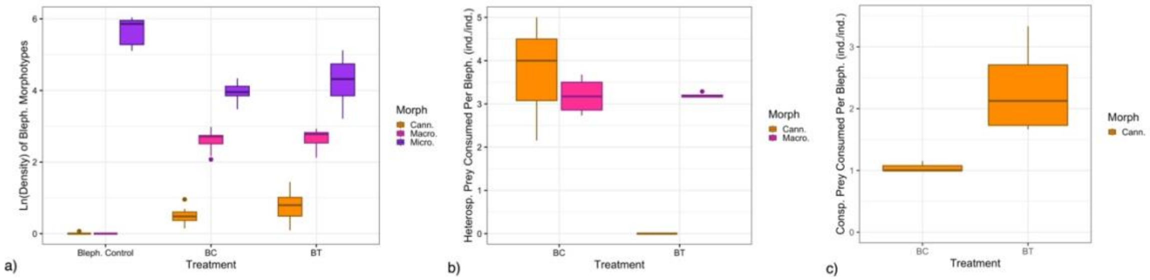


Figure 1.4. Preference dynamics in the first 40 simulated time steps (a, d) and throughout the 40 days of the experiment (b, e), which lag behind respective prey densities (c, f). Shown for BC treatment (a-c) and BT treatment (d-f). Time series start at day 7 when the first macrostomes with quantifiable vacuoles appeared in the experiment. Smoothed lines through the empirical data are regression lines using a locally estimated scatterplot smoothing function (LOESS) in the ggplot2 R package. Parameters for the simulations are listed in Table 1.1.



<u>Figure 1.5.</u> Comparison of long-term empirical and simulated data averaged over the time series for a) adaptive predator preferences and b) IG prey density. "Long-term" describes the experiment's 40 day duration and 100 simulated time steps of the model. The first 25 days of the empirical and simulated density time series were removed to avoid initial transient fluctuations that are not meaningful to long term equilibria. The different time scales are responsible for some of the quantitative differences, but the qualitative patterns between models and data are generally insensitive to the time scale used. Parameters for the simulations are listed in Table 1.1.



<u>Figure 1.6.</u> Blepharisma morphotype density across treatments (a), the number of heterospecific IG prey consumed by macrostomes and cannibals across treatments (b), and the number of conspecific prey consumed by cannibals across treatments. Individuals with conspecific microstomes in their vacuoles were deemed cannibals, whether or not they also had heterospecific IG prey in their vacuoles. Individuals that just had heterospecific IG prey in their vacuoles were deemed macrostomes.

Supplementary Information

Density dynamics of single species controls are shown in Figure S1.1. *Blepharisma* settled on a stable equilibrium after a slow increase to carrying capacity (Figure S1.1a). No macrostomes were observed given the lack of protist prey. Only one cannibal was observed in all replicate time series. *Euplotes* experienced relatively high-amplitude fluctuations and eventually began to decline to extinction (Figure S1.1b), corroborating *Euplotes'* weak relationship with bacteria and inability to persist on bacteria long-term. Both *Tetrahymena* (Figure S1.1c) and *Colpidium* (Figure S1.1d) quickly increased to carrying capacity and maintained relatively stable dynamics with bacteria.

Variable size changes between morphotypes allowed *Blepharisma* to exploit a wide range of resources and resource sizes (Figure S1.2). *Blepharisma* reached much larger and more variable sizes than *Euplotes*. *Euplotes* maintained a relatively similar size across treatments due to lack of phenotypic plasticity in size. *Blepharisma* had more variability in size particularly on the high end of the range, and especially prominent in BC, due to the large generalist cannibals that consumed both *Colpidium* and microstomes. *Blepharisma's* average size was much smaller in controls where *Blepharisma* were in microstome state feeding solely on bacteria.

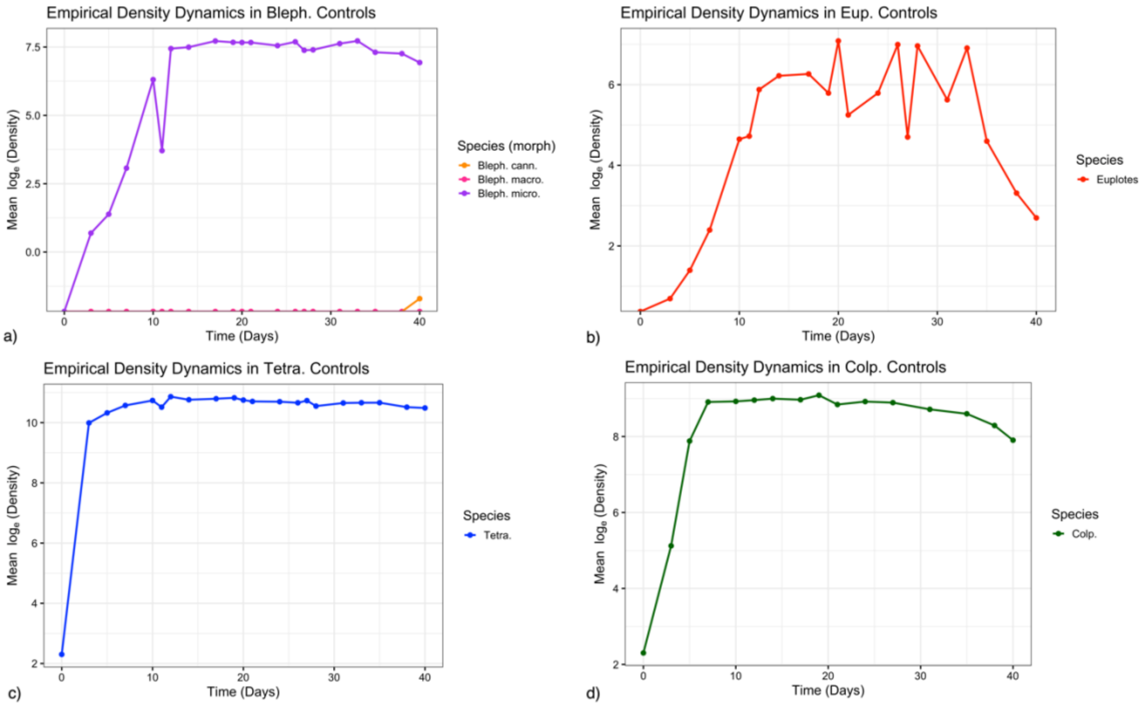


Figure S1.1. Density dynamics in single-species controls of a) *Blepharisma*, b) *Euplotes*, c) *Tetrahymena*, and d) *Colpidium*.

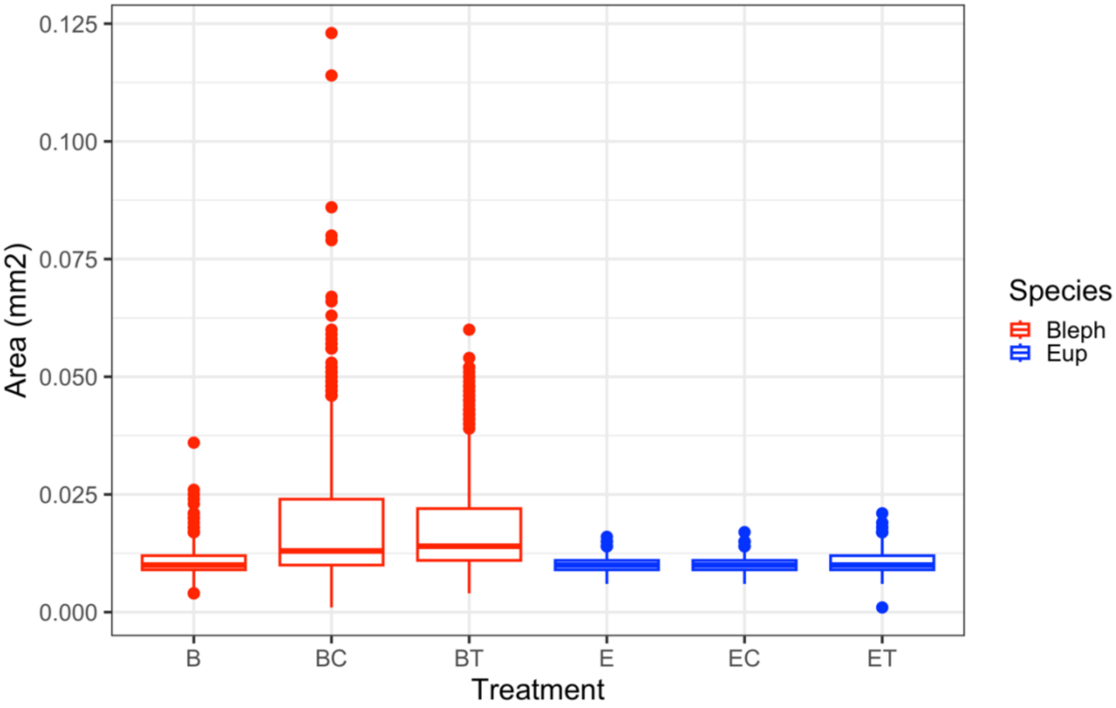


Figure S1.2. Area (mm^2) of each predator, *Blepharisma* or *Euplotes*, as a function of treatment.

Table S1.1. Generalized linear mixed effects model (GLMM) results on empirical *Blepharisma* preference dynamics as a function of treatment. A Beta distribution and logit link function was used given that the response variable is proportion data. Replicate ID was indicated as a random effect.

Empirical preference dynamics					
contrast	estimate	SE	p.value	95% Lower CI	95% Upper CI
con.BC-con.BT	-0.211	0.318	0.9100	-1.040	0.617
con.BC-hetero.BC	-2.520	0.379	*****<0.0001**	-3.509	-1.531
con.BT-hetero.BT	-2.097	0.355	*****<0.0001**	-3.024	-1.171
hetero.BC-hetero.BT	0.211	0.318	0.9100	-0.617	1.040

Table S1.2. Linear mixed effects model (LMM) results for the effects of treatment on logged IG prey density data. Replicate ID was included as a random effect.

Empirical IG Prey Density					
contrast	estimate	SE	p.value	95% Lower CI	95% Upper CI
BC-BT	4.824	0.200	*****<0.0001**	4.31	5.341
BC-EC	-0.808	0.200	*****0.0004**	-1.33	-0.291
BC-ET	6.830	0.209	*****<0.0001**	6.29	7.370
BT-EC	-5.631	0.188	*****<0.0001**	-6.12	-5.146
BT-ET	2.006	0.200	*****<0.0001**	1.49	2.523
EC-ET	7.638	0.200	*****<0.0001**	7.12	8.155

Table S1.3. Linear mixed effects model (LMM) results for the effect of treatment on logged *Blepharisma* morphotype density data. Replicate ID was included as a random effect.

Empirical Morphotype Density						
Group	contrast	estimate	SE	p.value	95% Lower CI	95% Upper CI
Within treatment	B.cann-B.macro	0.0107	0.172	1.000	-0.537	0.558
	B.cann-B.micro	-7.0998	0.172	*****<0.0001**	-7.648	-6.552
	B.macro-B.micro	-7.1106	0.172	*****<0.0001**	-7.658	-6.563
	BC.cann-BC.macro	-2.6217	0.180	*****<0.0001**	-3.196	-2.047
	BC.cann-BC.micro	-4.0046	0.180	*****<0.0001**	-4.579	-3.430
	BC.macro-BC.micro	-1.3829	0.180	*****<0.0001**	-1.957	-0.808
	BT.cann-BT.macro	-2.6271	0.164	*****<0.0001**	-3.151	-2.103
	BT.cann-BT.micro	-5.0677	0.164	*****<0.0001**	-5.592	-4.543
	BT.macro-BT.micro	-2.4406	0.164	*****<0.0001**	-2.965	-1.916
Within morphotype	B.macro-BC.macro	-3.5156	0.177	*****<0.0001**	-4.080	-2.951

	B.macro-BT.macro	-3.9694	0.168	*****<0.0001**	-4.506	-3.432
	BC.macro-BT.macro	-0.4539	0.173	0.1941	-1.006	0.098
	B.micro-BC.micro	2.2121	0.177	*****<0.0001**	1.648	2.776
	B.micro-BT.micro	0.7005	0.168	****0.0025**	0.163	1.238
	BC.micro-BT.micro	-1.5116	0.173	*****<0.0001**	-2.063	-0.960
	B.cann-BC.cann	-0.8832	0.177	*****<0.0001**	-1.447	-0.319
	B.cann-BT.cann	-1.3317	0.168	*****<0.0001**	-1.869	-0.795
	BC.cann-BT.cann	-0.4485	0.173	0.2069	-1.000	0.103

Table S1.4. Linear mixed effects model (LMM) results for the effect of treatment on logged *Blepharisma* vacuole data. Replicate ID was included as a random effect.

Empirical Vacuole Data					
contrast	estimate	SE	p.value	95% Lower CI	95% Upper CI
BC.cann.hetero-BC.macro.hetero	0.0884	0.1059	0.9886	-0.2692	0.4461
BT.cann.hetero-BT.macro.hetero	-1.4337	0.0969	*****<0.0001**	-1.7622	-1.1052
BC.cann.hetero-BT.cann.hetero	1.5166	0.1059	*****<0.0001**	1.1590	1.8742
BC.macro.hetero-BT.macro.hetero	-0.0055	0.0969	1.000	-0.3340	0.3230
BC.cann.consp-BT.cann.consp	-0.4600	0.1059	****0.0064**	-0.8177	-0.1024

Chapter 2

Preferential Cannibalism as a Key Stabilizing Mechanism of Intraguild Predation Systems with Trophic Polymorphic Predators

Abstract

Theory predicts intraguild predation (IGP) to be unstable despite its ubiquity in nature, prompting exploration of stabilizing mechanisms of IGP. One of the many ways IGP manifests is through inducible trophic polymorphisms in the intraguild (IG) predator, where a resource-eating predator morph competes with the intraguild (IG) prey for the shared resource while a top predator morph consumes the IG prey. Cannibalism is common in this type of system due to the top predator morph's specialization on the trophic level below it, which includes the resource-eating predator morph. Here, we explore the consequences of inducible trophic polymorphisms in cannibal predators for IGP stability using an IGP model with and without cannibalism. We employ linear stability analysis and identify regions of coexistence based on the top predator morph's preference for conspecifics vs. heterospecifics and the IG prey's competitive ability relative to the resource-eating morph. Our findings reveal preferential cannibalism (i.e. the preferential consumption of conspecifics) stabilizes the system when the IG prey and resource-eating morph have similar competitive abilities for the shared resource. Though original IGP theory finds the IG prey must be a superior resource competitor as a general criterion for coexistence, this is not typically the case when the predator has an inducible trophic polymorphism and the resource-eating morph is specialized in resource acquisition. Preferential cannibalism may therefore be a key stabilizing mechanism in

IGP systems with a cannibalistic, trophic polymorphic IG predators, providing further insight into what general mechanisms stabilize the pervasive IGP interaction.

Introduction

Inducible trophic polymorphisms (ITPs), a form of phenotypic plasticity in which consumers can alter morphology, physiology, or behavior to change the trophic level on which they feed (Banerji and Morin 2009), have profound implications on food web dynamics. ITPs occur in a diverse array of taxa, including bacteria (Berleman and Kirby 2007), rotifers (Gilbert 1973), protists (Williams 1961; Giese 1973), insects (Green 1989), gastropods (Padilla 2001), amphibians (Collins and Cheek 1983; Pfennig 1992), fish (Meyer 1990; Wainwright et al. 1991), and birds (Hulscher 1984; Matthysen 1989; Afik and Karasov 1995). ITPs are a flexible response to changing environmental conditions, enhancing an individual’s fitness in the present environment with regards to resource type and availability. Morphological traits related to feeding in particular are more flexible than once thought (Kishida et al. 2010). Consumption of a prey type can trigger a morphological shift and catalyze a positive feedback between consumption and morphological change (Padilla 2001). In some cases, morphology can even be flexibly reversed within an individual’s lifetime if conditions change (Eklov and Olsson 2005; Kishida and Nishimura 2006; Hoverman and Relyea 2007; Orizaola et al. 2012).

ITPs notably promote cannibalism by rearranging or expanding feeding apparatuses or increasing body size. This mitigates gape size limitation and facilitates consumption of larger prey, including conspecifics (Fox 1975; Polis 1981). The act of consuming larger prey itself can induce rapid growth and increased body size relative to conspecifics, further promoting cannibalism. Because of this, many taxa with ITPs also exhibit cannibal morphs, including fish (Persson et al. 2003; Ribeiro and Qin 2013; Hardie and Hutchings 2015; Amundsen 2016), reptiles (reviewed in Polis and Myers 1985), amphibians (Pfennig 1999; Takatsu and Kishida 2015), insects (de Block and Stoks 2004; Wissinger et al. 2004; Pervez et al. 2021), rotifers (Gilbert 1973), and protists (Kopp and Tollrian 2003; Banerji and Morin 2009). Though specialized morphology is required for some species to engage in cannibalism, for others it is simply behavioral, even among closely related species (Jefferson et al. 2014).

Cannibalism is common in systems with intraguild predation (IGP) (Polis et al. 1989), where the intraguild (IG) predator competes with the intraguild (IG) prey for a shared resource (Holt and Polis 1997). Despite its ubiquity in nature (Arim and Marquet 2004), original IGP theory predicts considerable regions of instability. A general criterion for coexistence in classic IGP theory is that the IG prey must be a superior competitor for the shared resource (Holt and Polis 1997). At low resource levels, the IG prey outcompetes the IG predator, and at high resource levels, the IG predator reaches densities high enough to overexploit the IG prey. Regions of stable coexistence are therefore limited to intermediate resource levels, in which the strengths of predation and competition are balanced. IGP studies building off the original theory have generally assumed IG prey superiority (Krivan 2000; Faria and Costa 2009; Pal et al. 2014). However, this is unlikely in systems where IG predators exhibit ITPs. A smaller, resource-eating IG predator morph may be as competitive for the shared resource as the IG prey due to morphological resource specialization (Smith and Skúlason 1996) and size-dependent scaling of foraging and metabolic demands (Claessen et al. 2000). Because trophic polymorphic predators challenge the criterion of IG prey competitive superiority, other mechanisms must be at play to enable coexistence.

Cannibalism in the IG predator has been shown to stabilize IGP systems by regulating the predator population when the predator is efficient at exploiting both the IG prey and the shared resource (Rudolf 2007; Toscano et al. 2017; Bassar et al. 2023). However, in nature, the effect of cannibalism depends on the foraging behavior of the cannibal. Cannibalism can divert predation pressure away from IG prey and regulate the predator population, promoting coexistence, or it can strengthen predation pressure on the IG prey due to the increased energetic demands of large cannibal morphs. For instance, Takatsu and Kishida (2015) show that cannibalistic salamander morphs intensify negative impacts on heterospecific prey (tadpole larvae) as a result of the accelerated growth of cannibals. Conversely, others have shown that consumption of heterospecific prey can induce cannibalism (Hoffman and Pfennig 1999; Michimae and Wakahara 2001), relieving the IG prey of consumptive pressure. Stabilizing effects of cannibalism are thus heavily dependent upon the cannibalistic predator’s preference for conspecifics vs. heterospecific IG prey. Studies often assume, however, that the predator has equal or indifferent preference. Evidence of preference in IGP systems is mixed, even among closely related species and sometimes among different populations of the same species. Some studies find preference for conspecifics (Lannoo and Bachmann 1984; Leonardsson 1991; Whiteman et al. 2003; Burgio et al. 2005; Rudolf 2008; Byström et al. 2013; Pervez et al. 2021), others find preference for heterospecifics (Loeb et al. 1994; Gerber and Echternacht 2000; Schausberger and Croft 2000; Montserrat et al. 2006), and still others find a lack of preference either way (Schausberger and Croft 2000; Yasuda et al. 2001; Rudolf 2008). Because predator preference directly alters the strengths of predation and competition experienced by the IG prey, preference is a key determinant of IGP coexistence. The consequences of predator preference, and how it interacts with other determining factors of IGP coexistence such as competitive ability, are nonetheless still unclear.

