UNIVERSITY OF CALIFORNIA
RIVERSIDE

The Contribution of Population, Spatial and Temporal Structure to Persistence in the Development of a Stream Community

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Evolutionary, Ecology and Organismal Biology

by

Joshua Fabri Goldberg

December 2019

Dissertation Committee:
Dr. David N. Reznick, Chairperson
Dr. Kurt Anderson
Dr. Jeffrey Diez

The Dissertation of Joshua Fabri Goldberg is approved:

_____

_____

_____

Committee Chairperson

University of California, Riverside

Acknowledgements

This dissertation represents the dedication and hard-work of many – more than I could reasonably name – each of whom have played an integral role in the success of this research in ways big and small.

I would like to extend my heartfelt thanks to my advisor, David Reznick, who has unconditionally trusted me to flit about the globe in pursuit of my research flights of fancy. His support and enthusiasm have improved the quality of my research and made graduate school more enjoyable.

Many others at UCR have made a positive impact on my dissertation. I am grateful to committee members, Kurt Anderson and Jeff Diez, for their expertise and constructive feedback on my research. Derek Roff also made suggestions that improve the quality of the work and it presentation. I am also thankful for the support, feedback and camaraderie of the Reznick lab: Andrew Furness, Keenan Morrison, Cindy Dick, Kristin Edwards, Robert Prather, Samantha Levell and Jeffrey Arendt. I am forever indebted to Yuridia Reynoso, the Reznick lab manager, for coordinating specimens from the field and dissections. I owed a special thank you to the many undergraduates who have taken the lead in maintaining the lab, caring for fish and performing dissections.

Many people have made my time in Trinidad productive and enjoyable. Thank you to Brad Lamphere, who first introduced me to the joys and frustrations of working with *Rivulus*. I am also grateful to Ron Bassar for showing

me the ropes at the mesocosms, helpful feedback and many interesting discussions. Matt Walsh and Joseph Travis also provided wise guidance and feedback at various stages of my research program. Thank you to Doug Fraser for sparking many conversations that improved the quality of this research. Fellow graduate students, Tomos Potter and Shannon Beston, provided an essential sense of academic community at the field station in Trinidad. Much of my work relied upon the resources and infrastructure of The Guppy Project, expertly managed by Andy Van Alst, Mark Charran, Jack Torresdal and many more. I am eternally grateful to the small army of interns that have contributed to collecting much of the long-term data, especially the *Rivulus* crew members: Erica Sarro, Samuel Bedgood, Bridget Sloat, Richard Evans, Guillermo García Costoya and Jana Riederer. I would not have survived without them. I thank the Ramdeen family for making the mesocosms available. The Ramlal family, Mahase, Roan, Jogi and Rohini, put a roof over my head and made me feel truly at home in Verdant Vale.

Finally, I am appreciative of the generous funding I have received during my graduate studies. My research would not have been possible without the support of the National Science Foundation, UCR Provost Research Fellowship, Society for Study of Evolution Rosemary Grant Award, UCR Academic Senate Grant and Irwin M. Newell Graduate Research Award.

ABSTRACT OF THE DISSERTATION

The Contribution of Population, Spatial and Temporal Structure to Persistence in the Development of a Stream Community

by

Joshua Fabri Goldberg

Doctor of Philosophy, Graduate Program in Evolution, Ecology and Organismal Biology
University of California, Riverside, December 2019
Dr. David N. Reznick, Chairperson

Ecologically similar species frequently occur together, but theory places restrictions on the conditions that allow for the coexistence of these species. This gap between predicted and observed distributions has proven particularly large for species with intraguild predation relationships that mix competitive and predatory interactions. A variety of ecological mechanisms have been proposed to explain this pattern, but these explanations fail to consider the role of evolution in species persistence. My dissertation explores the joint contributions of ecological and evolutionary factors to the persistence of killifish, which co-occur with guppies, an intraguild predator of killifish. I exploit variation in the duration of killifish-guppy interactions and the resulting evolution to assess how

population, spatial and temporal structure influence killifish persistence as the community develops.

In chapter one, I show that killifish persist across a range of intra- and interspecific population densities and size structures in a killifish-guppy community, although the long-term dynamics of the killifish population depends upon guppy predation on neonate killifish, intraspecific density-dependence and the population size structure of each species. In chapter two, I find that killifish population densities declined after guppy introduction into previously killifish-only streams and that guppies, but not killifish, used pools more than alternative habitats. This differential habitat use correlated with an increase in the mean of the killifish size distribution and a decrease in killifish recruitment, but not differences in individual growth rates, in pools with abundant guppies. In chapter three, I demonstrate that killifish habitat use and spawning site selection depends upon evolutionary experience with guppies, although diel activity patterns remain consistent as killifish-guppy communities age. As a whole, these results suggest that size- and stage-structured interactions among killifish and guppies vary in intensity across habitats and times of day, and contribute to the persistence of killifish in the presence of intraguild predator guppies. However, the contributions of each of these mechanisms to killifish dynamics fluctuate with the adaptation of killifish and guppies to the evolving ecology of

the community. Species persistence may rely on a dynamic interplay among multiple ecological and evolutionary mechanisms.