The present work is motivated by two factors. First, ITPs have uniquely strong effects on the balance of predation and competition in IGP systems by 1) promoting cannibalism, and 2) challenging the IG prey competitive superiority criterion. Second, not only is there evidence that IG prey are not always competitively superior to IG predators (Diehl 1995; Navarrete et al. 2000; Vance-Chalcraft et al. 2007; Crumrine 2010), multiple literature reviews find a high propensity for preferential cannibalism, i.e. preference for conspecifics (in piscivorous fish, Byström et al. 2013; across a wide range of taxa, Toscano et al. 2017). These two aspects of the IGP system–competitive superiority and preferential cannibalism–may therefore be inextricably linked in driving coexistence, particularly in IGP systems with trophic polymorphic predators. However, efforts to incorporate ITPs into IGP models have been limited (see Orlando et al. 2011 as the only exception to our knowledge). This is surprising given their disproportionately large potential for altering system stability through the nature of the two morphs and their consequences on coexistence.

In the present paper, we ask, how does the presence of cannibalism and preferential feeding in a trophic polymorphic IG predator interact with competitive ability of the IG prey to influence the long-term stability of an IGP system? We model an IGP system with a cannibalistic, trophic polymorphic IG predator. We include a preference term to explore the effects of the top predator morph's preference for conspecifics (resource-eating predator morph) vs. heterospecifics (IG prey) and alter the assumption of IG prey superiority. We find that preferential cannibalism (i.e. preference for conspecifics) expands the region of stable coexistence when the IG predator and IG prey are equal competitors for the resource. This prediction, which can be tested in natural systems, is compelling given that both cannibalism in the top predator morph and similar competitive ability between the resource-eating predator morph and IG prey are likely in IGP systems with trophic polymorphic IG predators. Since this is one of the many ways in which the intraguild predation interaction manifests in nature, preferential cannibalism may be a key stabilizing mechanism in systems with trophic polymorphic IG predators.

Methods

To examine the effect of preferential cannibalism in a trophic polymorphic predator on IGP system stability, we compared two models of varying complexity (Figure 2.1) under two scenarios pertaining to IG prey competitive ability. The first model (referred to herein as the "base" model) is an extension of the original Lotka-Volterra IGP model first proposed by Holt and Polis (1997) with the separation of the IG predator into two states: a resource-eating morph that competes with the IG prey for the shared resource, and a top predator morph that consumes the IG prey. Biomass moves from one state to the other as a function of resource density, which is intentionally general to encompass changes in frequency of morphs across generations or individuals switching between morphs in a lifetime. In the second model (referred to herein as the "full" model), we build upon the first model to include cannibalism in the IG predator, where the top predator morph consumes both the IG prey and the resource-eating predator morph. We further include a preference parameter, s, that controls the top predator morph's preference for conspecifics (resource-eating predator morph) or heterospecifics (IG prey). We explore preference over a range of s values, specifically three values of s which represent preference for conspecifics (s=0.7), preference for heterospecifics (s=0.3), and no preference (s=0.5).

Our base IGP model consists of a basal resource *R*, the IG prey *N*, and an IG predator, with two distinct states representative of the discrete morphotypes due to the ITP: morphotype P, which eats the resource (*R*), and morphotype Z, which eats the IG prey (*N*). The predator switches between the two states at a per capita rate dependent on resource density. This base model consists of four ordinary differential equations,

$$\frac{dR}{dt} = gR(1 - \frac{R}{K}) - c_{NR}NR - c_{PR}PR$$

$$\frac{dN}{dt} = e_{NR}c_{NR}NR - c_{ZN}ZN - d_N N$$

$$\frac{dP}{dt} = e_{PR}c_{PR}PR - u_{NP}NP + u_{RZ}RZ - d_P P$$

$$\frac{dZ}{dt} = e_{ZN}c_{ZN}ZN + u_{NP}NP - u_{RZ}RZ - d_Z Z \,. \qquad \text{(eq. 1)}$$

Model parameters are defined in Table 2.1. We assume the resource is self-regulated by logistic growth, and consumers forage with Type I linear functional responses and suffer constant, density-independent mortality. We also explored versions of these models where the consumers have a Type II saturating functional response, the results of which are qualitatively similar and presented in SI 3. We assume that individuals in the P state solely consume the resource and that individuals in the Z state solely consume the IG prey. We further assume density-dependent switching such that foraging effort switches from one state to the other as a function of the biomass density in their own state and availability of prey in the new state. This is to say that biomass of one morph is directed to that of the other morph when the former is crowded and when the resource of the latter is abundant. Without the discrete morphological states and switching between them, this base model collapses to the original IGP model.

Our full model includes cannibalism in the top IG predator morph and a preference parameter, s, to explore the effect of top predator preference for conspecifics (resource-eating predator morph, P) vs. heterospecifics (IG prey, N). Now, morphotype Z eats both the IG prey (N) and conspecifics (P). System dynamics are given by

$$\frac{dR}{dt} = gR(1 - \frac{R}{K}) - c_{NR}NR - c_{PR}PR$$

$$\frac{dN}{dt} = e_{NR}c_{NR}NR - c_{ZN}(1-s)ZN - d_N N$$

$$\frac{dP}{dt} = e_{PR}c_{PR}PR - c_{ZP}sZP - (u_{NP}N + u_{PP}P)P + u_{RZ}RZ - d_P P$$

$$\frac{dZ}{dt} = e_{ZN}c_{ZN}(1-s)ZN + e_{ZP}c_{ZP}sZP + (u_{NP}N + u_{PP}P)P - u_{RZ}RZ - d_Z Z\ .$$

(eq. 2)

Here, we assume that cannibalism occurs unidirectionally from predator morph Z onto predator morph P. This makes sense in the context of ITPs, in which one morph is either larger or has morphological, physiological or behavioral specializations that equips it to consume larger prey (i.e. the IG prey and smaller conspecifics) while the other morph is typically smaller and specialized to feed on the basal resource. Such trophic heterogeneity promotes the occurrence of cannibalism from the larger morph onto the smaller morph and not vice versa.

The switching function in the full model is slightly more complex compared to the base model due to the cannibalism link. Switching into the Z state (and out of the P state) is now a function of both N and P, because Z consumes both the IG prey and the resource-eating morph. Thus, there are two switching parameters dictating switching rate into the Z state: one dependent on IG prey density (u_{NP}), and the other dependent on P density (u_{PP}). As with the base model, biomass more readily switches from one state to the other when the former state is high in density and the prey species of the latter state is abundant. Following Orlando et al. (2011), we define fitness on the morphological level as the per capita growth rate of a morph's population excluding the addition or subtraction of individuals from the other morph. The purpose of defining fitness on the morphological level is that the dynamic fitness differences between the two morphs is a key aspect of our model and an important driver of system dynamics.

Model Parameterization

Model parameterization follows that used in the original IGP framework (Holt and Polis 1997) for comparability to earlier work (Table 2.1). By assuming equal attack rates and conversion efficiencies of the top IG predator morph on its prey, we explore preference by altering the preference parameter, s. We therefore interpret s=0.5 as being an equal preference for IG prey and resource-eating predator morph. We use the phrase "preferential cannibalism" to denote that s is greater than 0.5, and therefore the top predator morph Z preferentially consumes conspecifics, P. Similarly, "heterospecific preference" denotes situations when s is less than 0.5, and the top predator morph Z preferentially consumes heterospecific IG prey, N. We focus on three scenarios using the following parameterization: heterospecific preference ($s=0.3$), preferential cannibalism ($s=0.7$) and no preference ($s=0.5$).

We further explore two scenarios pertaining to the superiority of the IG prey, N, over the resource-eating predator morph, P, for the shared resource. Original IGP theory found a general criterion for coexistence to be that the IG prey is a superior resource competitor (Holt and Polis 1997), and subsequent IGP models have generally assumed IG prey superiority (Krivan 2000; Faria and Costa 2009; Pal et al. 2014). However, when the predator has an ITP that results in two separate states, each specialized on their given resource, it is safe to assume that the resource-eating morph is equipped with a similarly strong competitive ability for the shared resource as the IG prey. To explore the effects of IG prey competitive superiority, or lack thereof, we present two scenarios: one in which N and P are equal competitors, and one in which N is superior to P. We do not consider a situation in which the resource-eating morph is superior to the IG prey, as this would largely lead to IG prey extinction due to the predator's inherent advantage over the prey (consuming its competitor). Under the case of "equal competitors," the resource-eating predator morph and IG prey are equal competitors for the shared resource: $c_{NR} =$

c_{PR}=0.5. Under the case of "prey superiority," the IG prey is a superior resource competitor, such that c_{NR}=1 and c_{PR} =0.5.

We keep the predator morph switching parameters equal to 0.5 and assume that switching happens on a time scale similar to other demographic processes. Though studies quantifying switching rates between morphs are limited, this would reflect morphological switching in organisms such as protists (Banerji and Morin 2009; Orlando et al. 2011). However, lags in switching rates can destabilize population dynamics (Padilla and Adolph 1996; Abrams 2010), and switching that is too rapid can be maladaptive (Kath et al. 2022). These cases typically involve behavioral lags, such as lags in decision making on the part of the predator. Our implementation of switching, however, can be thought of as the sensitivity of biomass transfer rates from one state to the other in response to density changes. Nevertheless, we explore the effects of switching parameters in SI 2.

Lastly, we vary the resource carrying capacity between K=1 and K=50 to examine a wide range of productivity levels for the purpose of relating our results to previous work. Productivity is of interest for two reasons. First, high productivity has been shown to destabilize food webs in general (e.g. paradox of enrichment, Rosenzweig 1971). Second, productivity alters the relative strengths of competition and predation in IGP systems, heavily affecting coexistence outcomes (Holt and Polis 1997; Diehl and Feissel 2000). Original theory found the IG predator overexploits the IG prey at high resource carrying capacities, but work since then has found coexistence to be possible at high productivity levels with the incorporation of various stabilizing mechanisms (e.g.

adaptive foraging, Krivan 2000; alternative resources, Daugherty et al. 2007; cannibalism, Rudolf 2007; prey preference, Faria and Costa 2009). We therefore explore the consequences of preferential cannibalism across a gradient of productivity.

Analysis

Following numerical analyses performed in existing cannibalism studies (Rudolf 2007; Orlando et al. 2011; Bassar et al. 2023), we performed numerical simulations and explored stability in our models using linear stability analysis (Gurney and Nisbet 1998; Murdoch et al. 2003). In short, we linearized eqs. 1 and 2 around their interior equilibrium, and then examined the stability of these systems to small perturbations. We first solved for the equilibrium in which all species have positive, non-zero abundances using the “Solve” function in Mathematica (Wolfram Research, Inc., Mathematica, Version 12.0, Champaign, IL, 2019). We then evaluated the Jacobian matrix at this solution and numerically computed the eigenvalues using the “Eigenvalues” function, selecting the eigenvalue(s) in which the real part is negative and therefore stable. We further performed numerical simulations to show the effects of preference and competitive superiority on dynamics and equilibrium densities in SI 1. Dynamics were simulated in the R programming language (R Core Team 2023) using the package deSolve.

Results

Within the region of four-species coexistence, the preference parameter, s, is negatively related to the IG prey’s superiority over the resource-eating morph, P, for the shared resource (Figure 2.2). When the IG prey, N, is a similar competitor as P for the resource (c_{NR} is close to 0.5 and c_{PR}=0.5), the region of coexistence exists in the parameter space in which preference is skewed towards conspecifics (s>0.5, between ~0.6 and ~0.8). As *N* becomes increasingly superior to *P* for the resource (c_{NR} approaches 1 as c_{PR} remains 0.5), coexistence is maintained when preference switches from conspecific preference (s>0.5), to no preference (s=0.5), and eventually to heterospecific preference (s<0.5). Outside of the region of coexistence, if preference for conspecifics is too high, the IG predator drives itself extinct through heavy preferential cannibalism, resulting in a stable equilibrium of just the IG prey and the resource (*NR*). If the preference parameter is too low (preference heavily skewed towards heterospecifics), the IG predator drives the IG prey extinct through strong intraguild predation, resulting in a stable equilibrium of the IG predator morphs with the resource (*ZPR*). See Section 2 of the Supplementary Information for numerical simulations of the dynamics in each of these three regions (Figure S2.1).

When the IG prey, *N*, is a superior competitor for the shared resource, *R*, the model without cannibalism is stable across a wide range of top predator consumption rates on the IG prey and resource carrying capacities (Figure 2.3a). In the case of IG prey superiority, cannibalism greatly decreases coexistence overall (Figure 2.3b-d). The region of stable *NR* equilibrium increases when cannibalism is added. The IG predator has a disadvantage by cannibalizing the resource-eating morph, *P*, which suffers strong competitive pressure from the superior IG prey. Strong cannibalism and competition lead to a dwindling *P* population, reducing the amount of biomass that can switch into the top predator morph, *Z*, resulting in extinction. Note the large region of stable *ZPR* equilibrium that is introduced under the heterospecific preference scenario (s=0.3, Figure 2.3b). Here, *Z* excludes *N* through a combination of preferential consumption of *N* and benefit of having an alternative resource, *P*. Conversely, when *Z* preferentially consumes conspecifics (s=0.7, Figure 2.3d), *N* confers an advantage from not being consumed as heavily as its competitor. The IG predator largely drives itself extinct through the preferential consumption of conspecifics, *P*, which are competitively inferior to the IG prey, resulting in a large region of *NR* equilibrium. The region of coexistence is maximized when preference is not skewed either way (s=0.5, Figure 2.3c), wherein the IG prey's competitive advantage is balanced out by the top predator morph's equal consumption of *N* and *P*.

When the IG prey and resource-eating morph are equal competitors for the resource, the region of coexistence is nonexistent without cannibalism (Figure 2.3e). Cannibalism is not present here to regulate the predator population and prevent overexploitation of the IG prey, which no longer benefits from being the superior resource competitor. Including cannibalism and a preference for heterospecifics (s=0.3, Figure 2.3f) introduces a negligible region of coexistence. Without preference either way (s=0.5, Figure 2.3g), there is a slight increase in the space of coexistence. Coexistence greatly increases when cannibals preferentially consume conspecifics (s=0.7, Figure 2.3h) due to greater regulation of the IG predator population, reducing overexploitation of the IG prey. When the IG prey is not competitively superior, preferential cannibalism simultaneously reduces predatory pressure from *Z* and competitive pressure from *P* on the IG prey, facilitating its persistence over a larger range of IG predation rates.

Increasing the resource carrying capacity, K, does not lead to the extinction of the IG prey in any of the model formulations (Figure 2.3, a-h) due to the stabilizing nature of density-dependent switching. We find that all species' equilibrium densities increase and saturate with increasing values of resource carrying capacity (Figure S2.2), as has been shown before. We further find that the results presented in this paper are not sensitive to switching rates (Figure S2.3). The results do not change drastically when consumers have a Type II functional response (Figure S2.4). Though neither of the present models with Type I functional responses yield limit cycles, we find that these models with Type II functional responses cause limit cycles only under high values of the preference parameter (Figure S2.5), and the cycles increase in amplitude as carrying capacity increases (Figure S2.6).

The main result that conspecific preference maximizes coexistence when the prey and predator are equal competitors is robust to multiple parameter combinations (Figure 2.3, 4, 5). Comparing the top predator morph's consumption rate on the IG prey, c_{ZN}, against the top predator morph's conversion efficiency on the IG prey, e_{ZN}, produces similar results that preferential cannibalism maximizes the region of coexistence when the IG prey and resource-eating morph are similar resource competitors (Figure 2.4). When the IG prey is a superior competitor, coexistence is maximized without cannibalism (Figure 2.4a), and adding cannibalism to the model greatly reduces stability regardless of preference (Figure 2.4b-d). A lack of preference leads to the largest region of coexistence when cannibalism is present in the model (s=0.5, Figure 2.4c). When the IG prey and resource-eating predator morph are equal competitors, preferential cannibalism maximizes coexistence (s=0.7; Figure 2.4h). Here we begin to see regions of bistability appear, in which there exists a stable equilibrium of the IG predator morphs with the resource (*ZPR*) or just the IG prey with the resource (*NR*).

Finally, we look at the top predator's consumption rate on the IG prey, c_{ZN}, against the top predator's cannibalism consumption rate on conspecifics, c_{ZP} (Figure 2.5). Only the three preference scenarios are compared since the base model does not include cannibalism and therefore does not have the c_{ZP} term. Again, we find the same pattern, further supporting the main result that preferential cannibalism stabilizes the IGP system by maximizing the region of coexistence when the prey and predator are equal competitors (Figure 2.5g). Similar to Figure 2.4, bistability occurs in a small region where either the IG prey persists with the resource (*NR*) or the IG predator morphs persist with the resource (*ZPR*).

Discussion

Holt and Polis' (1997) seminal paper on intraguild predation (IGP) predicted unstable dynamics under most conditions. Studies have since found IGP to be ubiquitous in natural food webs (Arim and Marquet 2004), prompting an exploration of stabilizing mechanisms. IGP manifests in many ways, one being through inducible trophic polymorphisms in the IG predator, where the top predator morph consumes the IG prey and the resource-eating morph competes with the IG prey for the shared resource (Banerji and Morin 2009). ITPs promote cannibalism in the predator by causing a divergence in the trophic levels on which each morph feeds along with facilitating size heterogeneity (Kopp and Tollrian 2003). Our study produces predictions of IGP stability in systems with cannibalistic, trophic polymorphic IG predators: preferential cannibalism in the top predator morph relaxes the requirement for IG prey competitive superiority, promoting coexistence when the prey and predator are equal competitors for the resource. This result is robust across a wide range of parameter values (Figs. 3, 4, 5, and S3). Preferential cannibalism may therefore be a strong stabilizing mechanism in natural IGP systems when the IG predator has an inducible trophic polymorphism and is a strong competitor, providing further understanding as to the conditions in which IGP exists stably in nature. To our knowledge, this is the first theoretical study to jointly explore inducible trophic polymorphisms, cannibalism and preference on IGP stability.