Table of Contents

List of Figures

List of Tables

Prologue

In exploring the natural world, we encounter staggering biodiversity. The distribution of this diversity raises a key question: why do so many ecologically similar species occur together (Hutchinson 1959)? Coexistence theory defines the conditions required for the persistence of individual species in stable, coexisting communities. For species to coexist, each population must respond to intraspecific interactions more than interspecific interactions (Chesson 2000, Adler et al. 2007). This criterion allows the population of each species to increase when rare in a coexisting community. Despite the fundamental nature of coexistence, hundreds of empirical studies have not yielded any consensus around this key aspect of theory (Silvertown 2004, Siepielski and McPeek 2010).

Understanding coexistence has presented a particular challenge in species with intraguild predation (IGP) relationships. In IGP, two species compete for shared resources and one species serves as a predator of the other (Polis et al. 1989). Traditional theory suggests that this interaction should only allow both species to persist under limited conditions. In particular, both species coexist only at intermediate productivities of the basal resource and when the IG prey has superior competitive ability to the IG predator (Polis et al. 1989, Holt and Polis 1997, Mylius et al. 2001). The prospects for coexistence narrow even further when both species prey upon individuals of the other species (HilleRisLambers and Dieckmann 2003, Schellekens and van Kooten 2012).

Despite these predictions, IGP interactions commonly occur in nature (Arim and Marquet 2004, Janssen et al. 2007) and have been documented outside the expected range of conditions (Borer et al. 2003, Novak 2013).

Resolving the discord between IGP theory and observations has attracted considerable interest. A variety of mechanisms have been proposed that may enhance coexistence, including cannibalism (Rudolf 2007, Amarasekare 2008), alternative resources (Daugherty et al. 2007, Holt and Huxel 2007), shared predators (Hall 2011), adaptive predator foraging (Krivan 2000, Krivan and Diehl 2005), and spatial or temporal refuges (HilleRisLambers et al. 2006, Amarasekare 2008). These mechanisms act to reduce interspecific competition by concentrating intraspecific interactions and so expand the boundaries of coexistence in parameter space. However, these mechanisms do not eliminate the boundaries altogether, which limits their general utility in explaining coexistence under IGP.

An alternative approach introduces within species variation, relaxing the usual theoretical assumption that species serve as homogenous groups. This individual variation structures interactions within and between species, potentially altering the stability of the community. Intraspecific variation often takes the form of ontogenetic niche shifts, when individual development leads to differing resource use and needs, and predation risk (Werner and Gilliam 1984, Miller and Rudolf 2011a, Nakazawa 2015). These size- or stage-structured

interactions appear to play an important role in the dynamics of several empirical systems (Montserrat et al. 2008, Montserrat et al. 2012, Henkanaththegedara and Stockwell 2014, Toscano et al. 2016). However, introducing this additional structure to IGP interactions has mixed effects across models: in some cases expanding the parameter space supporting coexistence (Rudolf 2007, Abrams 2011, Hin et al. 2011), but not in others (Mylius et al. 2001, van de Wolfshaar et al. 2006, Yamaguchi et al. 2007). Thus, adding individual variation that structures interactions does not provide a panacea for explaining coexistence under IGP.

Adding individual variation also admits the possibility that the key traits governing species interactions might evolve. Limited work strongly implicates evolution as a potential stabilizing force in IGP interactions. Theory and replicated microcosm experiments have shown an expanded realm of potential population dynamics when a basal resource can evolve rapidly (Ellner and Becks 2011, Hiltunen et al. 2014a). These dynamics, however, do not necessarily promote stable coexistence nor do they address the evolution of the consumer species. Emerging IGP theory has shown that the evolution of foraging traits can produce novel coexistence outcomes (Patel and Schreiber 2015, Wang et al. 2016). IG prey evolution has been demonstrated in several natural systems by comparing traits from populations occurring with and without IG predators (Ingram et al. 2012, Urban 2013, Miller et al. 2015, Anderson and

Lawler 2016). These comparisons generally show that evolution operates in a fashion consistent with reducing the strength of interspecific interactions, which may promote coexistence. However, these comparative studies do not provide a test of evolutionary coexistence or examine the potentially important transient stages of IGP interactions that give rise to long-term coexistence (Amarasekare 2008, Maciel and Kraenkel 2017, Hastings et al. 2018). Evolutionary coexistence requires the interaction to persist long enough for one or both species to adapt. Thus, ecological responses may dominate the early phases IGP interactions before the development of longer-term evolutionary coexistence mechanisms.

In this work, I describe a system in which two species frequently co-occur as IG predators, which theory predicts should not persist. I conduct a series of experiments and observations to assess the contribution of size-structured interactions, spatial and temporal variation, and evolution to the persistence of one of these species. I characterize the changes in species demography upon initiation of IGP interactions and how ontogenetic, spatial and temporal structure facilitate persistence as the interaction develops.

Study System

In the streams of the Northern Range Mountains of Trinidad, the killifish *Rivulus hartii* occurs alone without predators in the headwaters (killifish-only: KO) and downstream locations with guppies (*Poecilia reticulata*) and large predators (killifish-guppy-predator: KGP) (Gilliam et al. 1993). Waterfalls

separate these locations into discrete communities, but guppies occasionally breach these waterfalls and invade KO habitats, leading to the formation of killifish-guppy (KG) communities.

In these newly formed KG communities, killifish and guppies have complex size-structured IGP interactions. Killifish compete with guppies, adult guppies prey upon newborn killifish and killifish prey upon guppies, predominantly of small size classes (Seghers 1973, Fraser and Lamphere 2013, Furness and Reznick 2015). Experiments with killifish and guppies further indicate that the relative competitive ability within and between species depends upon body size with large individuals generally having an advantage over small individuals (Bassar et al. 2016, Potter et al. 2019, Potter unpublished data, Goldberg unpublished data). Theory predicts that this sort of IGP interaction should be among the most difficult to sustain (HilleRisLambers and Dieckmann 2003, van de Wolfshaar et al. 2006, Schellekens and van Kooten 2012), yet KG communities can be found throughout the Northern Range Mountains. Moreover, coexistence is not merely historical, as guppies have been introduced and successfully established in previously KO reaches (Endler 1980, Reznick and Bryga 1987, Fraser and Lamphere 2013).

Where KG communities establish, several ecological changes take place. Once released from the predation pressure of KGP communities, guppy densities and body sizes increase, while individual growth rates decline (Rodd

and Reznick 1997, Reznick et al. 2012, Bassar et al. 2013, Travis et al. 2014). This pattern argues that KG guppies face strong intraspecific population regulation. At the same time, IGP interactions with abundant guppies appear to impose a cost on killifish. In the immediate aftermath of guppy establishment, killifish densities decrease, while body sizes increase (Fraser and Lamphere 2013). These changes in killifish population structure further alter the intraspecific interactions of killifish, leading to increases in individual growth rates (Gilliam et al. 1993, Walsh et al. 2011, Furness and Reznick 2015). Thus, the development of the KG community entails changes in both intra- and interspecific interactions that may modify the capacity of either species to persist.

The strength of interactions within the KG community likely have additional spatial and temporal dimensions. The stream environment consists of multiple habitat types, which vary in both abiotic (e.g. flow) and biotic characteristics (e.g., primary productivity) (Kohler et al. 2012). Guppies are most abundant in pool habitats (Reznick et al. *in review*), raising the possibility that distinctive habitat preferences or differential habitat use could enable the persistence of both species (Borer et al. 2004, Snyder et al. 2005). In a similar fashion, limited previous work suggests that killifish and guppies may have different diel activity patterns with guppies primarily active during the day and killifish during the night (Marshall et al. 2012). These contrasting habits may

reduce predatory or competitive interactions between species relative to intraspecific interactions. Thus, adding spatial and/or temporal axes to size-structured killifish-guppy interactions may open novel pathways for each of these species to persist.

Against this dynamic ecological backdrop of spatial, temporal and size-structured interactions, each species evolves a contrasting set of adaptations to life in KG communities that may further alter the prospects for persistence. Guppies rapidly evolve a suite of morphological, behavioral and life history adaptations to the KG environment (Reznick 1982, Reznick and Bryga 1996, Travis et al. 2014). These adaptations facilitate guppy persistence in the face of IGP interactions with killifish. KG guppies perform better than KGP guppies in the presence of killifish (Bassar et al. 2017a). However, killifish evolution does not have the same positive impact on killifish persistence in direct response to antagonistic IGP interactions with guppies (Bassar et al. 2017a). Instead, killifish life history appears to represent a response to the reduced intensity of intraspecific interactions. In laboratory experiments using second-generation individuals reared in a common environment, KG killifish outperform KO killifish when food is abundant but not when food is scarce (Walsh and Reznick 2010). Thus, KG killifish apparently adapt to the indirect effects of guppies reducing intraspecific competition for food. Evolution likely modifies spatial, temporal and size-structured intra- and interspecific interactions in this system and, in turn,

shapes the ultimate composition of the community

Research outline

This dissertation targets the overarching theme of structured interactions and evolution in facilitating the persistence of killifish in the presence of IGP interactions with guppies. To address this larger goal, I distill the problem into three parts. First, I use short-term experiments to examine the impact of ecological changes in the density and size structure of each species on killifish demography in newly formed KG communities. Second, I assess how the demographic consequences of these structured interactions unfold across alternative habitat types over 3-4 years after experimental guppy introduction in natural streams. Third, I investigate how stage-specific patterns of habitat use and temporal activity vary across an evolutionary gradient of killifish experience of IGP interactions. These aims synthesize the impact of population, spatial and temporal structure, and evolution on IGP interactions, and killifish demography and persistence.

Chapter 1: The role of structured interactions in the persistence and dynamics of resident species in an invaded community.

Abstract

Classic models of species interactions often neglect intraspecific variation, but recent theoretical and empirical work demonstrates that this variability structures intra- and interspecific interactions. These structured interactions raise the possibility that species persistence will depend on the density and distribution of traits within its population and those of interacting species. We explore this hypothesis in the context of a killifish (*Rivulus hartii*) community invaded by guppies (*Poecilia reticulata*). Upon first contact, these species have size-structured competitive and predatory interactions, and the density and size-structure of both species changes as the community moves toward a new equilibrium. Using replicated artificial stream experiments to parameterize integral project models, we examine how each of these changes in population structure alter the strength of these interactions and the ability of the killifish to persist. We show that killifish can persist across the range of ecological scenarios examined, but that the predicted equilibrium dynamics depended upon size-specific guppy predation at first contact, and the competitive effects of killifish density and population size structure of both species thereafter. While the greater effects of intraspecific density relative to interspecific density strongly suggest that killifish can persist, the approximately

equivalent effects of changes in intra- and interspecific size structure imply that distribution of traits in each species influences the long-term dynamics of killifish populations. We conclude that understanding species persistence and community dynamics in response to structured interactions requires considering both the density and frequency of traits within each species.