The present results are especially compelling given that 1) IG prey are not likely to be competitively superior when the IG predator exhibits an inducible trophic polymorphism due to morphological resource specializations (Smith and Skúlason 1996) and size-dependent scaling of foraging and metabolic demands (Claessen et al. 2000), and 2) preferential cannibalism is widespread (Byström et al. 2013; Toscano et al. 2017). Our work combines these two phenomena to show that the interaction between them promotes IGP stability when the IG predator has an inducible trophic polymorphism. The underlying mechanism is preferential cannibalism as a strong form of intraspecific density dependence in the IG predator population (Polis 1981). By preferentially consuming conspecifics, the top predator morph regulates its own population and promotes the persistence of the IG prey by both diverting predatory pressure away from the IG prey and limiting the population size of its equally strong competitor, the resource-eating morph. This allows the IG prey to coexist with the IG predator without being the superior resource competitor, a general criterion of original IGP theory (Polis and Holt 1992; Holt and Polis 1997). Our results therefore indicate that preferential cannibalism in trophic polymorphic IG predators may be a key reason why we often see in nature that the IG prey is not competitively superior (Diehl 1995; Vance-Chalcraft et al. 2007; Crumrine 2010). Though we did not examine the case of the IG predator as a superior resource competitor, others have shown that coexistence is similarly enhanced when stabilizing mechanisms are at play, such as a high cannibalism consumption rate (Rudolf 2007; Toscano et al. 2017), alternative prey (Daugherty et al. 2007), or prey switching (Wei et al. 2019).

Prey switching is a stabilizing mechanism that enhances coexistence over a broad range of conditions in omnivory models (Abrams and Matsuda 2004; Faria and Costa 2009; Pal et al. 2014; Wang et al. 2018; Wei et al. 2019), preventing IG prey overexploitation at high carrying capacities (Krivan 2000; Krivan and Diehl 2005; Faria and Costa 2010). Though the switching mechanism we consider here is not explicitly behavioral, we see a similar stabilizing effect from the density-dependent switching between morphs. This stabilizing effect is most clearly illustrated in the large regions of coexistence in Figs. 3a, 4a and 5a. This scenario is closest to the original Lotka-Volterra IGP model, which predicts limited coexistence even when the prey is a superior competitor, resulting in IG prey overexploitation at high carrying capacities (Holt and Polis 1997). The only difference in our base model is the inclusion of switching between morphs. Without switching, we recover the original IGP prediction of reduced coexistence as carrying capacity increases. Instead, we see coexistence maintained at high carrying capacities (Figure 2.3a). When the IG prey is not competitively superior, switching alone is not enough to stabilize the system, as has been found in similar IGP models, such as those that employ adaptive foraging (Krivan 2000).

Studies show that switching is stabilizing unless there is a significant lag in switching between states (Padilla and Adolph 1996; Abrams 2010) or switching occurs at a high rate (Kath et al. 2022). Although we do not incorporate explicit time lags in shifts between morphological states, our results are robust to a broad range of switching parameter values (SI 2). Nonetheless, many species, notably protists with inducible trophic polymorphisms, have quick response times. For example, *Tetrahymena vorax* takes about 4.5 hours to switch states, which is about half of their generation time of 8 hours (Orlando et al. 2011).

The present study is intentionally general to encompass the many forms that inducible trophic polymorphisms can take. Our separate IG predator state variables and switching functions represent changes in biomass as a function of prey availability, which can occur within or across generations. In some species, morphotypes are induced during development and individuals are more or less fixed in that morphology throughout their lifetime, such as distinct cannibal fish morphotypes (e.g. perch, Persson et al. 2003; barramundi, Ribeiro and Qin 2013; cod, Hardie and Hutchings 2015; charr, Amundsen 2016). Others can flexibly reverse morphology in their lifetime, typically up until a point in development (e.g. jaw morphology in cichlids, Meyer 1990; broad-headed morphology in salamanders, Michimae and Wakahara 2002; snout and body shape in perch, Olsson and Eklov 2005; body and tail depth in tadpoles, Kishida and Nishimura 2006, Orizaola et al. 2012). Still others, like protists and rotifers, can respond to changing conditions at almost any point in their life cycle, rearranging buccal cavities when larger prey becomes available and dividing to typical morphs when that prey is depleted (Williams 1961; Giese 1973; Kopp and Tollrian 2003; Banerji and Morin 2009). Because we assume biomass is shifting from one predator state to another, our model provides a general framework that can be modified in the future to explore more specific forms of ITPs.

Our study is motivated by a well-known protist system: IG predator *Blepharisma*, IG prey *Tetrahymena*, and shared resource, bacteria (Diehl and Feissel 2000; Price and Morin 2004). *Blepharisma* is an omnivorous protist that has an inducible trophic polymorphism and also engages in cannibalism (Giese 1973; Lennartz and Bovee 1980). The microstome state is small and specialized on bacteria, while the macrostome state is large with gape structures specialized for feeding on smaller protists, such as bacterivorous *Tetrahymena* and conspecifics. When small protists are present, *Blepharisma* individuals that are large enough to capture smaller protists experience a positive feedback of enlargement and rearrangement of the buccal cavity and oral ciliature, facilitating growth into macrostomes. Macrostomes can then either divide into microstomes, if protist prey is depleted, or macrostomes, if protist prey is still available (Woodie, personal observation). This inducible expression of morphology is similar to that seen in an amphibian or fish, where the large cannibal morphs can be induced during development if conditions call for it, but their future offspring can flexibly take on a different morphology if conditions change.

Although this is the first study to examine preferential cannibalism in a trophic polymorphic IG predator, the results can be compared to the only other study to our knowledge of cannibalism and ITPs in IG predators (Orlando et al. 2011). Orlando et al. (2011) modeled cannibalism and different switching strategies between morphs in the protist, *Tetrahymena vorax*. They found constant switching rates between cannibals and typical morphs stabilize population dynamics, whereas variable switching (switching rates that increase fitness) leads to exclusion of the IG prey. This makes sense in light of the model parameterization; the cannibalistic top predator morph has a higher attack rate and conversion efficiency on the IG prey than conspecifics. The predator thus confers too much of an advantage, switching between morphs to maximize their fitness along with consuming IG prey more heavily than conspecifics. There is no mechanism at play to prevent the exclusion of the IG prey (e.g. preferential cannibalism). Our dynamic switching function is similar to their variable switching function in that predators more readily switch out of morphological states when intraspecific competition is high or their given resource is in low abundance, but the mechanism preventing the predator from having too much of a benefit is the preferential consumption of conspecifics when the predator and prey are similar resource competitors (s = 0.7; Figure 2.3h, 4h, 5f). When the prey has a bit more of an advantage through superior resource competition, conspecific preference is no longer necessary, and cannibalism alone–without preference either way–is enough to facilitate coexistence (s = 0.5; Figure 2.3c, 4c, 5b).

To date, cannibalism in IGP systems has primarily been studied in the context of life history IGP, in which adult predators prey on juvenile conspecifics and heterospecific

IG prey (Rudolf 2007; Toscano et al. 2017; Hin and de Roos 2019; Bassar et al. 2023). These studies find cannibalism in LHIGP systems can promote coexistence, even when the IG prey is not competitively superior, suggesting that cannibalism plays a similar stabilizing role regardless of the type of stage structure (LHIGP or ITPs). For instance, Toscano et al. (2017) found in a study of cannibalism in LHIGP systems that only if juvenile IG predators are superior competitors for the resource can cannibalism promote coexistence. The mechanism is the same as in the present study: when the IG prey is competitively superior, strong cannibalism reduces the juvenile (or resource-eating predator morph) population, leading to competitive exclusion. This is why we see large regions of *NR* equilibrium when the IG prey is superior and the top predator morph preferentially consumes conspecifics (Figs. 3d, 4d, 5c). Furthermore, Hin and de Roos (2019) find that a high cannibalistic preference, in combination with juvenile predator resource specialization, leads to coexistence in LHIGP systems. It is compelling that the conditions leading to the results in the present study of a particular type of stage structure (ITPs) align well with studies that employ a different type of stage structure (LHIGP).

Since the consumption of conspecifics necessarily reduces overall population size, cannibalism generally increases the fitness of individuals but not populations (Polis 1981). Because of this, cannibalism studies have consistently considered fitness at levels lower than the whole population, typically the individual level (see reviews and citations within: Fox 1975; Polis 1981; Rosenheim and Schreiber 2022) or the morphological level (the present study, and in Orlando et al. 2011). This is because cannibalism, by nature of removing individuals from the population, naturally has a negative effect on population growth rate. The negative population-level effect is a crucial population regulation mechanism that has been shown to stabilize many models with cannibalism (see reviews and citations within: Claessen et al. 2004, Rosenheim and Schreiber 2022), especially those involving IGP interactions (Rudolf 2007; Toscano et al. 2017; Bassar et al. 2022). However, previous IGP models define fitness on the population level (Krivan 2000). Under this definition of fitness, cannibalism is often considered maladaptive especially when parameterization allows for the population regulation effect. Considering fitness at the population level is interesting for future cannibalism studies. The potential for cannibalism to be stabilizing while simultaneously increasing total population growth rate will likely depend on the type of cannibalism, mentioned briefly in a recent review (Rosenheim and Schreiber 2022). For instance, cannibalism in the form of cannibal morphotypes almost always decreases overall population growth rates by nature of cannibal morphs increasing in density quickly and inflicting strong conspecific mortality (Persson et al. 2003; Amundsen 2016). Conversely, filial cannibalism can induce positive population growth rate as it is a unique form of parental care (Rosenheim and Schreiber 2022). Future studies should explore the potential for population regulation in IG predators with cannibal morphotypes using a population-level definition of fitness, i.e. can cannibalism have a regulatory effect while also increasing the growth rate of the population.

Conclusion

Despite decades of focused attention, there are still major gaps in our understanding of what mechanisms stabilize intraguild predation interactions, which are widespread in nature and diverse in the ways they manifest. Inducible trophic polymorphisms are one way that IGP manifests in nature, yet efforts to incorporate them into the theoretical framework of IGP are extremely limited (but see Orlando et al. 2011). The present study finds that preferential cannibalism is the mechanism responsible for enhancing coexistence between cannibalistic trophic polymorphic IG predators and IG prey that lack competitive superiority. These results are compelling given that both cannibalism and similar competitive ability between the resource-eating IG predator morph and IG prey are particularly likely in IGP systems with trophic polymorphic IG predators. This is because ITPs challenge the assumption of IG prey superiority and promote cannibalism. The results of the present study may help explain why evidence suggests two common occurrences in IGP systems are preferential cannibalism (reviewed by Byström et al. 2013 and Toscano et al. 2017) and lack of IG prey competitive superiority (Diehl 1995; Navarrete et al. 2000; Vance-Chalcraft et al. 2007; Crumrine 2010). Preferential cannibalism may therefore be a key stabilizing mechanism in systems with trophic polymorphic IG predators that compete strongly with their IG prey. The present work contributes to broader efforts to understand what mechanisms drive coexistence of the ubiquitous IGP interaction in order to bridge the gap between theory and nature.

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Tables & Figures

Table 2.1. A description of the parameters and their values used in this study.

Parameter	Description (units)	Default Value
g	Resource, *R*, intrinsic growth rate (time^{-1})	5
K	Resource, *R*, carrying capacity (biomass)	50
c_{NR}	Consumption rate of IG prey, *N*, on resource, *R* (time^{-1})	Varied: 0.5 when “equal competitors” or 1 when “prey superior”
c_{PR}	Consumption rate of resource-eating predator morph, *P*, on resource, *R* (time^{-1})	0.5
c_{ZN}	Consumption rate of top predator morph, *Z*, on IG prey, *N* (time^{-1})	0.5
c_{ZP}	Consumption rate of top predator morph, *Z*, on resource-eating predator morph, *P* (time^{-1})	0.5
e_{NR}	Conversion efficiency of IG prey, *N*, on resource, *R* (biomass of *N*/unit *R* consumed)	0.5
e_{PR}	Conversion efficiency of resource-eating predator morph, *P*, on resource, *R* (biomass of *P*/unit *R* consumed)	0.5
e_{ZN}	Conversion efficiency of top predator morph, *Z*, on IG prey, *N* (biomass of *Z*/unit *N* consumed)	0.5
e_{ZP}	Conversion efficiency of top predator morph, *Z*, on resource-eating predator morph, *P* (biomass of *Z*/unit *P* consumed)	0.5
d_N	IG prey, *N*, mortality rate (time^{-1})	0.5
d_P	Resource-eating predator morph, *P*, mortality rate (time^{-1})	0.5

d_Z	Top predator morph, *Z*, mortality rate (time^{-1})	0.5
u_{RZ}	Switching rate from top predator morph, *Z*, to resource-eating predator morph, *P* ($\text{density}^{-1}\text{time}^{-1}$)	0.5
u_{NP}	Switching rate from resource-eating predator morph, *P*, to top predator morph, *Z*, dependent on IG prey, *N*, population ($\text{density}^{-1}\text{time}^{-1}$)	0.5
u_{PP}	Switching rate from resource-eating predator morph, *P*, to top predator morph, *Z*, dependent on conspecific resource-eating predator morph, *P*, population ($\text{density}^{-1}\text{time}^{-1}$)	0.5
s	Preference parameter (unitless)	Varied: 0.3 for heterospecific preference, 0.5 for no preference, 0.7 for preferential cannibalism

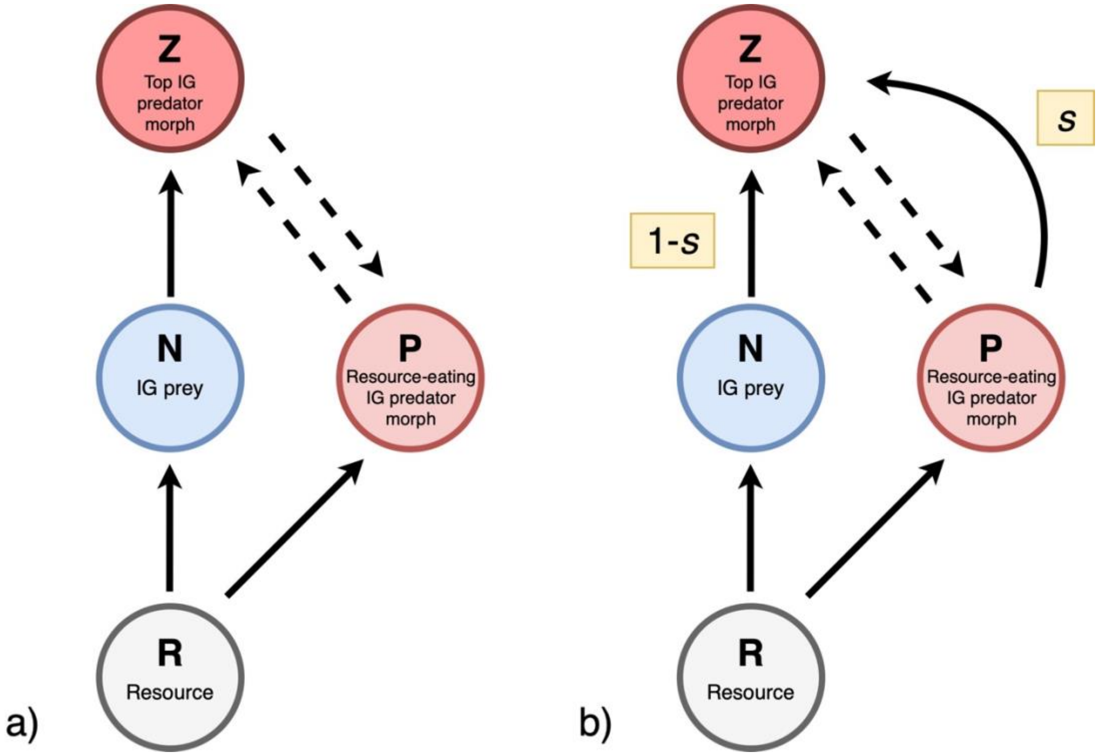

Figure 2.1. Visual depictions of the two intraguild predation models used in this study. (a) The base model (eq. 1) includes a trophic polymorphic IG predator that switches between two states as a function of prey density: a top predator morph, *Z*, that feeds on the IG prey, *N*, and a resource-eating morph, *P*, that feeds on the shared resource, *R*. (b) The full model (eq. 2), which builds on the base model to include cannibalism and a preference parameter. Preference for conspecifics occurs when $s>0.5$; preference for heterospecifics occurs when $s<0.5$; and no preference occurs when $s=0.5$. Solid arrows indicate feeding relationships, and broken arrows indicate switching between the two IG predator morphs.

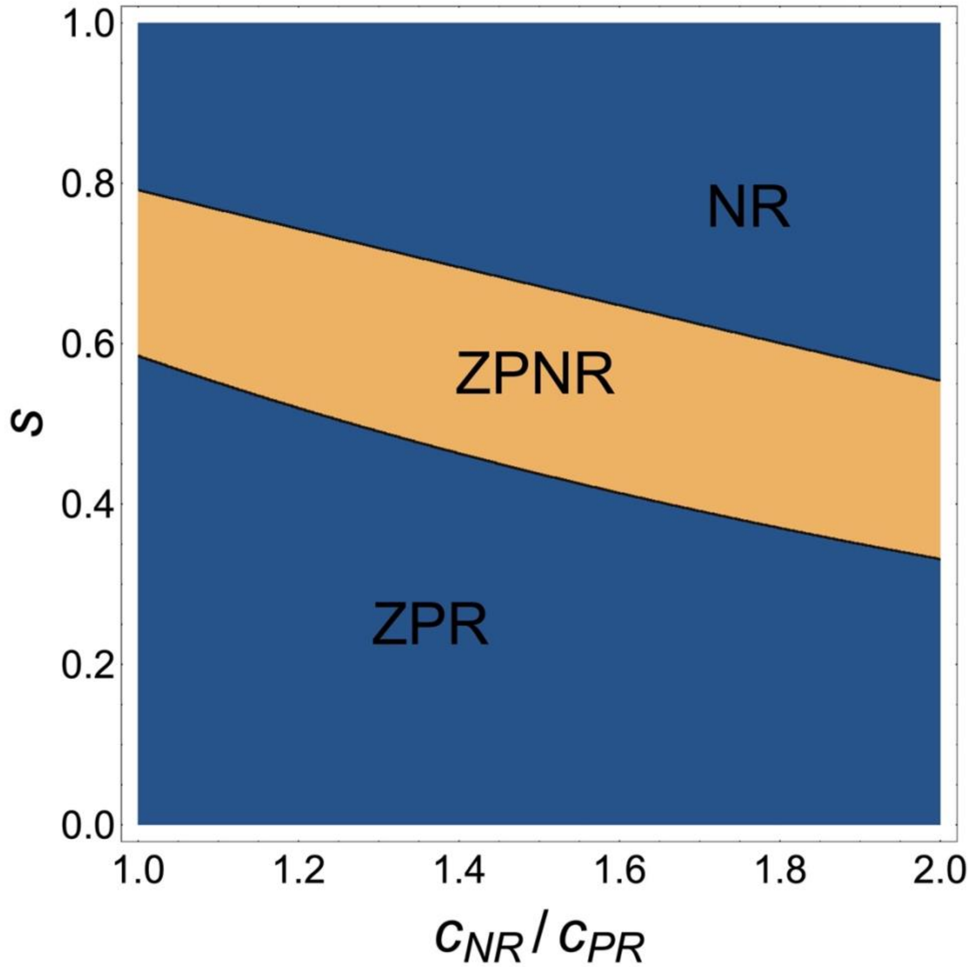

Figure 2.2. Regions of stable coexistence across the ratio of resource consumption rate by the IG prey to that of the resource-eating predator morph, c_{NR}/c_{PR}, and preference parameter, s. Orange regions denote stable coexistence between all species and blue regions denote stable equilibria between certain species. R is the resource, N is the IG prey, P is the resource-eating IG predator morph, and Z is the top IG predator morph. When $c_{NR}/c_{PR}=1$, the IG prey and resource-eating morph are equal competitors for the shared resource. As c_{NR}/c_{PR} increases, the IG prey becomes increasingly more competitively superior to the resource-eating morph.