Introduction

The immigration of a new species into a community raises the question as to how each species will respond to the novel interactions that occur. Coexistence theory provides a framework for understanding the persistence of the immigrant and resident species. For species to stably coexist, intraspecific interactions must regulate the population of each species more strongly than interspecific interactions (Chesson 2000, Adler et al. 2007). Thus, the population of each species can increase when rare in a coexisting community. Alternatively, if the interspecific interactions limit populations more than intraspecific interactions, then the species with greater sensitivity to interspecific interactions will be excluded from the community. Despite the broad importance of understanding the mechanisms that generate coexistence, hundreds of empirical studies have not provided convincing support for this fundamental condition (Silvertown 2004, Siepielski and McPeek 2010).

While this lack of consensus may derive in part from the difficulty of testing coexistence conditions even in simple communities (Chesson 2000,

Adler et al. 2007), another limitation may arise from the treatment of species as homogenous groups. Many species exhibit substantial variation in resource use, and interactions with conspecifics and heterospecifics (Bolnick et al. 2003, Araújo et al. 2011, Bolnick et al. 2011). This variation between individuals often structures interactions, opening new avenues for species coexistence (or exclusion). Moreover, the key traits governing species interactions may not remain fixed over an individual's lifetime when organisms undergo an ontogenetic niche shift, and use or require different resources over their development (Werner and Gilliam 1984, Miller and Rudolf 2011b, Nakazawa 2015). For example, dragonfly larvae and adults occupy discrete aquatic and terrestrial niches, respectively, with the diet of larvae further depending upon body size and instar number (Corbet 1980). Thus, the outcome of competition depends upon both the density of each species, and the frequency of stages and/or sizes within each species.

Theory provides some guidance as to how these structured competitive interactions shape the composition of communities. In models with two competing species with two discrete life stages (e.g., juveniles and adults), coexistence depends upon the extent of changes in the niche of each life stage, the relative competitive ability of each species during the different stages and the way each stage limits the population growth of each species (Loreau and Ebenhoh 1994, Moll and Brown 2008, De Roos and Persson 2013). Thus, the

two species can coexist when a different life stage limits the population of each species and the limiting life stage in each species outcompetes that of the other species. Incorporating multiple life stages and/or continuously varying traits allows even more dynamic conditions for coexistence to emerge (Bassar et al. 2017b). However, neither intraspecific variation in general nor ontogenetic niche shifts in particular provide a panacea for the problem of coexistence. Variation within species may either enhance or diminish the prospects for species coexistence (Bolnick et al. 2011, Lankau 2011, Miller and Rudolf 2011b) and coexistence depends upon the population structure and density of the competitors, as well as the broader ecological context (Hart et al. 2016, Bassar et al. 2017b). Thus, the density and/or distribution of traits of an immigrant and/or a resident species in a newly formed community may impact the ability of both species to persist.

We evaluate this hypothesis using the freshwater stream fish communities of Trinidad as a model. In these streams, persistent communities of killifish (*Rivulus hartii*) and guppies (*Poecilia reticulata*; killifish-guppy: KG) occur across the Northern Range Mountains (Endler 1978, Gilliam et al. 1993). In these communities, killifish and guppies have antagonistic interactions. Guppies introduced into previously KO streams lead to immediate declines in killifish density that remain over the long-term (Gilliam et al. 1993, Fraser and Lamphere 2013, Furness and Reznick 2015). Similarly, simple competition experiments

suggest that killifish negatively impact the growth of guppies (Gilliam et al. 1993, Fraser and Lamphere 2013). Despite these mutually antagonistic interactions, guppies have successfully established in all experimental introductions into previously killifish-only (KO) communities (Endler 1980, Reznick and Bryga 1987, Fraser and Lamphere 2013, Dick et al. 2018), suggesting that coexistence in KG communities is not merely probabilistic. While both killifish and guppies show a suite of evolutionary adaptations to life in KG communities over the long-term (Reznick 1982, Reznick and Bryga 1996, Walsh and Reznick 2009, 2010, 2011, Travis et al. 2014), these evolutionary changes cannot explain the persistence of killifish or guppies at first contact. Understanding the persistence of each species to reach any evolutionary endpoint requires examining interactions during the initial phase of KG community establishment.

Killifish and guppies have size-structured intra- and interspecific interactions. Upon initially colonizing KG habitats, guppy diets contain primarily aquatic invertebrates with relatively little algae or detritus (Zandonà et al. 2011, Sullam et al. 2015, Zandonà et al. 2015), leading to declines in invertebrate density and increases in algal biomass (Bassar et al. 2010, Bassar et al. 2012, Simon et al. 2017). Killifish have primarily insectivorous diets, including a range of both aquatic and terrestrial insects (Fraser et al. 1999), suggesting that killifish and guppies may have intense competitive interactions. Moreover, the result of these interactions likely depend upon the body sizes of the competitors.