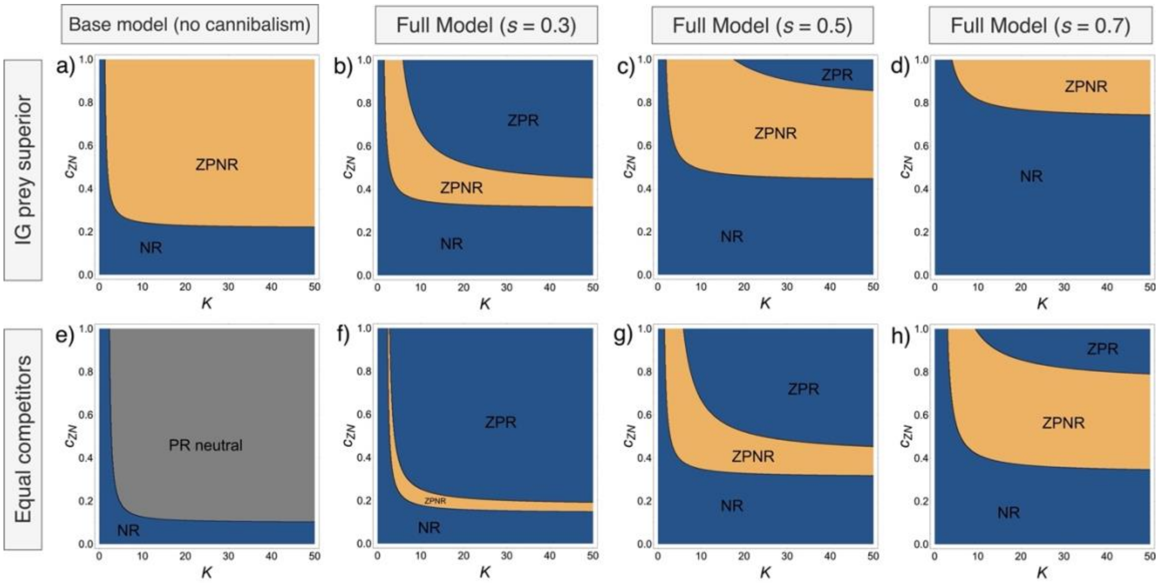

Figure 2.3. Regions of stability across carrying capacity, *K*, and the top predator morph's consumption rate on the IG prey, c_{ZN}, when the prey is superior (a-d) and when the prey and predator are equal resource competitors (e-h). Examined across four scenarios: base model without cannibalism (eq. 1, a, e), and full model (eq. 2) with heterospecific preference (b, f), no preference (c, g), conspecific preference (d, h). Variables are defined in Figure 2.2. Orange regions denote stable coexistence between all species, blue regions denote stable equilibria between certain species, and gray regions denote neutral equilibria.

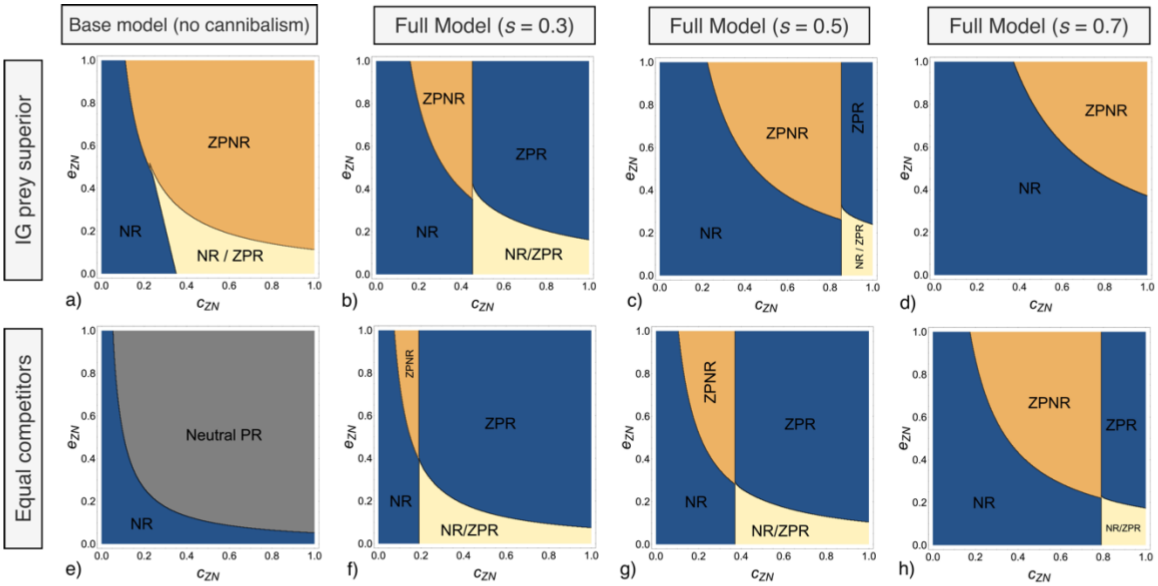

Figure 2.4. Regions of stability across the top predator morph's consumption rate on the IG prey, c_{ZN}, and the top predator morph's conversion efficiency on the IG prey, e_{ZN}, when the prey is superior (a-d) and when the prey and predator are equal resource competitors (e-h). Examined across four scenarios: base model without cannibalism (eq. 1, a, e), and full model (eq. 2) with heterospecific preference (b, f), no preference (c, g), conspecific preference (d, h). Variables are defined in Figure 2.2. Orange regions denote stable coexistence between all species, blue regions denote stable equilibria between certain species, gray regions denote neutral equilibria, and yellow regions denote bistability.

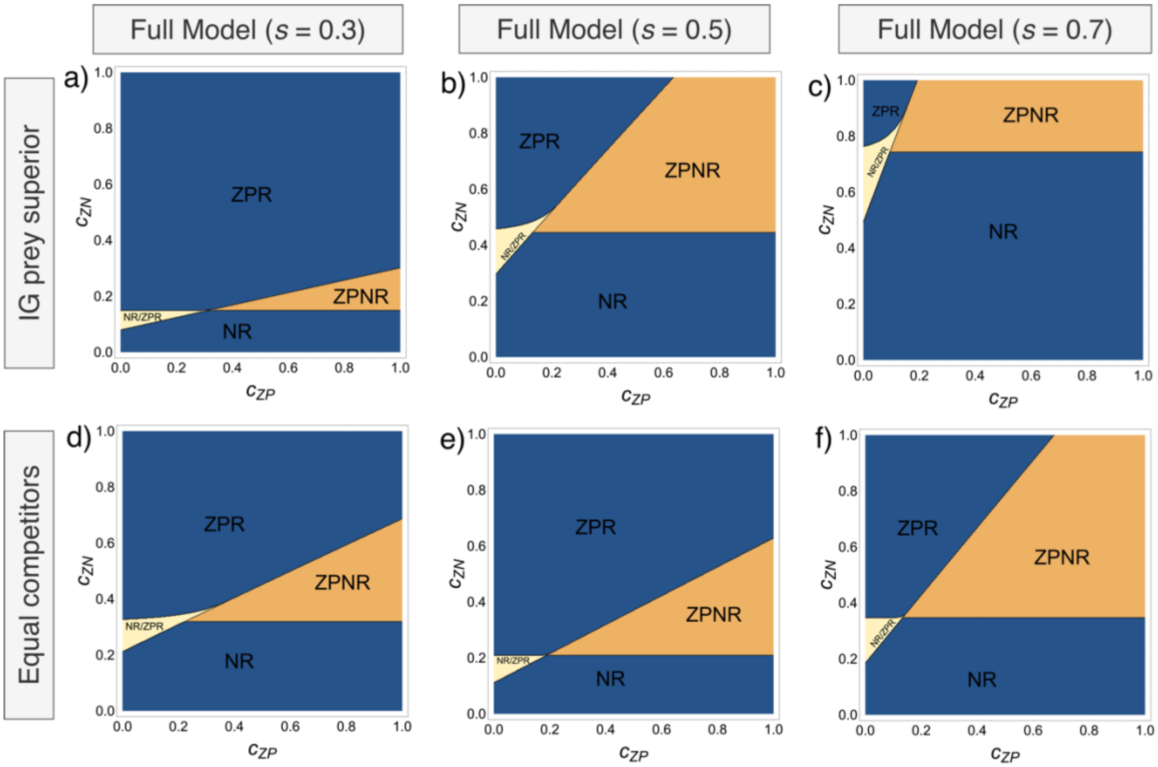

Figure 2.5. Regions of stability across the top predator morph's consumption rate on the IG prey, c_{ZN}, and the top predator morph's consumption rate on conspecifics, c_{ZP}, when the prey is superior (a-c) and when the prey and predator are equal resource competitors (d-f). Examined across three scenarios: the full model (eq. 2) with heterospecific preference (a, d), no preference (b, e), conspecific preference (c, f). Variables are defined in Figure 2.2. Orange regions denote stable coexistence between all species, blue regions denote stable equilibria between certain species, gray regions denote neutral equilibria, and yellow regions denote bistability.

Supplementary Information

Figure S2.1 shows numerically simulated dynamics in the three regions of interest from Figure 2.2 of the main text corresponding to different equilibrium states. We kept the prey and predator equal competitors here for consistency, but dynamics are qualitatively similar under the IG prey superiority scenario. Dynamics equilibrate quickly, and those that reach a positive equilibrium have densities far from zero. Figure S2.2 shows equilibrium densities of all species across a carrying capacity gradient. At very low carrying capacity values, the predator morphs cannot yet establish. As values increase, all species' equilibrium densities increase and eventually saturate. This pattern is analogous to what others have shown, particularly with regards to cannibalism (Rudolf 2007). Furthermore, this pattern is the same regardless of preference or prey superiority. Cannibalism stabilizes the system at high resource carrying capacities, such that the IG prey does not go extinct from overexploitation by the IG predator, as others have shown (Rudolf 2007; Toscano et al. 2017; Hin and de Roos 2019). Original theory predicts that resource equilibrium density increases with increasing carrying capacity, because the IG predator drives the IG prey extinct and persists with the resource alone (Holt and Polis 1997). Because the IG prey persists at high resource carrying capacities, the resource density saturates, instead of increases, as resource carrying capacity increases.

We explored the sensitivity of our results to the three switching parameters present in the full model. Our switching parameters act as sensitivity parameters, which scale how fast biomass moves from one state to another as a function of density. Figure S2.3 illustrates that regions of coexistence do not change across ranges of switching rates and preference parameters. We varied u_{NP} and u_{PP} together for simplicity given that they both govern the switching rate into the Z state, as a function of heterospecific N density and conspecific P density respectively. The same pattern arises within each scenario (prey superiority or equal competitors), across ranges of u_{RZ}, u_{NP}, and u_{PP}, indicating the results are not sensitive to switching rates. Regardless of switching rates, when the prey is superior (Figure S2.3a-c), the top predator morph's preference must be within the range of about 0.3-0.5 for coexistence (no preference or slightly towards heterospecifics). Similarly, when the prey and predator are equal competitors (Figure S2.3d-f), the preference must be within the range of about 0.6-0.8 for coexistence (preference towards conspecifics). This illustrates clearly that preference is primarily driving regions of coexistence as opposed to switching rates. The pattern remains the same for significantly higher switching rates than shown in Figure S2.3.

We explored if our results change when the consumers have a nonlinear, saturating Type II functional response, which has been shown to best represent consumer functional responses in IGP systems (Sentis et al. 2013). The models with Type II functional responses in the consumer species are as follows for the base model,

$$\frac{dR}{dt} = gR(1 - \frac{R}{K}) - \frac{c_{NR}NR}{1+c_{NR}h_{NR}R} - \frac{c_{PR}PR}{1+c_{PR}h_{PR}R}$$

$$\frac{dN}{dt} = \frac{e_{NR}c_{NR}NR}{1+c_{NR}h_{NR}R} - \frac{c_{ZN}ZN}{1+c_{ZN}h_{ZN}N} - d_N N$$

$$\frac{dP}{dt} = \frac{e_{PR}c_{PR}PR}{1+c_{PR}h_{PR}R} - u_{NP}NP + u_{RZ}RZ - d_P P$$

$$\frac{dZ}{dt} = \frac{e_{ZN}c_{ZN}ZN}{1+c_{ZN}h_{ZN}N} + u_{NP}NP - u_{RZ}RZ - d_Z Z \qquad \text{(eq. 3)}$$

and the full model,

$$\frac{dR}{dt} = gR(1 - \frac{R}{K}) - \frac{c_{NR}NR}{1+c_{NR}h_{NR}R} - \frac{c_{PR}PR}{1+c_{PR}h_{PR}R}$$

$$\frac{dN}{dt} = \frac{e_{NR}c_{NR}NR}{1+c_{NR}h_{NR}R} - \frac{c_{ZN}(1-s)ZN}{1 + c_{ZN}h_{ZN}(1-s)N + c_{ZP}h_{ZP}sP} - d_N N$$

$$\frac{dP}{dt} = \frac{e_{PR}c_{PR}PR}{1+c_{PR}h_{PR}R} - \frac{c_{ZP}sZP}{1 + c_{ZN}h_{ZN}(1-s)N + c_{ZP}h_{ZP}sP} - (u_{NP}N + u_{PP}P)P + u_{RZ}RZ - d_P P$$

$$\frac{dZ}{dt} = \frac{e_{ZN}c_{ZN}(1-s)ZN + e_{ZP}c_{ZP}sZP}{1 + c_{ZN}h_{ZN}(1-s)N + c_{ZP}h_{ZP}sP} + (u_{NP}N + u_{PP}P)P - u_{RZ}RZ - d_Z Z \qquad \text{(eq. 4)}$$

where the new parameter introduced is h, handling time. h_{NR}, h_{PR}, h_{ZN}, and h_{ZP} are the handling times for *N* on *R*, *P* on *R*, *Z* on *N*, and *Z* on *P* respectively. Handling time introduces saturation into the consumer's functional response, limiting their ability to consume increasingly more prey as prey density increases infinitely. All variables and other parameters are defined in the main text.

We found results did not change qualitatively (Figure S2.4), which is consistent with previous studies that compare linear Type I and nonlinear Type II functional responses in IGP systems (Mylius et al. 2001; Revilla 2002; Krivan and Diehl 2005; Rudolf 2007). Similar to Type I, when the prey and predator are equal competitors for the shared resource (Figure S2.4e-h), preferential cannibalism (s=0.7) significantly expands the region of coexistence (Figure S2.4h). The main difference between models with the Type I and Type II functional response here and with Type I is that when the IG prey is a superior competitor, preferential cannibalism is as stabilizing as the equal competitor scenario such that the region of coexistence remains large when preference is increased from no preference (s=0.5; Figure S2.4c) to preferential cannibalism (s=0.7; Figure S2.4d). When the prey is superior, lack of preference is most stabilizing when consumers have a Type I functional response, but lack of preference and preferential cannibalism are equally stabilizing when consumers have a Type II functional response. This further supports and even strengthens the general result that preferential cannibalism is a key stabilizing mechanism of IGP systems with trophic polymorphic IG predators. With Type II, this effect is not dependent on the competitive ability of the IG prey, suggesting that preferential cannibalism is stabilizing regardless of the IG prey's competitive advantage over the resource-eating predator morph or vice versa.

The Type II functional response includes a handling time parameter, which describes the time between encountering a prey individual and looking for the next prey. When prey density increases, the number of prey a predator can eat eventually saturates due to the limitation of handling prey. Thus, prey mortality by predation decreases as prey density increases. This has been shown to be stabilizing in IGP systems, because predation rates are more limited with a Type II functional response, weakening the strength of predation that the IG predator can impose on the IG prey. Abrams and Fung (2010) in particular find that a Type II functional response can be more stabilizing than Type I in IGP systems under certain scenarios, one of them being a high handling time. The results here contribute to the evidence that including a handling time into the functional responses can expand conditions for coexistence between IG predator and IG prey.

When the consumers have a Type II functional response, dynamics switch from a stable equilibrium to limit cycles as values of the preference parameter increase past a high threshold value ($s>0.8$, strong preference for conspecifics, Figure S2.5). When values of s reach close to one (full preference for conspecifics) the predator morphs go extinct. Additionally, high resource carrying capacity can amplify limit cycles (Rosenzweig 1971), which is what we find: when s is high enough to produce these limit cycles (s=0.9), increasing the carrying capacity, K, results in cycles of ever-increasing amplitude (Figure S2.6).

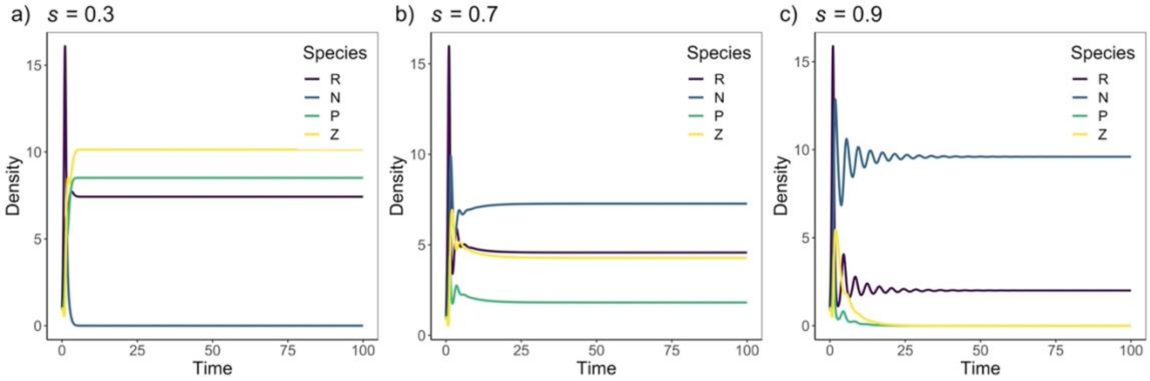

Figure S2.1 Numerical simulations corresponding to the three equilibrium regions in Figure 2.2. The prey and predator are equal competitors for the shared resource.
a) $s=0.3$, in which the predator morphs and resource persist (*ZPR*), b) $s=0.7$ in which all species coexist (*ZPNR*), c) $s=0.9$ in which the IG prey and resource persist (*NR*). All other parameter values are found in Table 2.1.