Experiments with guppies and killifish show that their relative competitive abilities depend upon body size, such that large individuals generally have an advantage over small individuals (Bassar et al. 2016, Potter et al. 2019, Potter unpublished data, Goldberg unpublished data). Furthermore, large individuals of each species may occasionally consume small members of the other species (Seghers 1973, Mattingly and Butler IV 1994, Fraser and Lamphere 2013, Furness and Reznick 2015). Thus, the population consequences of killifish-guppy interactions likely depend upon both the number and size frequency distribution of each species.

The population density and size structure of killifish and guppies vary as the KG community develops. In the lowlands, guppies and killifish co-occur with many other species, including large predators (killifish-guppy-predator: KGP communities). Occasionally, small groups of guppies manage to breach the barrier waterfalls separating KGP and KO communities, leading to the formation of KG communities in intermediate reaches of streams (Alexander et al. 2006). Thus, initial guppy population density is low and body sizes are likely small because abundant predators in KGP habitats increase mortality and prevent guppies from reaching large body sizes (Reznick et al. 1996, Rodd and Reznick 1997, Reznick et al. 2001). Released from predation pressure, guppies in KG communities reach high density and grow to larger body sizes (Reznick et al. 1996, Rodd and Reznick 1997, Reznick et al. 2001). At the same time as these

guppy population dynamics unfold, killifish population density and size structure also change in KG areas. After guppy introduction into a previously KO community, killifish population density decreases, while mean body size increases (Fraser and Lamphere 2013), although only declines in density, and not differences in killifish population size structure, continue over the long-term (Gilliam et al. 1993, Furness and Reznick 2015). The nature of the killifish-guppy interaction suggests that each of these changes in population density and size structure impact the persistence of the KG community, but how do each of these shifts contribute to the outcome?

We explore the impact of these changes in intra- and interspecific population density and size structure on the equilibrium population growth rate and mean body size of killifish in a newly formed KG community. Coexistence theory predicts that the effects of varying intraspecific density and size structure should exceed the corresponding effects of interspecific density and size structure. Similarly, we expect the mean of the equilibrium size distribution should respond most strongly to combinations of density and size structure in each species that lead to severe competition. In response to this competition, we predict that the mean size will shift towards those sizes that experience relatively less intense antagonistic interactions.

We test these predictions using factorial artificial stream experiments pairing KO killifish with KGP guppies with varying density and size structures of

each species. In these experiments, we parameterize our experimental populations to capture the effects of competition across a broad range of body sizes in both species, but exclude the smallest size classes of killifish vulnerable to guppy predation. This approach allows us to attribute any killifish responses to competition without any contribution of guppy predation. We then develop integral projection models (IPMs; Easterling et al. 2000) to assess the response to the treatments in terms of the asymptotic population growth rate and the mean of the stable size distribution. Each of these measures provides an index of killifish population density and size structure dynamics. The population growth rate, in particular, offers an assessment of population persistence with values greater than 1 predicting growing, stable populations and values less than 1 indicating declining populations at risk of extinction. Finally, we use size-specific perturbations of survival to explore how a range of plausible guppy predation levels impact killifish populations. This approach provides an approximate means of assessing how guppy competition and predation contribute to killifish population dynamics across the varying densities and size structures of each species as KG communities develop.

Methods

Artificial Stream Preparation

The experimental facility had 16 artificial streams or mesocosms located adjacent to a natural stream in the Arima valley, Trinidad, West Indies. To

approximate the lighting conditions of a natural KG stream, we covered the mesocosms with a commercial grade shade-cloth supported by a steel frame structure. Each 3 m x 0.5 m mesocosm was constructed of cinder-block and mortar with a flow-through channel design. Water for the mesocosms came from an uphill section of a spring-fed stream, and passed through PVC pipes and 2 settling tanks. The final settling tank had 8 independent 3/4-inch outlets which allowed connections to commercial grade garden hoses. These hoses carried water to each set of 2 mesocosms and we subdivided the water from each hose to feed both channels with ball valves at the head of each mesocosm. These ball valves further allowed us to adjust the flow rates in each mesocosm so that each received equal flow. Water exited the mesocosms through a mesh covered drain at the foot of each channel. We attached a gooseneck fitting to the drain pipe to set the water level of each mesocosm at 15 cm.

We prepared the interior of the mesocosms to mimic the conditions of a natural stream. First, we covered the bottom of each mesocosm with a mixture of sand and gravel from local watersheds. We flushed this material with water to remove fine silts and distributed it evenly across the benthic area of each mesocosm. Next, we allowed water to flow at a constant rate for about 1 week to allow the accumulation of diatoms and fine benthic organic matter delivered through the water supply. After sufficient organic material had accumulated, we

collected invertebrates and coarse organic material from the adjacent natural stream. To do so, we used kicknets with 250 μm mesh over an area approximately equal to the benthic area of all mesocosms. We placed kicknet samples into a plastic sorting tray to remove any fish and all large predatory odonate larvae, since they can potentially consume the smallest size classes of killifish or guppies and alter experimental treatments. We pooled the remainder of the kicknet sample into buckets until we had completed sampling the prescribed area of stream. We then homogenized the mixture of coarse organic material and invertebrates and distributed it evenly among the mesocosms. We left the mesocosms with flowing water for an additional week to allow invertebrates to acclimate and distribute themselves in the mesocosms.