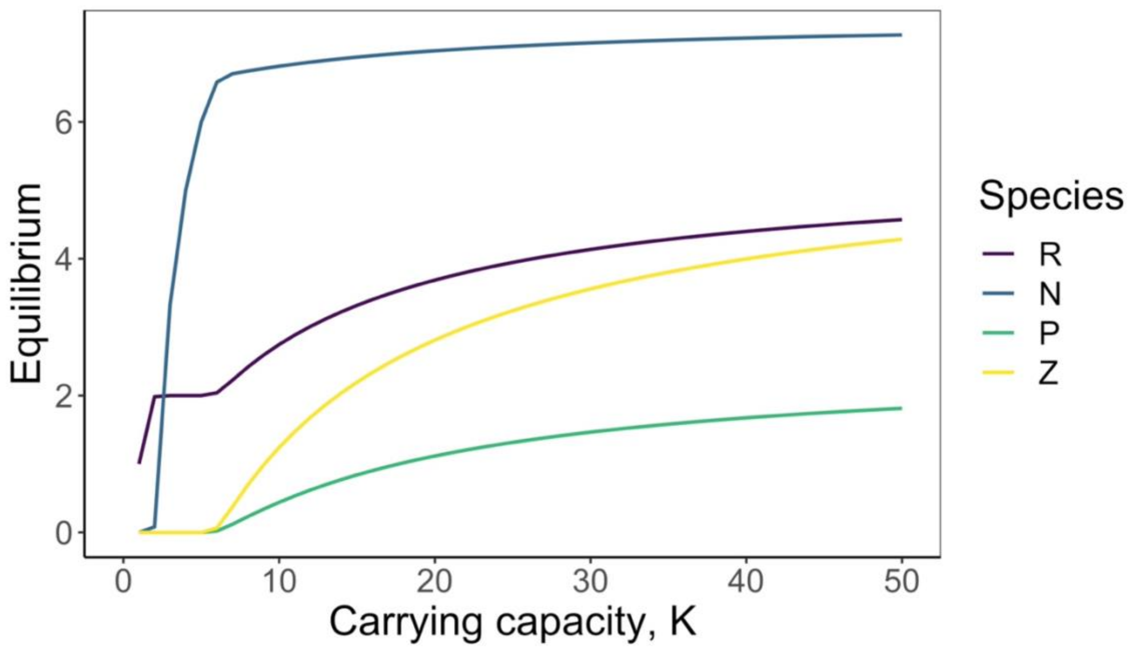

Figure S2.2 Equilibrium densities across a range of resource carrying capacity, *K*. Here, preference is for conspecifics, $s=0.7$, and the prey and predator are equal competitors. All other parameters are the same as in Table 2.1.

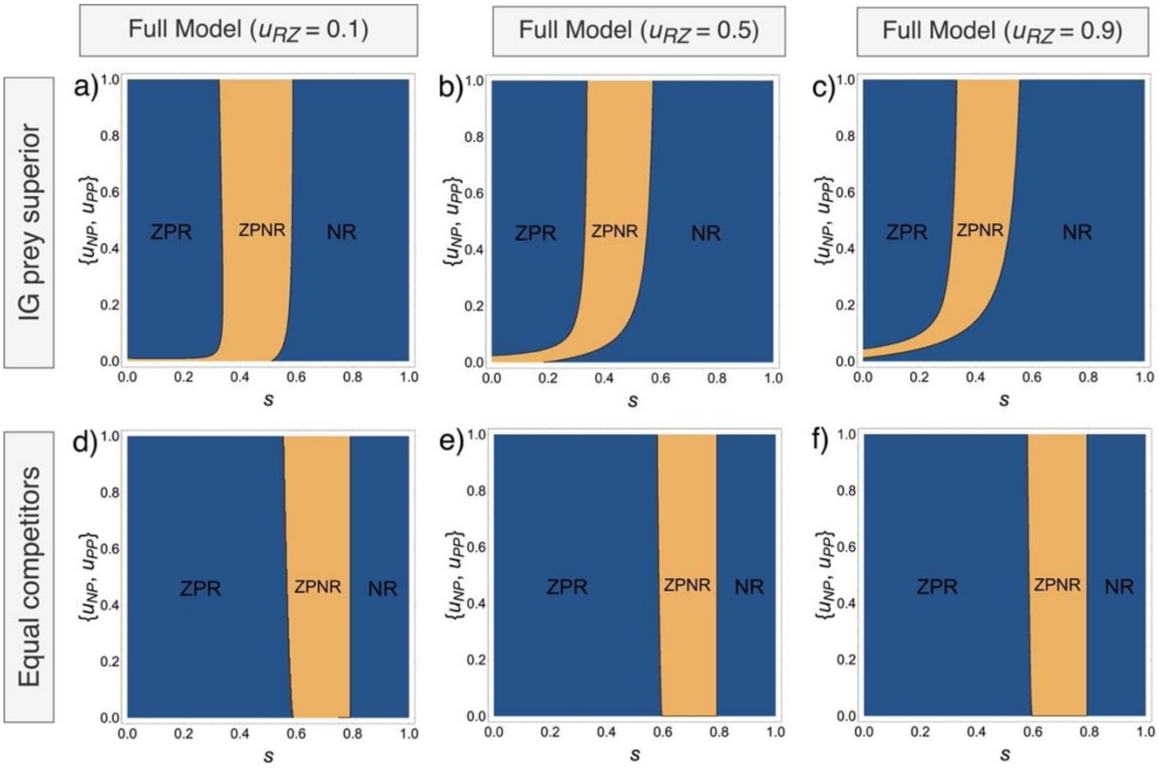

Figure S2.3 Regions of stability across preference parameter, *s*, and both switching parameters into the *Z* state, u_{NP} and u_{PP} (varied simultaneously), when the prey is superior (a-c) and when the prey and predator are equal competitors for the resource (d-f). Examined across three values of switching parameter into the *P* state, u_{RZ}: low switching rate into *P* state (u_{RZ} =0.1), intermediate switching rate into *P* state (u_{RZ} =0.5), high switching rate into *P* state (u_{RZ} =0.9). Orange regions denote stable coexistence between all species, and blue regions denote stable equilibria between certain species. *Z* is the top predator morph, *P* is the resource-eating predator morph, *N* is the IG prey and *R* is the basal resource.

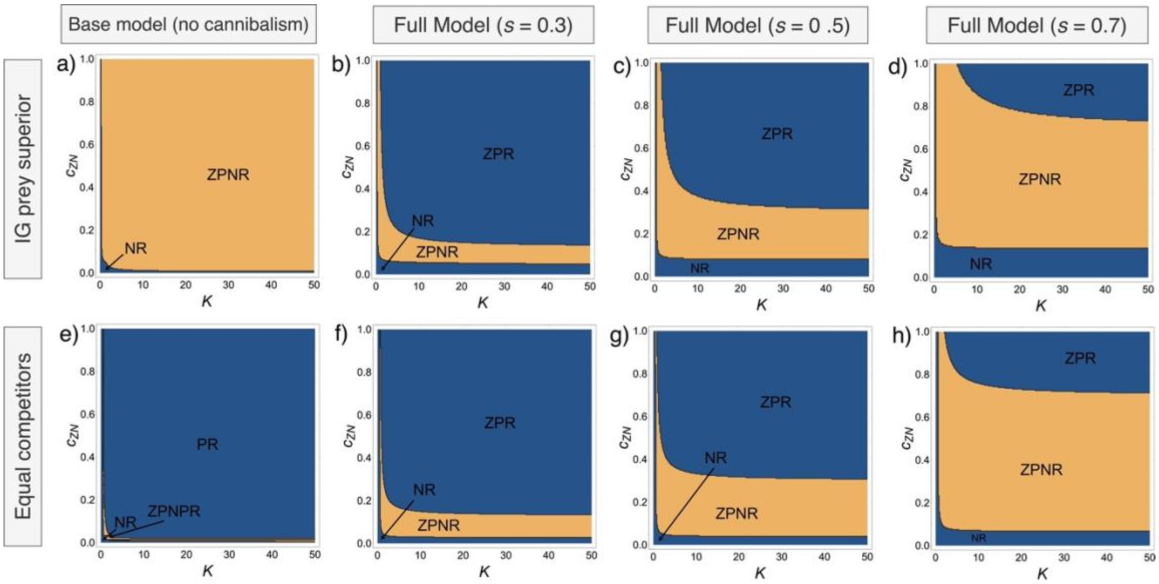

Figure S2.4 Regions of stability across carrying capacity, *K*, and the top predator morph's consumption rate on the IG prey, c_{ZN}, when the prey is superior (a-d) and when the prey and predator are equal competitors for the resource (e-h). Examined across four scenarios: base model without cannibalism (a, e), heterospecific preference (b, f), no preference (c, g), conspecific preference (d, h). Orange regions denote stable coexistence between all species, and blue regions denote stable equilibria between certain species. Consumers have a Type II functional response. Parameter values used are the same as in Table 2.1, with the exception of all death rates being 0.1. All handling times are equal to 1.

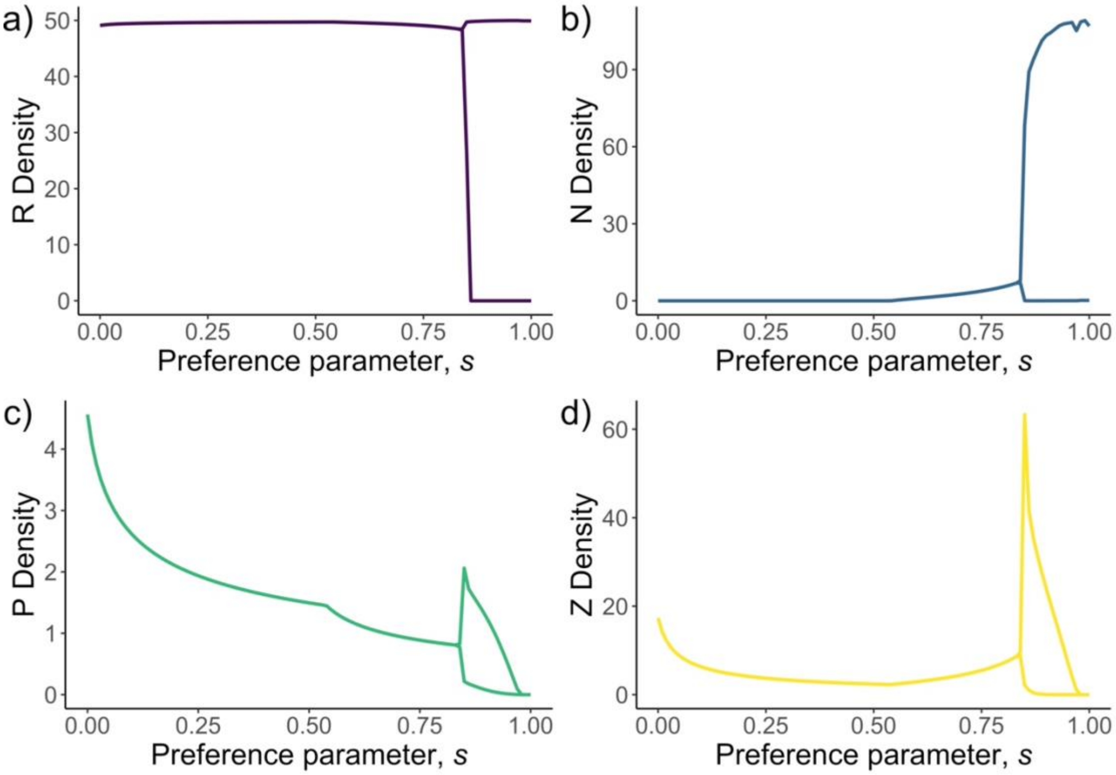

Figure S2.5 Bifurcation diagrams showing the switch from stable equilibrium to limit cycles past a high preference value, $s>0.8$. Density refers to the minimum and maximum density of the final 500 out of 2,000 time steps, in which oscillations have stabilized. Consumers have a Type II functional response. The prey and predator are equal competitors for the shared resource, but results do not change qualitatively when the prey is superior. All other parameters are the same as in Table 2.1, with the exception of all death rates being 0.1. All handling times are equal to 1.

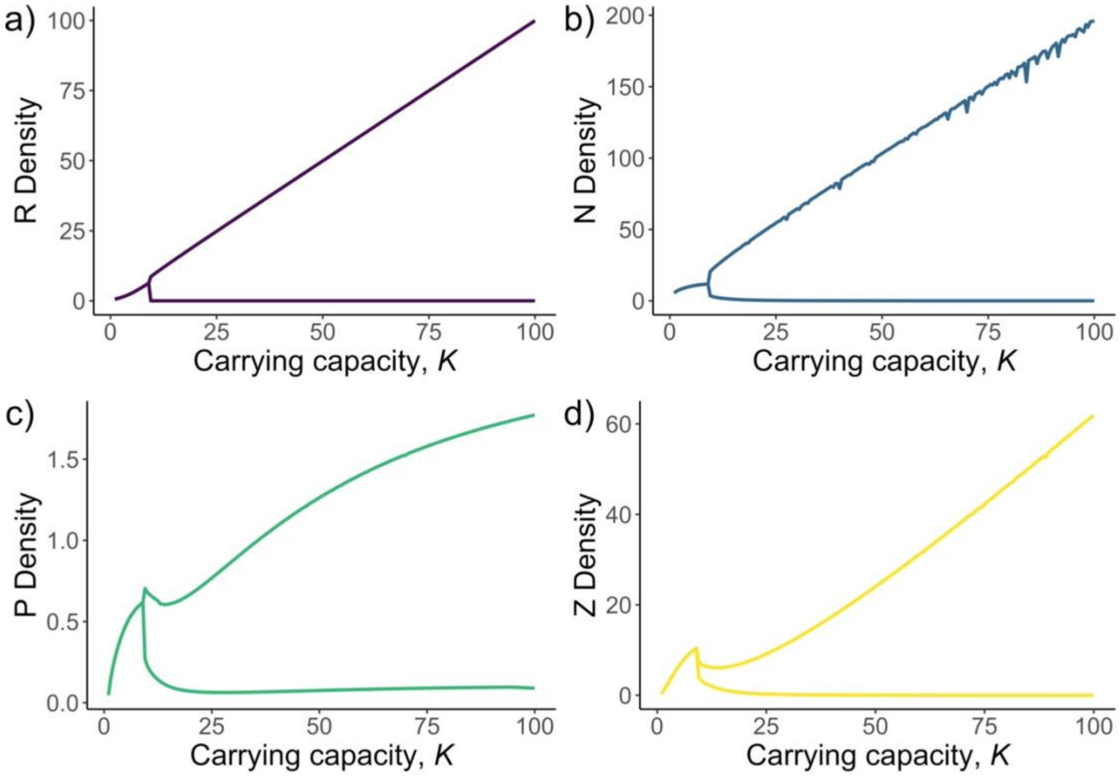

Figure S2.6 Bifurcation diagram showing the switch from stable equilibrium to limit cycles of increasing amplitude as resource carrying capacity, *K*, increases. Density refers to the minimum and maximum density of the final 500 out of 2,000 time steps, in which oscillations have stabilized. Consumers have a Type II functional response and preference is skewed towards conspecifics (s=0.9). The prey and predator are equal competitors for the shared resource, but results do not change qualitatively when the prey is superior. All other parameters are the same as in Table 2.1, with the exception of all death rates being 0.1. All handling times are equal to 1.

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Chapter 3

Spatial resource heterogeneity and differential habitat use promote coexistence of an intraguild predation system at local and regional scales

Abstract

Theory on intraguild predation (IGP; the consumption of one's competitor) predicts specific patterns of long-term population dynamics across a productivity gradient, where exclusion occurs at low and high productivity levels and coexistence is possible only at intermediate levels. However, IGP theory that incorporates space predicts that dispersal among habitats of low, medium, and high productivity enables coexistence in all patches. This variable distribution of resource productivity is known as spatial resource heterogeneity, hereafter SRH. Despite spatial IGP theory being nearly 20 years old, explicit tests of model predictions are nonexistent. We fill this important gap in the literature by testing spatial IGP theory using a protist microcosm experiment that allows us to manipulate a spatial productivity gradient, generate long-term population data, and establish causality between spatial mechanisms and coexistence. We assembled 3-patch networks of uniformly-distributed low, medium, or high productivity (i.e., homogeneous networks); networks with SRH where each patch contains a different productivity level (i.e., heterogeneous networks); and isolated communities of each productivity level as controls. The densities of the IG predator (ciliate, *Blepharisma*) and IG prey (ciliate, *Tetrahymena*) were quantified for 90 days, corresponding to approximately 270 *Tetrahymena* generations and 180 *Blepharisma* generations. We analyze local and regional occupancy, amplitude, and coexistence as measures of stability. Results show strong local and regional stabilizing effects of SRH. Because the IG predator and IG prey reacted to productivity in opposite ways, SRH enabled predator and prey to coexist in their respective suboptimal patches via consistent recolonization in heterogeneous networks. Heterogeneous networks provided refuges for IG predator from strong competitive pressure and IG prey from strong predatory pressure. Our results add to a growing body of knowledge highlighting the importance of differential habitat use to IGP coexistence, and this is the first explicit test of spatial IGP theory involving SRH.

Introduction

Intraguild predation (IGP), the predation of one's competitor, is a ubiquitous interaction in all major taxa in nature (Polis et al. 1989; Arim and Marquet 2004) despite original theory predicting limited coexistence between intraguild (IG) predator and IG prey (Holt and Polis 1997). Coexistence requires a competition-predation tradeoff such that the IG predator, the inferior resource competitor, gains an advantage by consuming the IG prey. However, too much predatory pressure on top of competitive pressure from the IG predator can drive the IG prey extinct. A consequence of this tradeoff is that coexistence is achieved only at intermediate resource productivity levels as predicted by original theory (Holt and Polis 1997). At low productivity, the IG prey outcompetes the IG predator, while at high productivity, the IG predator over exploits the IG prey (Holt and Polis 1997).

Though initial tests of IGP theory provided some support for the predicted productivity-abundance patterns (Morin 1999; Diehl and Feissel 2000, 2001; reviewed by Kratina et al. 2012), evidence of IG prey persistence at high resource productivity in the field accumulated rapidly (Amarasekare 2007b; Borer et al. 2003; Novak 2013). Additionally, meta-analyses reveal that IGP is a common interaction in natural food webs (Arim and Marquet 2004), contradicting the limited coexistence predicted by original theory. This discrepancy between theory and empirical studies prompted theoretical exploration of stabilizing mechanisms, including cannibalism (Rudolf et al. 2007), adaptive foraging (Okuyama and Ruyle 2003), alternative resources (Daugherty et al. 2007), prey defenses (Ingeman and Novak 2022), and spatial effects (Amarasekare 2006). However, through attempts to refine original theory to better explain natural phenomena, theoretical advancements have far outpaced empirical tests of theory.

Spatial resource heterogeneity (hereafter SRH; the variable spatial distribution of resources) is one realm of IGP theory that has far outpaced empirical tests. Given that natural systems are spatially explicit, IGP theory was extended to incorporate space less than a decade after the development of the original theoretical framework (Amarasekare 2006). In the first spatially-explicit theoretical IGP framework, Amarasekare (2006) modeled a 3-patch spatial network with SRH, where each patch’s resource productivity level corresponds to low, medium and high, to elucidate the productivity-abundance relationship under dispersal. The study makes several predictions with regard to dispersal rates and tradeoffs, but a core result is that with dispersal, the IG predator and IG prey both maintain positive abundances in all patches. In a later study with increased network size, Okuyama (2008) compared homogeneous and heterogeneous networks with regards to productivity and found that SRH can prevent the exclusion of IG prey at high productivity whereas homogeneous environments maintain the predictions of non-spatial models. Numerous other theoretical studies have examined the role of spatial heterogeneity with respect to dispersal rates (Nguyen and Nguyen-Ngoc 2015), dispersal strategies (Amarasekare 2007a), and habitat preference (Snyder et al. 2005) on IGP persistence.