We captured experimental guppies from KGP sections and killifish from KO reaches of the Aripo River 10-14 days after water began to flow in the mesocosms. We transported all fishes to our laboratory facility near the mesocosms, where we housed them in glass and acrylic aquaria. Approximately 24-48 hours prior to the beginning of the experiment, we anesthetized experimental fish in a buffered MS-222 solution, measured wet mass and length (standard length [SL] for guppies, total length [TL] for killifish), and marked each individual with subcutaneous injections of colored elastomer (Northwest Marine Technologies, Shaw Island, WA) that uniquely identified each individual. We then opportunistically assigned each individual to a treatment replicate (mesocosm)

to fulfill the desired density and size structure. When all individuals had recovered from anesthesia, we transported fishes to the mesocosm facility and released them into the designated mesocosm to begin the experiment.

Experimental design

We used a factorial design with four treatment factors: KGP guppy density and size structure, and KO killifish density and size structure (Table 1.1). Each treatment factor had two levels. For guppy density, low density treatments contained 8 individuals, while high density treatments contained 16 individuals. For guppy size structure, small size structured populations had a mean ± S.D. of 13.8 ± 3.31 mm SL and large size structured populations had a mean ± S.D. of 15.5 ± 4.67 mm SL. Similarly, for killifish density, low density treatments contained 6 individuals and high density treatments contained 12 individuals. For killifish size structure, small size structured populations had a mean ± S.D. of 40.9 ± 14.44 mm TL, while large size structured populations had a mean ± S.D. of 44.3 ± 17.23 mm TL. We chose these densities and size structures to represent observed differences in density and size structure between KGP and KG guppy populations (Rodd and Reznick 1997, Reznick et al. 2001), and between KO and KG killifish populations (Gilliam et al. 1993, Fraser and Lamphere 2013, Furness and Reznick 2015).

To allow adequate replication of treatments, we implemented a fractional factorial experimental design. Treatment 1 captures the state of a typical KO

community prior to guppy invasion in which killifish occur at high density with a small size structure. This treatment includes no guppies. Treatments 2 through 8 assess the competitive interactions among KO killifish and KGP guppies. For these treatments, our design assesses the effects of manipulating the density and size structure of one species against a common backdrop of density and size structure in the other species (Table 1.1). We chose a low density, small size structured population as this backdrop, since we expected a relatively small competitive effect of this treatment combination, so that any response would reflect differences in the density and/or size structure of the species in which these factors varied.

Demographic response and statistical analysis

We left guppies and killifish undisturbed in the mesocosms for a 28-day experimental period. During this time, we monitored and adjusted the flow rates in all mesocosms to ensure equal flow, removed fishing spiders and cleaned any debris from the drain pipe. At the completion of the 28-day experiment, we captured all fishes using aquarium dipnets and returned them to the laboratory facility. We then euthanized them with a lethal dose of MS-222, measured wet mass and length as before, and persevered all specimens in 10% formalin. We then performed dissections following standard procedures (Reznick and Endler 1982, Reznick 1982, Walsh and Reznick 2008, Reznick et al. 2012, Bassar et al. 2013) in our laboratory at the University of California, Riverside to obtain

information about the reproductive status of mature females, including the number and dry mass of mature killifish oocytes. We repeated the experiment twice in January and March 2016 to achieve four-fold replication of each treatment.

We transformed dry mass of oocytes obtained from killifish dissections into an approximate length at hatching using two intermediate regressions. First, we used data from a previous experiment that measured the dry mass of both freshly laid eggs and hatchlings from the same female (Walsh and Reznick 2008) to construct a no-intercept linear regression of hatchling mass on egg mass. This regression accounts for changes in mass over the course of egg development and allowed us to predict the dry mass of hatchlings in this experiment. We then estimated the approximate length of these hatchlings by fitting a log-log regression of total length on dry mass to killifish from the experiment. These steps place offspring size on the same scale of measurement as fish (total length) and allow us to estimate the transition between these killifish life stages.

We estimated the effect of the treatments on killifish growth, survival, and number and size of offspring, using generalized linear mixed models with appropriate link functions and error distributions. For growth, we used a piecewise linear mixed model with normally distributed errors. The piecewise model allows us to account for the complex observed pattern of killifish growth

over ontogeny. Juvenile growth rates rapidly decelerated with increasing body size, while adult growth rates declined much more slowly with increasing body size. In our piecewise model, the slope of growth rate with body size differs on either side of a breakpoint to account for these two distinct phases of growth. For survival, we employed a model with a binomial error structure and logit link function. For fecundity, we used a hurdle negative binomial model that decomposed the number of mature eggs produced during the experiment into two processes: probability of reproduction (having at least one mature oocyte) and the number of eggs conditional on reproducing. The probability of reproduction (hurdle) component of the model used a binomial error structure with logit link function, and fecundity conditional on reproduction used a negative binomial error structure with log link function. Finally, we used a model with normally distributed errors for the transformed offspring size.

For each analysis, we began with a full model containing terms for initial TL (in cm and centered at the mean of all individuals), treatment and their interaction, as well as a random intercept for mesocosm number. In the growth model, we considered length $\times$ treatment interactions with respect to both the juvenile and adult phases of growth. Similarly, for fecundity, we included interaction effects in both the hurdle and negative binomial facets of the model. The random intercept of mesocosm accounted for random variation among channels within and across replicates of the experiment.

We fit these models using STAN (Carpenter et al. 2017) via the brms package (Bürkner 2017) in R (R Core Team 2018). We specified weakly informative prior distributions to provide some domain knowledge about the anticipated scale of effects and regularize the posterior distributions (Gelman et al. 2017). Preliminary investigation indicated that our scaling and centering of initial TL placed the range of variation in length on a similar scale as that of the categorical treatment variable. We, therefore, defined somewhat generic priors on the population-level effects of initial TL, treatment and their interaction. For models with Gaussian or negative binomial error structures, we adopted $N(0, 1^2)$ prior distributions on the population-level effects to capture our belief that the experimental factors would have a relatively small effect on the observed responses. For models with binomial error structures and logit links, we applied $N(0, 2.5^2)$ prior distributions on population-level effects to cover values from approximately 0.01 to 0.99 on the response scale. In all models, we used $N(0, 1^2)$ prior distributions on the random intercepts to reflect a conservative view that differences in the average response across mesocosms should be relatively small. Prior distributions on the model intercept, which represents the grand mean across all population-level effects, varied across models. We used a $N(0, 2.5^2)$ prior for the model of growth, a $t_3(0, 10^2)$ prior for the model of survival, a logistic$(0, 1^2)$ prior for the probability of reproduction, a $t_3(-2, 10^2)$ for the negative binomial component of fecundity conditional on reproducing, and $t_3(1, 10^2)$ for

the offspring size model. For models with family-specific variance or dispersion terms, we specified $t_3(0, 10^2)$ prior distribution on the residual standard deviation, σ, of the Gaussian growth and offspring size models, and a $\Gamma(0.01, 0.01)$ prior distribution on the shape parameter of the negative binomial model of fecundity conditional on reproduction. For each model, we ran 12 chains with 2,000 total iterations per chain, the first 1,000 of which we discarded as warm-up.

After fitting the model, we evaluated model sampling convergence on the posterior distribution by inspecting parameter trace plots and the Gelman-Rubin convergence diagnostic, $\hat{R}$ (Gelman et al. 2013). We also monitored a several diagnostics specific to the Hamiltonian Monte Carlo methods used by STAN (e.g., divergent transitions, tree depth and kinetic energy) and tuned sampling accordingly. For converged models, we used posterior predictive checks to assess discrepancies between the model and the observed data, paying particular attention to any apparent residual heteroscedasticity. These checks revealed a strong pattern in the residuals of the growth model with initial TL, so we expanded our growth model to incorporate a covariate of initial TL on σ, using a log link function. We placed a $N(0, 1^2)$ prior distribution on this covariate. Our investigation of residual heteroscedasticity revealed no other strong deviations from model assumptions.

Having validated model assumptions, we then assessed the relative support for models with length × treatment interactions as compared to models with additive effects of length and treatment. For models that included interactions in multiple components (growth and fecundity), we considered all combinations of interaction and additive model components. We compared models using Pareto-smoothed importance sampling (PSIS) leave-one-out (LOO) cross-validation (Vehtari et al. 2017) and Bayesian stacking weights (Yao et al. 2018) to compare the predictive performance of each model parameterization. In computing the PSIS LOO information criteria, the Pareto k diagnostics indicated some data points were strong outliers (i.e., $k > 0.7$) that would negatively impact the reliability of model comparisons. To improve reliability, we substituted the PSIS LOO by sampling from the LOO posterior distribution with respect to each problematic data point. In practice, PSIS LOO and stacking weights present similar output as AIC and AIC weights (Burnham and Anderson 2002), but incorporate some important advantages. For example, model comparisons based upon PSIS LOO include standard errors. Likewise, stacking weights jointly optimize the estimated predictive performances of each model and the relative performance of these models. As a result, stacking weights perform well in scenarios with similar models and/or potentially irrelevant covariates, as we might expect if interaction terms play a small role in

model predictions. On the basis of these comparisons, we removed unsupported interactions from further analysis.

Integral Projection Models

After settling upon the best model formulation for each vital rate, we moved to account for the correlations across vital rates. To do so, we extend the Bayesian bootstrapping procedure of Rubin (1981) to incorporate the hierarchical sampling design of the experiment. The Bayesian bootstrap generalizes classical bootstrap methods by adopting a continuous set of sampling probabilities or weights on the observations. Although the Bayesian bootstrap comes with very strong assumptions (i.e., only observed combinations of values for each vital rate treated as possible), this method does provide a valid and readily implemented alternative to other Bayesian methods of accounting for demographic correlations, such as multivariate models that explicitly include covariances across vital rates (Gelman et al. 2013, Bürkner 2017), or the “hierarchical centering” approach of Evans et al. (2010).