Although spatial IGP theory has progressed, tests of theory have languished. The empirical tests that do exist lack causality and fail to elucidate a mechanism (Novak 2013), occur on short time frames that cannot be extrapolated to long-term dynamics predicted by theory (Briggs and Borer 2005), or lack a productivity gradient for testing productivity-abundance predictions (Reichstein et al. 2013; Goldberg et al. 2022). An exception to this is the study by Amarasekare (2007a), but this study focuses predominantly on temporal coexistence mechanisms. Most empirical spatial IGP studies examine spatial complexity or forms of heterogeneity other than resource distribution, typically finding stabilizing effects via reduced IGP strength (reviewed in Janssen et al. 2007). Such studies on the effect of habitat complexity nevertheless offer insights into coexistence-enhancing mechanisms: spatial predator avoidance (Sergio et al. 2003, 2007; Webb et al. 2009; Van der Hammen et al. 2010; Kozlowksi et al. 2012; Grassel et al. 2015; Lonsinger et al. 2017); spatial refugia (Finke and Denno 2002, 2006; HilleRisLambers et al. 2006; Janssen et al. 2007; Carter et al. 2018; Richards et al. 2024); and differential habitat preference or use (Gompper et al. 2016; Goldberg et al. 2022). These mechanisms are likely to play a role in environments with SRH, but the specific effects of SRH on causal mechanisms of long term IGP stability have yet to be confirmed with tests of theory.

Microcosm experiments are ideal for testing model predictions, as they are easily controlled and replicated, variables can be manipulated on large spatial scales relative to the organisms, and they can generate long-term population dynamics quickly (Jessup et al. 2004; Altermatt et al. 2015). A common misconception is that the results of microcosm experiments are meant to scale up to larger ecosystems. Instead, microcosm experiments are an important stepping stone between model predictions and comparative field studies and provide evidence that our models are biologically sound (Holyoak and Lawler 2005; Benton et al. 2007). For instance, several early tests of original IGP theory were able to reproduce certain model results while challenging others (Morin 1999; Diehl and Feissel 2000, 2001), inspiring further theoretical and empirical explorations of IGP dynamics. Moreover, a recent review calls for the use of microcosm experiments to study landscape-level IGP interactions (Kuppardt-Kirmse and Chatzinotas 2020).

Here we fill an ©mportant gap in the literature by conducting the first test of SRH on long-term IGP stability. We aim to disentangle the effects of dispersal, productivity level, and productivity distribution through networks of homogeneous productivity distribution (networks of uniform low, medium, and high productivity), heterogeneous productivity distribution where each patch has a different productivity level, and isolated communities. Specifically, we test the broad prediction generated by Amarasekare (2006) that dispersal among three interconnected patches corresponding to low, medium, and high productivity can facilitate local coexistence in patches of all productivity levels. Our results support this prediction, finding that SRH enhances each species' persistence and coexistence regionally and locally in all patches. We find that the IG predator and IG prey respond in opposite directions to productivity. SRH therefore enables continual recolonization of each species into their respective suboptimal habitats from more optimal ones, maintaining long-term persistence of each species in all patches. To our knowledge, this is the first test of spatial IGP theory in the context of SRH, despite the theory being developed almost 20 years ago.

Methods

Study System

Our study system consisted of two ciliated, free-swimming freshwater protozoan species commonly used in protist microcosm studies (Diehl and Feissel 2000, 2001). The IG predator, *Blepharisma 116utria116num* (hereafter *Blepharisma*) competes with its IG prey, *Tetrahymena pyriformis* (hereafter *Tetrahymena*) for a shared resource, bacteria. The shared resource was a mix of three bacteria species, *Bacillus cereus, Bacillus subtilis*, and *Serratia marcescens*. All protist and bacteria species were purchased from Carolina Biological Supply Company (Burlington, North Carolina, USA). This *Blepharisma-Tetrahymena* system is the same one used in Diehl and Feissel (2000, 2001), which were original tests of IGP theory that reproduced the predicted IGP abundance-productivity patterns.

Tetrahymena is a bacterivore, i.e. consumes only bacteria. Conversely, *Blepharisma* feeds adaptively via an inducible trophic polymorphism (ITP), a form of phenotypic plasticity in which consumers can alter morphology, physiology, or behavior to change the trophic level on which they feed (Banerji and Morin 2009). *Blepharisma* has two distinct morphological states: bacterivorous microstomes and predatory macrostomes (Giese 1973, 1973). Microstomes are small, slender and have short oral ciliature that facilitates the capture and ingestion of small particles such as bacteria. Macrostomes are much larger, with enlarged organelles, oral ciliature and buccal cavity, along with a prominent undulating membrane, that facilitates the capture of larger protist prey (Giese 1938, 1973). *Blepharisma* undergoes the morphological switch from microstomes to macrostomes when protist prey is available in high density. This morphological switch is due to a combination of increased competition with IG prey, decreased bacteria densities, and opportunistic feeding on more nutritional prey. Though we did not explicitly quantify the distinct morphotypes in the present study, this adaptive foraging behavior makes *Blepharisma* an effective omnivore with a strong predation-competition tradeoff (Woodie and Anderson, unpublished manuscript).

Experimental Design

The present study consisted of three treatments with the following factors: productivity level (low, medium, high), productivity distribution (homogeneous, heterogeneous), and dispersal (isolated, network). Figure 3.1 shows a visualization of the experimental design. We refer to “spatial treatment” as isolated bottles versus networks and “productivity distribution” as heterogeneous versus homogeneous networks. Spatial networks consisted of three bottles connected by tubes allowing for active dispersal. Networks had either a homogeneous productivity distribution (i.e., a constant distribution of either low, medium or high productivity) or a heterogeneous productivity distribution (i.e., each bottle had a different productivity level). Controls were isolated bottles of either low, medium, or high productivity levels. There were 8 replicates per treatment for a total of 32 networks (96 total network bottles) and 24 isolated control bottles.

Bacterial productivity was manipulated via the amount of protozoan pellets (Carolina Biological Supply Company), which are largely made of alfalfa leaf. We chose a wide range of productivities to ensure that dynamics were vastly different for each level in order to clearly delineate spatial effects. Nutrient levels comprised 0.28g/L (low productivity), 1.4g/L (medium productivity), and 5.6g/L (high productivity), encompassing nearly the full range of productivity levels used in previous protist microcosm experiments (Holyoak and Lawler 1996; Morin 1999; Liess and Diehl 2000, 2001; Fox and McGrady-Steed 2002; Liess and Diehl 2006; Green et al. 2023). The medium was made by mixing the given amount of protozoan pellets and 0.1g Reptivite with 1 liter of deionized water in a large flask, autoclaving to sterilize it, and inoculating once cool with equal parts of each bacteria species. We gave the bacteria five days to grow to carrying capacity prior to the start of the experiment. Local microcosm communities were assembled in 175 mL polypropylene Nalgene bottles filled with 50 mL medium of the respective productivity level. Each bottle contained one autoclaved wheat seed for a slow release of nutrients throughout the experiment (Morin 1999; Diehl and Feissel 2000, 2001).

Networks consisted of three bottles connected by silicon rubber tubing of 22.23 cm long and 0.2 cm in diameter, similar to previous spatial microcosm experiments (Holyoak and Lawler 1996; Holyoak 2000; Green et al. 2023). All three bottles in each metacommunity were connected uniformly such that each bottle had a connectivity degree of two. We allowed active dispersal, such that individuals of all species could freely and naturally move through the tubes into neighboring bottles.

Sampling

Sampling followed standard microcosm protocol (Altermatt et al. 2015). In short, we measured protist density every Monday, Wednesday, and Friday until day 91. The duration of the experiment comprised approximately 364 generations for *Tetrahymena* and 182 generations of *Blepharisma*. We did not quantify bacteria levels; differences between productivity treatments were so large that any changes within a productivity level were likely negligible, as shown in a previous study (Green et al. 2023). On day 0, we added approximately 100 individuals of *Tetrahymena* and 100 individuals of *Blepharisma* microstomes to each bottle and began sampling on day 3. We added *Blepharisma* at the same time as *Tetrahymena* given that *Blepharisma* is an omnivore. To sample, we thoroughly mixed the medium in a bottle, pipetted 10 drops of 20 microliters onto a tared petri dish, identified and counted protist individuals in each drop using a compound light microscope, and calculated density. We replaced 10% of each bottle's medium once a week starting on day 14 to remove waste and replenish nutrients to a limited extent. We did this by removing 5 mL from the bottle and replacing it with 6 mL of sterile medium of the corresponding productivity level. The extra 1 mL of sterile medium was added to replace weekly sampling (total of 0.6 mL/week removed from sampling), and the extra 0.4 mL replaced natural weekly evaporation (calculated from a side experiment). Previous experiments show that standard medium renewal does not strongly affect ciliate growth rates (Diehl and Feissel 2001).

Analysis

We analyzed data on the local patch (bottle) level and the regional (network) level. Local patch-level analysis lends itself to disentangling the effects of patch productivity within different spatial treatments, while regional-level analysis lends itself to exploring productivity distribution effects on the metacommunity as a whole. We used two ecologically-relevant measures of stability to give a holistic idea of each species' long term persistence: occupancy and amplitude. We measured occupancy and amplitude for both IG predator and IG prey on the patch and regional levels. We further calculated coexistence using occupancy. We used occupancy instead of density because of the highly variable dynamics and regular zero occurrences, in which density fell below detection in sampling. The first 10 days of data were omitted to avoid initial fluctuations due to growth.

We defined occupancy based on density: $O_{i,t} = \begin{cases} 1\ if\ D_{i,t} > 0 \\ 0\ otherwise \end{cases}$ where $O_{i,t}$ denotes occupancy in patch © and time step t. To visualize patch occupancy, we summed up the occupancy values $O_{i,t}$ for each time step t and divided by the total number of time steps (T) to get average patch occupancy for each patch © across the time series. Patch occupancy was thus defined as: $\frac{1}{T}\sum_{t=1}^{T} O_{i,t}$. For regional occupancy, we first calculated the average occupancy across the three bottles for each time step, and then averaged across the time series. Regional occupancy was thus defined as $\frac{1}{T}\sum_{t=1}^{T}\left(\frac{1}{n}\sum_{i=1}^{n} O_{i,t}\right)$ where *n*=3 patches.

For patch amplitude, we calculate the amplitude in each patch © by taking the maximum and minimum values across the entire time series, and calculating the logarithm base 10 of the ratio of maximum to minimum: $log_{10}\left(\frac{max(D_{i,t})}{min(D_{i,t})}\right)$. For regional amplitude, we first summed the densities of patches in a network at each time step, determined the maximum and minimum values across the time series and calculated amplitude from there. Regional amplitude was defined as: $log_{10}\frac{max(\sum_{i=1}^{n} D_{i,t})}{min(\sum_{i=1}^{n} D_{i,t})}$ where n=3 patches.

Finally, coexistence at time step t, C_t, was calculated as 0 when one or neither species was present in a patch and 1 when both species were present. The average patch coexistence across the time series is therefore: $\frac{1}{T}\sum_{t=1}^{T} C_t$. For average regional coexistence, we average coexistence across patches in a network first and then across the time series: $\frac{1}{T}\sum_{t=1}^{T}\left(\frac{1}{3}\sum_{i=1}^{3} C_t\right)$.

We fit generalized linear mixed effects models (GLMMs) for each species with different network predictors for regional vs. patch level statistics, defaulting to linear mixed effects models (LMMs) when a Gaussian distribution was appropriate. We used the package glmmTMB in R (version 0.4.6; Brooks et al. 2017, R Core Team 2024). GLMMs handle both fixed and random effects well, can be applied to various types of data distributions, and can handle hierarchical data with issues of unequal weights, balance or non-independence (Bolker et al. 2009). Replicate ID was maintained as a random effect in all models to account for repeated measures through time within each replicate time series. We further nested bottle ID within replicate ID in bottle-level analyses to account for issues of 1) non-independence between the three bottles of the homogeneous treatments and 2) unbalanced data, given that the homogeneous treatment has three times the amount of data.

At the patch level, many of the comparisons are not meaningful (e.g. a medium bottle in a homogeneous network compared to a high bottle in a heterogeneous network). Comparisons are only meaningful on the patch level across bottles of the same productivity within and across networks or across isolated bottles of different productivity. We therefore ran separate patch-level GLMMs grouped by productivity, with a fixed predictor of spatial treatment (isolated, heterogeneous, homogeneous). We also ran GLMMs within the isolated treatment with productivity level as a fixed predictor to compare the effects of productivity without space. At the regional level, comparisons are only meaningful across network types, which excluded isolated control bottles. We therefore ran regional-level GLMMs with a fixed predictor of productivity distribution (heterogeneous, homogeneous low, homogeneous medium, homogeneous high).

We employed separate GLMMs based on the nature of the response variable. For response variables with a binary outcome of 0 and 1 (i.e. patch-level occupancy and coexistence), we employed a GLMM with a binomial family and logit link function. For response variables with a continuous outcome (i.e. patch amplitude and regional amplitude), we employed a Gaussian family (i.e., LMMs). For the analysis of regional occupancy and regional coexistence, where data are bounded between 0 and 1 and include values at these boundaries, we first applied an arcsine square root transformation, which is common for bounded proportional data (Gotelli and Ellison 2004), and then used a Gaussian family. Although a beta distribution was initially considered, it is generally less effective at handling data points near the boundaries of 0 and 1, which characterizes our dataset. Nonetheless, models employing a beta distribution performed similarly well.

All models were assessed with the DHARMA package (version 0.4.6; Hartig 2022, R Core Team 2024). This package provides a simulation based approach to assess the fit and adherence to our model assumptions, helping identify issues such as overdispersion and model misspecification. After building and assessing each GLMM, we performed pairwise comparisons of estimated marginal means (EMMs) to assess the differences between the levels of our factors of interest. These comparisons were performed using the emmeans package in R (version 1.8.6; Lenth et al. 2024; R Core Team 2024). The Tukey HSD adjustment method was applied to the resulting p-values and confidence intervals to manage the risk of Type I errors, ensuring the reliability of our results.

Results

Population dynamics

Blepharisma and *Tetrahymena* had unique population dynamics as a function of productivity level, spatial productivity distribution, and dispersal (Figure 3.2). While *Blepharisma* and *Tetrahymena* persisted for the length of the experiment in isolated low and medium bottles, *Blepharisma* went extinct in isolated high bottles (Figure 3.2a) and bottles of homogeneous high networks (Figure 3.2e). Consistent recolonization from neighboring bottles of different productivity facilitated long-term *Blepharisma* persistence in high productivity bottles of heterogeneous networks (Figure 3.2b). Dynamics were qualitatively similar across bottles of the same productivity within homogeneous networks (Figure 3.2c, 3.2d, 3.2e). Dynamics between bottles in homogeneous networks were qualitatively similar to their isolated counterparts, while bottles in heterogeneous networks were much more variable compared to their isolated counterparts.

Local level effects

Blepharisma and *Tetrahymena* responded to productivity in opposite directions. While *Blepharisma's* patch occupancy decreased with productivity (Figure 3.3a), *Tetrahymena's* occupancy increased with productivity (Figure 3.3b) regardless of spatial treatment. *Blepharisma's* occupancy was significantly different across all isolated bottles (Table S2.1; low-med: est.=3.41, 95% CI: 1.86 to 4.96; high-med: est.=-1.86, 95% CI: -2.92 to -0.80; high-low: est.=-5.27, 95% CI: -6.83 to -3.71). *Tetrahymena's* occupancy was also significantly different across all isolated bottles (Table S2.1; iso.low-iso.med: est.=-1.23, 95% CI: -2.05 to -0.41; iso.high-iso.low: est.=4.89, 95% CI: 3.37 to 6.41; iso.high-iso.med: est.=3.66, 95% CI: 2.15 to 5.17).

Dispersal alone (i.e., in homogeneous networks) positively affected *Blepharisma's* patch occupancy in all productivity levels compared to isolated bottles (Figure 3.3a), significantly for medium and high productivity (Table S2.1; homo.med-iso.med: est.=2.08, 95% CI: 1.41 to 2.76; homo.high-iso.high: est.=0.53, 95% CI: 0.12 to 0.94). SRH significantly increased *Blepharisma's* patch occupancy in its most suboptimal environment, high productivity, compared to both homogeneous high bottles (Table S2.1;

hetero.high-homo.high: est.=0.70, 95% CI: 0.31 to 1.08) and isolated high bottles (Table S; hetero.high-iso.high: est.= 1.23, 95% CI: 0.74 to 1.72). Subsequently, *Blepharisma* experienced a slight buffering effect in the heterogeneous low bottles (Table S2.1; hetero.low-homo.low: est.=-1.80, 95% CI: -3.12 to -0.48) and heterogeneous medium bottles (Table S2.1; hetero.med-homo.med: est.=-0.90, 95% CI: -1.62 to -0.17). The latter had a significantly higher occupancy than ©solated medium bottles (Table S2.1; hetero.med-iso.med: est.= 1.19, 95% CI: 0.41 to 1.96), leading to a net stabilizing effect in heterogeneous networks for *Blepharisma*.

Unlike *Blepharisma*, *Tetrahymena's* patch occupancy generally only benefited from SRH and not so much from dispersal in homogeneous networks. (Figure 3.3b; Table S2.1). Similar to *Blepharisma*, SRH provided significantly increased patch occupancy in its most unfavorable environment, i.e. low productivity (Table S2.1; hetero.low-homo.low: est.=2.57, 95% CI: 1.84 to 3.31, hetero.low-iso.low: est.=2.88, 95% CI: 2.02 to 3.74). The same is true for medium productivity, where heterogeneous medium bottles supported significantly increased *Tetrahymena* occupancy compared to homogeneous medium bottles (Table S2.1; hetero.med-homo.med: est.=1.83, 95% CI: 0.90 to 2.75) and isolated medium bottles (Table S2.1; hetero.med-iso.med: est.=2.23, 95% CI: 1.17 to 3.29). *Tetrahymena* occupancy is similarly high in high productivity bottles regardless of spatial treatment.

Both species experienced a buffering effect in patch amplitude in heterogeneous networks. Patch amplitude generally increased with productivity in homogeneous and isolated bottles for both *Blepharisma* (Figure 3.3c) and *Tetrahymena* (Figure 3.3d), consistent with the paradox of enrichment (Rosenzweig 1971). However, patch amplitude generally stayed the same or even decreased with productivity in heterogeneous networks. This resulted in a significant increase in patch amplitude in heterogeneous low bottles compared to homogeneous and isolated low bottles for both *Blepharisma* (Table S2.2; hetero.low-iso.low: est.=1.57; 95% CI: 0.73 to 2.41; hetero.low-homo.low: est.=2.58, 95% CI: 1.95 to 3.21) and *Tetrahymena* (Table S2.2; hetero.low-iso.low: est.=2.77, 95% CI: 1.20 to 4.33; hetero.low-homo.low: est.=3.28, 95% CI: 2.11 to 4.44). The buffering effect subsequently reduced the amplitude of fluctuations in high heterogeneous bottles, resulting in patch amplitude values that were relatively stable across heterogeneous bottles for both species.

Regional level effects

Homogeneous networks of a given productivity level generally benefit whichever species thrives in that productivity level (low for *Blepharisma*, high for *Tetrahymena*; Figure 3.4). Heterogeneous networks support high regional occupancy for both *Blepharisma* (Figure 3.4a) and *Tetrahymena* (Figure 3.4b). While *Blepharisma* regional occupancy is increased in homogeneous networks relative to isolated bottles, *Tetrahymena*’s regional occupancy is similar to isolated bottles. All homogeneous networks have significantly different regional occupancy values from one another for both *Blepharisma* and *Tetrahymena* (Table S2.3). *Blepharisma’s* regional occupancy in heterogeneous networks is approximately in between the homogeneous values (Table S2.3; hetero-homo.high: est.=0.42, 95% CI: 0.28 to 0.57; hetero-homo.med: est.=-0.23, 95% CI: -0.36 to -0.10; hetero-homo.low: est.=-0.39, 95% CI: -0.52 to -0.26).

Tetrahymena's regional occupancy in heterogeneous networks is closest to its optimal high productivity environment (Figure 3.4b; Table S2.3). Though significantly reduced compared to homogeneous high networks (Table S2.3; est.=-0.16, 95% CI: -0.32 to -0.001), heterogeneous networks have a significantly increased regional occupancy compared to homogeneous medium (Table S2.3; hetero.homo.med: est.=0.30, 95% CI: 0.15 to 0.45) and homogeneous low networks (Table S2.3; hetero-homo.low: est.=0.60; 95% CI: 0.45 to 0.75).

SRH reduces regional amplitude due to averaging effects of asynchrony, where high-amplitude local fluctuations average out to lower regional fluctuations (Briggs and Hoopes 2004). SRH reduces regional amplitude to mid-level values for *Blepharisma* (Figure 3.4c) and low values for *Tetrahymena* (Figure 3.4d). *Tetrahymena's* regional amplitude in heterogeneous networks is similar to homogeneous high and low networks (Table S2.4), lower than homogeneous medium but not significantly. *Blepharisma's* regional amplitude in heterogeneous networks is closest to medium homogeneous networks, significantly higher than low homogeneous networks (Table S2.4; hetero-homo.low: est.=3.27, 95% CI: 1.95 to 4.60) and significantly lower than high homogeneous networks (Table S2.4; hetero-homo.high: est.=-1.92, 95% CI: -3.53 to -0.31). *Blepharisma's* regional amplitude increases significantly with productivity across homogeneous networks (Table S2.4).

Coexistence across scale

Local coexistence in each productivity level increases with spatial complexity (Figure 3.5a), from isolated bottles to homogeneous networks to heterogeneous networks.

Coexistence is similarly low between isolated bottles of each productivity level. Coexistence increases significantly in homogeneous medium and high bottles compared to isolated counterparts (Table S2.5; homo.med-single.med: est.=1.10, 95% CI: 0.44 to 1.75; homo.high-single.high: est.=0.59, 95% CI: 0.23 to 0.94). Lastly, bottles in heterogeneous networks of all productivity levels have significantly higher coexistence than those in homogeneous networks (Table S2.5).

Similar to local-level, regional coexistence is highest in medium homogeneous networks (Figure 3.5b; Table S2.5), significantly higher than homogeneous low networks (Table S2.5; homo.low-homo.med: est.=-0.33, 95% CI: -0.45 to -0.21) and homogeneous high networks (Table S2.5; homo.high-homo.med: est.=-0.35, 95% CI: -0.51 to -0.18). Regional coexistence in heterogeneous networks is highest, significantly different from low and high homogeneous networks (Table S2.5; hetero-homo.low: est.=0.43, 95% CI: 0.31 to 0.55; hetero-homo.high: est.=0.45, 95% CI: 0.29 to 0.61).

Discussion

IGP theory was extended to spatial systems almost 20 years ago (Amarasekare 2006), yet explicit tests of the theory are surprisingly nonexistent to our knowledge. Here we utilize a spatial protist microcosm experiment to quantify multigenerational population dynamics of an IG predator and its IG prey to test predictions from spatial IGP theory. Our findings support theoretical predictions that SRH, the variable distribution of resource productivity, is a strong stabilizing mechanism of IGP dynamics. First, heterogeneous networks maximized both local coexistence, regardless of patch productivity level, and regional coexistence. Second, in heterogeneous networks, each species' persistence was significantly enhanced in their most suboptimal habitats (low productivity for *Tetrahymena* and high productivity for *Blepharisma*) compared to homogeneous networks and isolated controls. Third, because of each species' opposing responses to productivity, regional occupancy was greatly enhanced, and regional amplitude minimized, in heterogeneous networks for each species. Within the homogeneous networks, coexistence is maximized in homogeneous environments of medium productivity, a level that balances the advantages conferred to each species at the productivity extremes.

The opposite responses of the IG predator and IG prey to productivity drove a mismatch in their respective ideal conditions. *Blepharisma* thrived in low productivity environments while *Tetrahymena* thrived when productivity was high. These results were robust to spatial treatment (i.e., isolated communities vs. spatial networks) and spatial scale (i.e., local vs. regional level). Such differential habitat use has been shown to stabilize IGP systems (Gompper et al. 2016; Rodriguez-Luna et al. 2021), especially when the two species prefer different habitats, both theoretically (Snyder et al. 2005) and empirically (Goldberg et al. 2022). We find this stabilizing effect is facilitated by SRH, because SRH not only increases species' occupancy in their suboptimal habitats but also keeps occupancy high in their preferred habitats (i.e., weak buffering effect). Rescue effects between patches of differing productivity bolster populations in less favorable habitats through dispersal from populations in more favorable habitats, while keeping persistence high in the latter. Overall, this leads to maximized local coexistence in each habitat type, and maximized regional coexistence, in heterogeneous networks.

Blepharisma's extinction-prone dynamics in high productivity environments are due to factors other than the paradox of enrichment (Rosenzweig 1971), because *Blepharisma* experiences lower amplitude in high productivity bottles compared to medium. While *Tetrahymena* followed the expected pattern of increasing abundance with enrichment, *Blepharisma* experienced a stress response to increased pH with enrichment. The130utriant pellets used to create the medium are basic relative to the deionized water, increasing the medium's pH with enrichment (C.W., personal observation). Due to their large size, *Blepharisma* macrostomes struggle to maintain homoeostasis under alkaline stress, challenging osmoregulation and disrupting metabolic processes (Giese 1973). Previous microcosm experiments faced similar issues growing *Blepharisma* at high nutrient levels (Morin 1999; Diehl and Feissel 2000). However, *Blepharisma's* struggle to persist in high productivity environments arguably makes our results more compelling: although *Blepharisma* cannot persist long term in high productivity environments, as exhibited in both isolated and homogeneous high productivity bottles, *Blepharisma* was able to maintain prolonged persistence in high productivity bottles of heterogeneous networks due to consistent recolonization and/or rescue effects (Brown and Kodric-Brown 1977; Holyoak and Lawler 1996). The mechanism here necessitates patches of variable suitability (e.g., SRH) such that *Blepharisma* can consistently disperse from more suitable patches to rescue or recolonize less suitable ones. Overall, these findings illustrate the importance of heterogeneous environments in providing recolonization opportunities for species that may not be able to sustain a population in a closed system or homogeneous environment.

Blepharisma's functional traits (i.e., inducible trophic polymorphism, ITP) interact with habitat suitability to influence spatial IGP dynamics, especially in heterogeneous landscapes. Our results support Amarasekare's (2006) prediction that dispersal can be a mechanism of coexistence in enriched environments if the competition-IGP trade-off is strong or the IG prey has an advantage, both of which are true in our system. *Blepharisma's* ITP drives a strong competition-IGP trade-off, allowing *Blepharisma* to forage adaptively through morphological specializations on bacteria vs. protist prey. ITP expression is further mediated by the abiotic environment, wherein basic (high productivity) environments prohibit the induction of large macrostome cells due to osmoregulation issues discussed above. We therefore see dynamics are more predation-driven in low productivity and competition-driven in high productivity (note this is the opposite of what original IGP theory predicts). As a result, *Tetrahymena*, the superior competitor, benefits greatly from a predation refuge in high productivity patches where it thrives, while *Blepharisma* benefits from a physiological refuge in lower productivity patches. IG prey consistently recolonized bottles with increased predation risk while IG predators consistently recolonized bottles that presented higher physiological stress as a trade-off for foraging in a high density resource patch. Our system is a good example of how the competition-IGP tradeoff can be enhanced by different habitat suitability requirements in spatial networks with SRH, thereby promoting IGP stability. Our work addresses the first step of varying spatial productivity, but future work should manipulate dispersal rates by varying distances among patches as proposed by Amarasekare (2006).

Our results support a related study's prediction that interspecific segregation, where IG predator and IG prey are restricted to patches of different productivity, promotes coexistence (Amarasekare 2007a). Such spatial segregation can occur behaviorally from habitat-mediated avoidance by the IG prey, often at the expense of access to lower quality resources (Morris 2005; Sergio et al. 2003, 2007; van der Hammen et al. 2010; Grassel et al. 2015; Lonsinger et al. 2017). In our study, avoidance at the expense of fitness is not necessary given that species prefer different environments, enabling them both to be in their preferred habitats without much behavioral modification. There is no trade off between predation risk and habitat quality for the IG prey, which is often the case (Webb et al. 2009). This raises the question of whether SRH would still maximize coexistence if the IG predator was not physiologically constrained in higher productivity environments. Future studies should employ species that have similar habitat preferences to test if long-term coexistence is still maximized in heterogeneous networks where the IG prey is restricted to suboptimal habitats. We posit that differential habitat preference and/or suitability plays a significant role in the stabilizing role of SRH in the present study.

We find that the effect of space alone (i.e., homogeneous treatment) generally benefited the IG predator on local and regional scales while having a neutral effect on the IG prey. Although coexistence increased in homogeneous networks compared to isolated counterparts, it did so primarily by increasing *Blepharisma's* occupancy locally and regionally. This effect of dispersal in networks of homogeneous productivity has been shown to promote predator occupancy, while prey occupancy is more strongly influenced by other factors such as predation (Green et al. 2023). While the predator benefits from sampling the environment at a larger spatial scale, the prey is largely constrained by predation due to lack of refuges in homogeneous networks. Future studies should expand the spatial scale of the experiment, such as in the theoretical work by Okuyama 2008, including different resource distribution patterns. For instance, SRH in large networks has been predicted to be important to predator-prey stability (Woodie and Anderson, unpublished manuscript) and different network structures have been shown to heavily influence predator-prey dynamics (Green et al. 2023). Increased connectivity may support highly mobile generalist omnivores and negate the opportunity for IG prey to find refuge (Liao et al. 2020). However, if SRH is included, and omnivores have to navigate through patches that are less ideal for them, this can slow them down, canceling out the effects of heightened connectivity.

In our heterogeneous networks, species persistence in a patch was strongly driven by local environmental conditions, species traits and habitat suitability, and dispersal. We therefore see effects of three metacommunity dynamics frameworks: species sorting, patch dynamics, and mass effects (Leibold et al. 2004; Leibold and Loueille 2015). Evidence for species sorting was observed through the distinct distribution of species across the productivity gradient, sorted by their fitness in local environments, in which each species thrived in environments that matched their biological requirements. Evidence for patch dynamics lies in how different environments influenced species' population dynamics through both colonization and extinction processes. Although local productivity provides a foundational environmental context, the dynamic interplay between dispersal and local extinctions, driven by factors such as predatory and competitive pressures and habitat suitability, shapes local population dynamics. Lastly, mass effects are evidenced by the fact that *Blepharisma* is not able to sustain a population in high productivity patches without consistent immigration from patches with positive growth rates, overriding the deterministic effects of local conditions by supplying a continuous influx of individuals from the regional pool.

Many pests and their natural enemies engage in intraguild predation, so spatial IGP dynamics have important biological control implications. Conservation biology goals are generally compatible with biological control goals such that preserving diversity of natural enemies, including those that engage in intraguild predation, positively affects biological control (Janssen et al. 2006), but not always (Straub et al. 2008). Biological control goals can clash with conservation goals, especially with regards to the IG predator. We advocate for a nuanced approach to biological control that emphasizes understanding the ways in which species sample the environment and their habitat preferences. When the two species exhibit niche complementarity, biological control will be enhanced (Straub et al. 2008). Landscape heterogeneity can promote complementarity and lead to net positive effects on pest control (Martin et al. 2015). Our study as a whole represents the ideal conditions that enhance both biodiversity and biocontrol: the different habitat preferences for predator and prey in our study suggests that hypothetical biocontrol of the shared resource is enhanced, while spatial mechanisms in heterogeneous landscapes support persistence of both predators. Future studies should quantify resource density as well for more explicit information on biocontrol implications.

Our highly controlled microcosm experiment reveals that SRH significantly enhances long term-IGP stability on both local and regional scales, providing strong support for spatial IGP theory that has yet to be tested. Our study illustrates that although dynamics can appear unstable in the short term, populations can be maintained long-term through mechanisms that enable recolonization and rescue effects. By executing an experiment that closely adheres to the assumptions of spatial IGP theory, our results provide biological support for model predictions and provide a stepping stone between theory and comparative field studies. Future field studies should explicitly disentangle SRH from other mechanisms to identify whether SRH is in fact a strong, generalizable mechanism of IGP stability in nature. Because of the influence of productivity on IGP dynamics, the prevalence of omnivory in natural food webs, and the fact that species interact in space, understanding the mechanisms of spatial IGP interactions with regards to productivity is key for conservation management and biological control.

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Tables & Figures

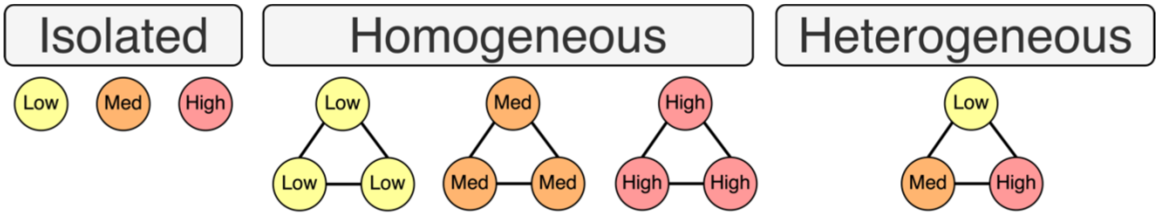


Figure 3.1. Visualization of the experimental set up, consisting of three treatments with the following levels: isolated control bottles of low, medium, or high productivity; homogeneous networks with a constant distribution of low, medium, or high productivity; heterogeneous networks consisting of a bottle of low, medium, and high productivity. The isolated controls and each network were replicated 8 times.

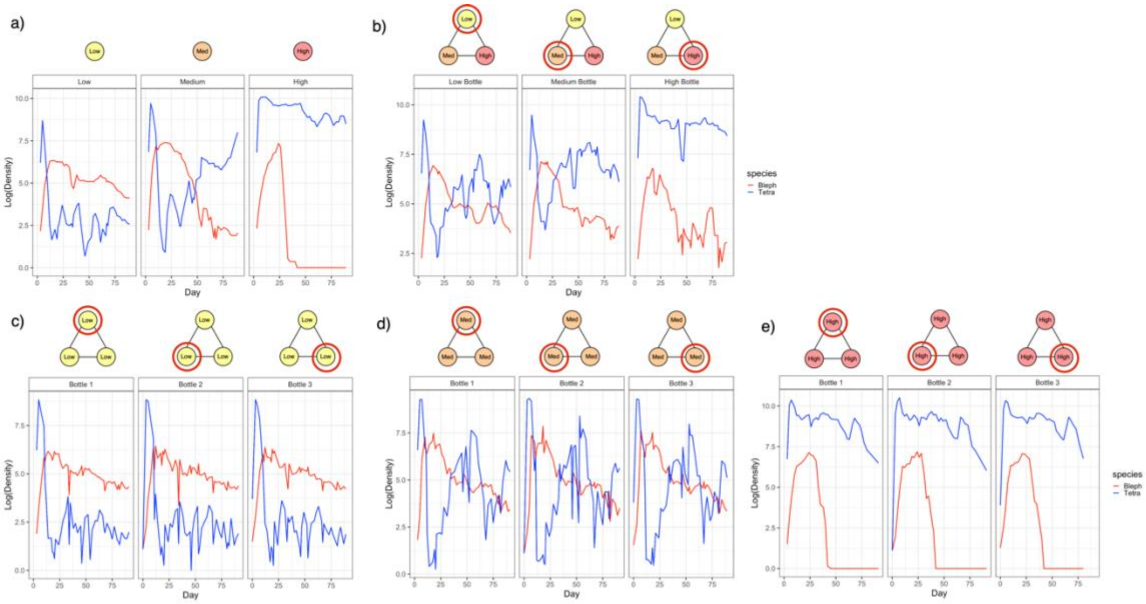


Figure 3.2. Time series averaged across 8 replicates for (a) isolated controls, (b) heterogeneous networks, (c) homogeneous low networks, (d) homogeneous medium networks, and (e) homogeneous high networks. A moving average with a window size of four time steps was computed to reduce noise.

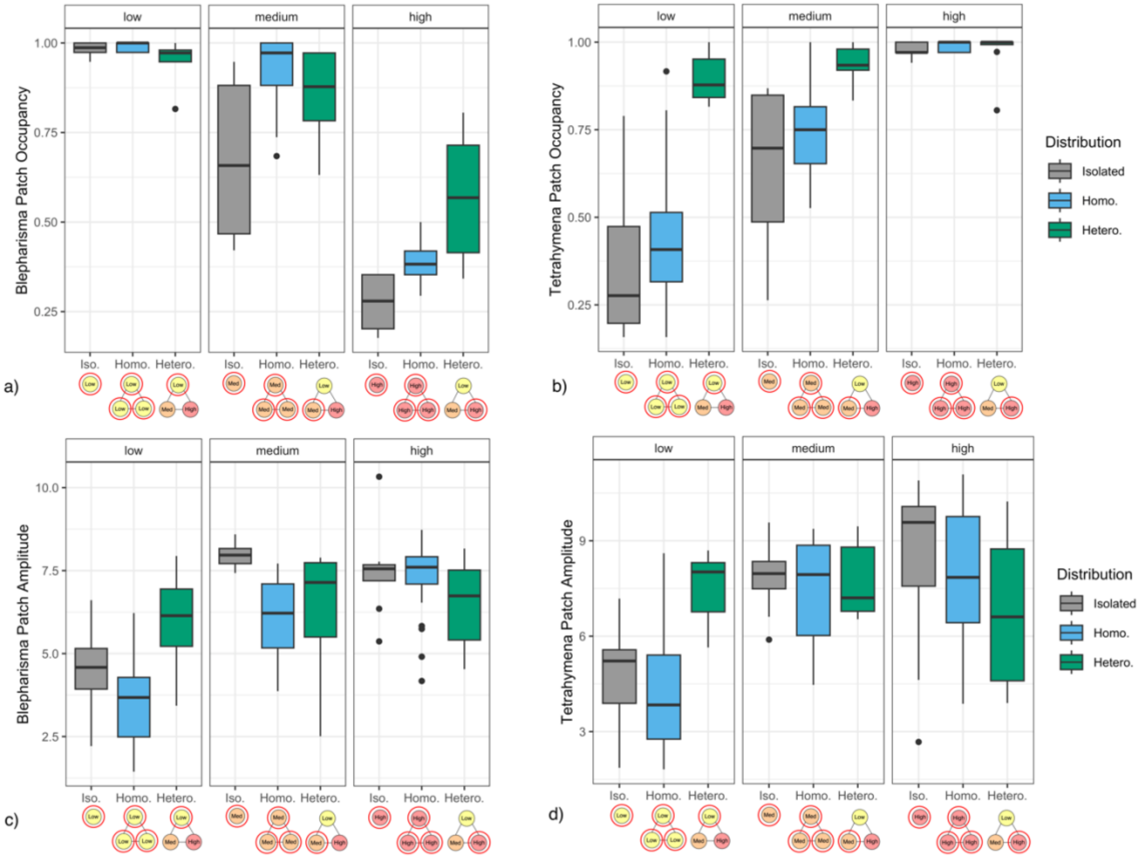
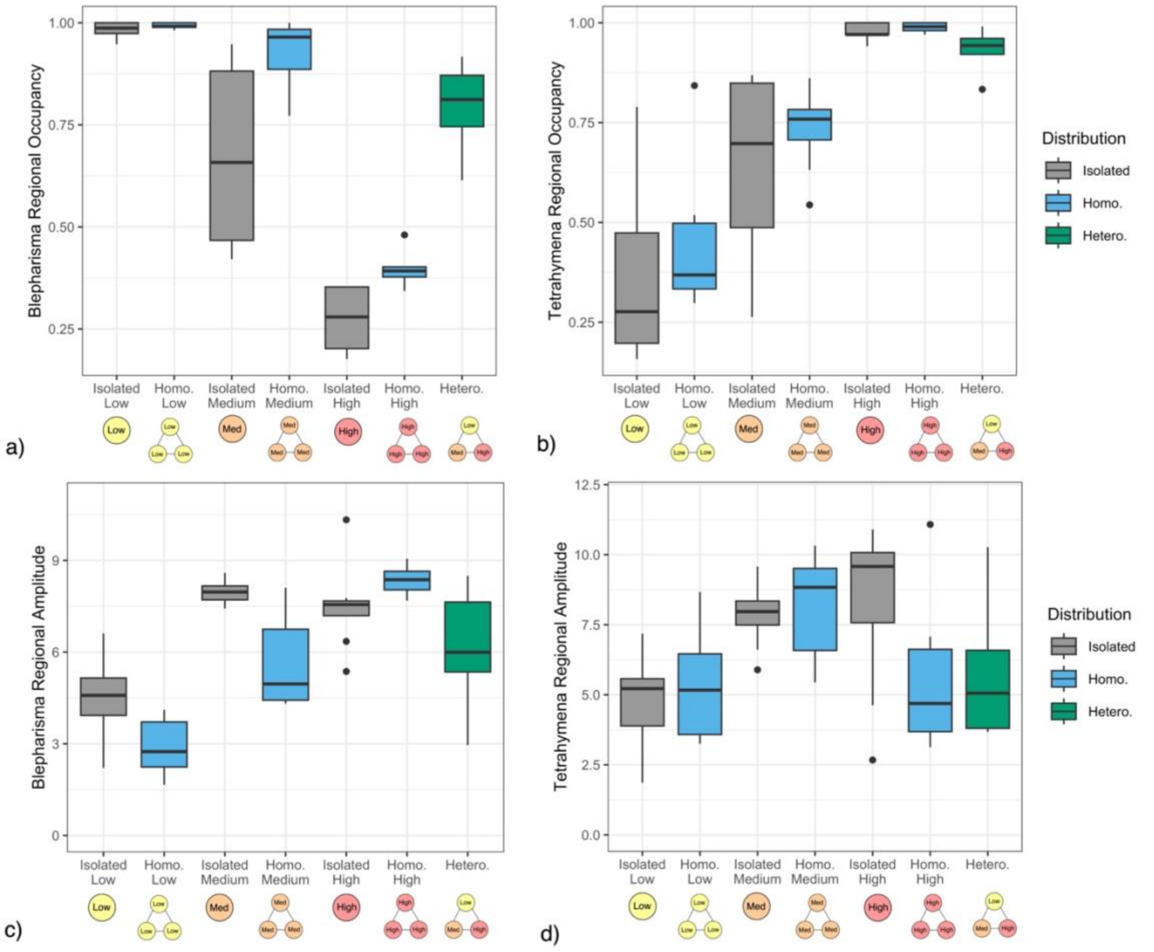


Figure 3.3. Local patch occupancy (a, b) and patch amplitude (c, d) as a function of spatial treatment and patch productivity for *Blepharisma* (a, c) and *Tetrahymena* (b, d).



<u>Figure 3.4.</u> Regional occupancy (a, b) and regional amplitude (c, d) as a function of spatial treatment and productivity distribution for *Blepharisma* (a, c) and *Tetrahymena* (b, d). Isolated bottles are shown for comparison purposes only.

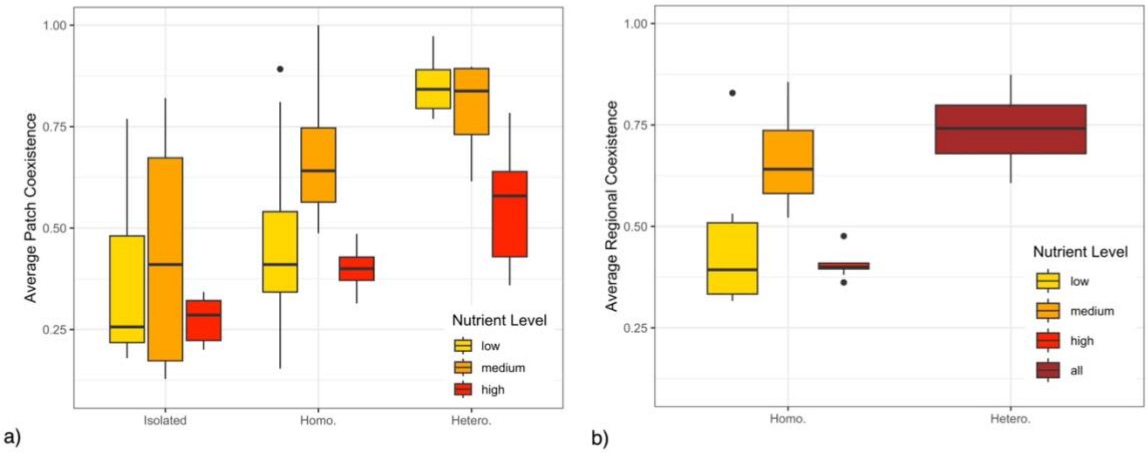


Figure 3.5. Coexistence as a function of spatial treatment and (a) local-level patch productivity on the local level and (b) productivity distribution on the regional level. Coexistence is defined as occurrences in time in which both species have an occupancy of one.

Supplementary Information

Table S3.1. Results from generalized linear mixed effects models (GLMMs) of the effect of spatial treatment (isolated, homogeneous, heterogeneous) and productivity level (low, medium, high) on patch occupancy for *Blepharisma* and *Tetrahymena*. We ran separate GLMMs within each productivity level so as to compare only meaningful effects. GLMMs were run with a Binomial family and Logit link on the occupancy (presence/absence) of each species. Bottle ID was nested within replicate ID as random effects in all models.

Patch Occupancy							
Species	Group	contrast	estimate	SE	p.value	95% Lower CI	95% Upper CI
Bleph	Isolated bottles	iso.high - iso.low	-5.27	0.616	*****<0.0001**	-6.83	-3.705
		iso.high - iso.med	-1.86	0.419	*****<0.0008**	-2.92	-0.797
		iso.low - iso.med	3.41	0.612	*****<0.0001**	1.86	4.964
	High prod.	hetero.high - homo.high	0.696	0.157	*****0.0002**	0.313	1.079
		hetero.high - iso.high	1.228	0.199	*****<0.0001**	0.740	1.715
		homo.high - iso.high	0.532	0.167	****0.0084**	0.122	0.941
	Medium prod.	hetero.med - homo.med	-0.898	0.297	***0.0126**	-1.624	-0.171
		hetero.med - iso.med	1.185	0.317	****<0.0019**	0.409	1.961
		homo.med - iso.med	2.083	0.275	*****<0.0001**	1.411	2.755

	Low prod.	hetero.low - homo.low	-1.799	0.540	**0.0057	-3.12	0.478
		hetero.low - iso.low	-1.040	0.620	0.2286	-2.56	0.479
		homo.low - iso.low	0.759	0.645	0.4750	-0.82	2.338
Tetra	Isolated bottles	iso.high - iso.low	4.89	0.597	***<0.0001	3.37	6.408
		iso.high - iso.med	3.66	0.593	***<0.0001	2.15	5.167
		iso.low - iso.med	-1.23	0.324	**<0.0033	-2.05	-0.409
	High prod.	hetero.high - homo.high	-0.156	0.835	0.9809	-2.199	1.89
		hetero.high - iso.high	0.539	0.834	0.7957	-1.502	2.58
		homo.high - iso.high	0.695	0.572	0.4527	-0.705	2.10
	Medium prod.	hetero.med - homo.med	1.825	0.378	***0.0001	0.899	2.75
		hetero.med - iso.med	2.230	0.434	***<0.0001	1.166	3.29
		homo.med - iso.med	0.405	0.305	0.3901	-0.342	1.15
	Low prod.	hetero.low - homo.low	2.570	0.300	***<0.0001	1.835	3.305
		hetero.low - iso.low	2.878	0.351	***<0.0001	2.019	3.737
		homo.low - iso.low	0.308	0.253	0.4523	-0.312	0.927

Table S3.2. Results from linear mixed effects models (LMMs) of the effect of spatial treatment (isolated, homogeneous, heterogeneous) and productivity level (low, medium, high) on patch amplitude for *Blepharisma* and *Tetrahymena*. We ran separate LMMs for each productivity level so as to compare only meaningful effects. LMMs were run with a Gaussian family on the continuous amplitude data. Bottle ID was nested within replicate ID as random effects in all models.

Patch Amplitude							
Species	Group	contrast	estimate	SE	p.value	95% Lower CI	95% Upper CI
Bleph	Isolated bottles	iso.high - iso.low	3.073	0.573	*****0.0001**	1.61	4.535
		iso.high - iso.med	-0.468	0.573	0.6974	-1.93	0.994
		iso.low - iso.med	-3.541	0.573	*****<0.0001**	-5.00	-2.079
	High prod.	hetero.high - homo.high	-0.822	0.425	0.1358	-1.84	0.193
		hetero.high - iso.high	-1.109	0.536	0.1021	-2.39	0.169
		homo.high - iso.high	-0.287	0.401	0.7550	-1.25	0.671
	Medium prod.	hetero.med - homo.med	0.228	0.286	0.7056	-0.455	0.912
		hetero.med - iso.med	-1.626	0.384	*****0.0002**	-2.543	-0.709
		homo.med - iso.med	-1.854	0.286	*****<0.0001**	-2.538	-1.171
	Low prod.	hetero.low - homo.low	2.58	0.262	*****<0.0001**	1.953	3.207

		hetero.low - iso.low	1.57	0.352	***<0.0001	0.729	2.410
		homo.low - iso.low	-1.01	0.262	***0.0007	-1.637	-0.384
Tetra	Isolated bottles	iso.high - iso.low	3.479	0.956	**0.0071	0.977	5.98
		iso.high - iso.med	0.336	0.703	0.8829	-1.505	2.18
		iso.low - iso.med	-3.143	0.438	***0.0001	-4.290	-2.00
	High prod.	hetero.high - homo.high	-1.055	0.808	0.3959	-2.98	0.873
		hetero.high - iso.high	-1.448	0.995	0.3176	-3.82	0.927
		homo.high - iso.high	-0.394	0.750	0.8596	-2.18	1.398
	Medium prod.	hetero.med - homo.med	0.313	0.316	0.5844	-0.441	1.067
		hetero.med - iso.med	-0.172	0.424	0.9131	-1.184	0.839
		homo.med - iso.med	-0.485	0.316	0.2794	-1.239	0.269
	Low prod.	hetero.low - homo.low	3.275	0.488	***<0.0001	2.11	4.440
		hetero.low - iso.low	2.768	0.655	***0.0002	1.20	4.331
		homo.low - iso.low	-0.507	0.488	0.5545	-1.67	0.658

Table S3.3. Results from linear mixed effects models (LMMs) of the effect of productivity distribution (homogeneous low, homogeneous medium, homogeneous high, heterogeneous) on regional occupancy for *Blepharisma* and *Tetrahymena*. Bottle occupancy was averaged across bottles in a network first, transformed with an arcsine square root transformation to normalize and unbound the data, and then modeled with a Gaussian distribution. Replicate ID was included as a random effect in all models.

Regional Occupancy						
Species	contrast	estimate	SE	p.value	95% Lower CI	95% Upper CI
Bleph	hetero - homo.high	0.424	0.0521	*****<0.0001**	0.2813	0.5673
	hetero - homo.low	-0.393	0.0479	*****<0.0001**	-0.5240	-0.2612
	hetero - homo.med	-0.229	0.0479	*****0.0003**	-0.3604	-0.0976
	homo.high - homo.low	-0.817	0.0521	*****<0.0001**	-0.9599	-0.6739
	homo.high - homo.med	-0.653	0.0521	*****<0.0001**	-0.7963	-0.5103
	homo.low - homo.med	0.164	0.0479	***0.0106**	0.0322	0.2950
Tetra	hetero - homo.high	-0.162	0.0583	***0.0467**	-0.322	-0.00186
	hetero - homo.low	0.601	0.0551	*****<0.0001**	0.450	0.75265
	hetero - homo.med	0.298	0.0551	*****<0.0001**	0.147	0.44947
	homo.high - homo.low	0.763	0.0583	*****<0.0001**	0.603	0.92337
	homo.high - homo.med	0.460	0.0583	*****<0.0001**	0.300	0.62019

	homo.low - homo.med	-0.303	0.0551	*****<0.0001**	-0.454	-0.15192

Table S3.4. Results from linear mixed effects models of the effect of productivity distribution (homogeneous low, homogeneous medium, homogeneous high, heterogeneous) on regional amplitude for *Blepharisma* and *Tetrahymena*. Patch amplitude was first averaged across bottles in a network, and LMMs were run with a Gaussian family. Replicate ID was included as a random effect in all models.

Regional Amplitude						
Species	contrast	estimate	SE	p.value	95% Lower CI	95% Upper CI
Bleph	hetero - homo.high	-1.92	0.586	***0.0147**	-3.527	-0.314
	hetero - homo.low	3.27	0.483	*****<0.0001**	1.945	4.597
	hetero - homo.med	0.44	0.483	0.7993	-0.886	1.767
	homo.high - homo.low	5.19	0.586	*****<0.0001**	3.585	6.798
	homo.high - homo.med	2.36	0.586	****0.0023**	0.755	3.968
	homo.low - homo.med	-2.83	0.483	*****<0.0001**	-4.157	-1.504
Tetra	hetero - homo.high	0.0563	1.05	0.9999	-2.82	2.935
	hetero - homo.low	0.1955	1.05	0.9976	-2.68	3.074
	hetero - homo.med	-2.555	1.05	0.0952	-5.43	0.323
	homo.high - homo.low	0.1392	1.05	0.9991	-2.74	3.018
	homo.high - homo.med	-2.612	1.05	0.0854	-5.49	0.267
	homo.low - homo.med	-2.751	1.05	0.0649	-5.63	0.128

Table S3.5. Results from generalized linear mixed effects models (GLMMs) of the effect of spatial treatment (isolated, homogeneous, heterogeneous) and productivity level (low, medium, high) on patch-level coexistence, and linear mixed effects models (LMMs) of the effect if productivity distribution (homogeneous low, homogeneous medium, homogeneous high, heterogeneous) on regional-level coexistence. For the patch models, we nested Bottle ID within Replicate ID and ran separate GLMMs with a Binomial distribution and logit link within each productivity level so as to compare only meaningful effects. For the regional models, patch coexistence was first averaged across bottles in a network. The data was transformed with an arcsine square root transformation to normalize and unbound the data, and then LMMs were run with a Gaussian distribution and Replicate ID as a random effect.

Coexistence						
Spatial scale	contrast	estimate	SE	p.value	95% Lower CI	95% Upper CI
Local patch	homo.low - single.low	0.343	0.241	0.3298	-0.223	0.908
	homo.low - hetero.low	-2.141	0.268	*****<0.0001**	-2.771	-1.512
	single.low - hetero.low	-2.484	0.319	*****<0.0001**	-3.234	-1.735
	homo.med - single.med	1.097	0.279	*****0.0003**	0.442	1.7520
	homo.med - hetero.med	-0.716	0.290	***0.0364**	-1.397	-0.0357
	single.med - hetero.med	-1.813	0.351	*****<0.0001**	-2.637	-0.9886
	homo.high - single.high	0.586	0.150	*****0.0003**	0.233	0.938
	homo.high - hetero.high	-0.609	0.135	*****<0.0001**	-0.925	-0.292
	single.high - hetero.high	-1.194	0.176	*****<0.0001**	-1.607	-0.782

Regional	hetero - homo.high	0.4482	0.0632	***<**0.0001**	0.2856	0.611
	hetero - homo.low	0.4318	0.0460	***<**0.0001**	0.3135	0.550
	hetero - homo.med	0.1028	0.0459	0.1135	-0.0153	0.221
	homo.high - homo.low	-0.0164	0.0632	0.9939	-0.1790	0.146
	homo.high - homo.med	-0.3454	0.0632	***<**0.0001**	-0.5079	-0.183
	homo.low - homo.med	-0.3289	0.0460	***<**0.0001**	-0.4472	-0.211

Synthesis

Connecting theory and empiricism is crucial to understanding widespread, generalizable mechanisms of species coexistence. This is especially important for species that engage in the ubiquitous species interaction called intraguild predation (IGP; the consumption of one’s competitor), which has historically experienced a disconnect between theory and empirical evidence. By developing and testing theory regarding various stabilizing mechanisms of IGP, we found that certain mechanisms are strong drivers of IGP stability and likely play fundamental roles in the ubiquity of IGP in nature. We found that adaptive foraging, including cannibalism, is a causal driver of long-term coexistence between IG predators and IG prey (Chapter 1). IG predators that had the ability to forage adaptively coexisted with their prey long-term, across a range of interaction strengths, supporting predictions from theory. Systems with IG predators that lacked adaptive foraging ability led to the exclusion of either IG predator or IG prey. To dive deeper into foraging preferences of IG predators, in Chapter 2 we developed theory regarding inducible trophic polymorphisms in the IG predator to help explain two phenomena commonly documented in the literature: cannibalism and strong resource competition in the IG predator. We found that preferential cannibalism is a mechanism of stable coexistence in IGP systems with trophic polymorphic, cannibalistic predators that have strong resource competition relative to their IG prey (Chapter 2). Zooming out to mechanisms on the spatial scale, in Chapter 3 we tested spatial IGP theory regarding spatial resource heterogeneity (SRH; the variable spatial distribution of resources). Supporting predictions from multiple bodies of theory, we found that SRH is a strong mechanism of long-term coexistence between IG predators and IG prey on both local and regional scales. SRH enabled rescue effects, which prevented population extinction and prolonged persistence in patches of given productivity level that otherwise experienced instability in homogeneous networks and isolated communities. The research in this dissertation provides strong support for otherwise-untested IGP theory, stimulating field studies and further theoretical development by providing biological validity to existing theories.