One derivation of the standard Bayesian bootstrap is to sample the weights on each observation from the posterior distribution of a Dirichlet process, letting the concentration parameter go to zero (Gasparini 1995). To incorporate the structure of our data, in which individuals occur within mesocosms and mesocosms receive different treatments, we sample from the posterior of a hierarchical Dirichlet process (Teh et al. 2006), where the

concentration parameters at each level of the hierarchy go to zero. Thus, for each bootstrap iteration, we draw a probability weight for each channel and for each individual within each channel from independent Dirichlet distributions. Multiplying the weight for each mesocosm and the weight for each individual within that mesocosm gives the overall weight associated with each observation in the dataset. We then scale these probabilities to frequencies given the total sample size. We use these frequencies as the weights in weighted generalized linear mixed models with the best model parameterization fit by restricted maximum likelihood techniques for Gaussian models or maximum likelihood estimation for models with non-Gaussian response distributions (Bates et al. 2015, Brooks et al. 2017). We repeated this procedure 10,349 times to characterize the posterior distribution of the model parameters and the covariance of parameters across demographic rates.

For each experimental treatment and bootstrap iteration, we constructed an IPM that allowed us to characterize the differences in killifish population growth rate and stable size distributions among treatments or treatment combinations. IPMs represent discrete time, structured population models, where the structure depends upon a continuous trait (Easterling et al. 2000). We use body size (z) as this continuous trait, measured in terms of TL (in cm). Our IPM of killifish reflects a single sex (female only), two stage (eggs, fish) IPM. While female killifish females produce eggs continuously (Walsh and Reznick

2008, 2010, 2011), eggs hatch after approximately two weeks. Given the developmental schedule of eggs, we partition the overall projection kernel for the experiment into a composite of two, 14-day projection kernels. While this approach represents a simplification of egg production, it did not alter population growth rates or the means of the stable size distributions in test comparisons of models with discrete and continuous reproduction (Bassar pers comm). The 14-day projection equations for each stage are:

$$n_e\left(z', t+\frac{1}{2}\right) = \frac{1}{2}F(z)S(z)n_f(z,t),$$

$$n_f\left(z', t+\frac{1}{2}\right) = \int D(z'|z)vn_e(z,t) + G(z'|z)S(z)n_f(z,t)dz,$$

where the subscripts on the population size functions (n) denote the egg stage (e) and the fish stage (f). The population size functions, $n(z,t)$, give the density of individuals in a stage at the beginning of the experiment. Thus, integrating $\int_L^U n_f(z,t)dz$ gives the number of fish between L and U cm TL at the beginning of the experiment. $F(z)$ is a continuous function representing the number of offspring produced by an individual of length z, and is the product of 1-$B(z)$ and $M(z)$, where $B(z)$ is the probability of producing zero eggs (not breeding) as a function of body size, z, and $M(z)$ is the number of eggs produced by an individual of size z. $S(z)$ yields the probability of an individual of length z surviving the time interval as a continuous function. $D(z'|z)$ is a conditional probability density function representing the distribution of offspring lengths, z', produced

from eggs of females of size z at the beginning of the time interval. Similarly, $G(z'|z)$ is the conditional probability function that describes growth transitions from length z to z' during the time interval. Finally, v reflects the probability of surviving from the egg stage to hatch. We set this parameter to 0.75, since we have no information about egg survival. Setting v constant means that this transition does not influence the outcome of treatment contrasts.

We analyzed the continuous trait IPMs by using the midpoint rule of calculus to transform the projection equations to high dimensional matrices. We used minimum and maximum sizes of 0 and 15 cm total length, respectively. In practice, killifish never reach these extreme sizes, which we adopt as the limits of integration to prevent individuals on the boundaries from being evicted from the population (Williams et al. 2012). We employed 450 mesh points for each stage in our approximation of the IPM to yield the projection matrix, $\boldsymbol{A}$. We then construct the composite projection kernel, $\bar{\boldsymbol{A}} = \boldsymbol{AA}$, to approximate the IPM over the full 28-day experiment. We calculate the asymptotic population growth rate by taking the dominant eigenvalue of $\bar{\boldsymbol{A}}$, λ. Similarly, we estimate the stable size distribution by finding the dominant eigenvector of $\bar{\boldsymbol{A}}$, which we scale sum to 1. We then take the mean of the stable size distribution, $\bar{z}$, by multiplying the stable size distribution by the body sizes (mesh points), assuming eggs have length of 0, and taking the sum.

We used *a priori* contrasts to evaluate how each vital rate, λ and $\bar{z}$ differed among combinations of experimental treatments (Table 1.1). The first contrast compares a high density, small size structured killifish population in the presence and absence of a low density, small size structured guppy population. This contrast reflects the expected effect on killifish of the initial colonization of a previously KO community. The next set of three contrasts examine the interspecific effect of varying guppy density, size structure and their interaction on killifish (with a low density and small size structure population). The final three contrasts examine the intraspecific effect of varying killifish density, size structure and their interaction on killifish in the presence of a low density, small size structured guppy population.

We then compared the magnitude of the competitive impact of varying density, size structure and their interaction on killifish dynamics. This comparison provides a test of the canonical condition for coexistence: that intraspecific effects must exceed interspecific effects to stabilize interactions. To perform this test, we took the difference of the absolute values of the corresponding effects. For each species, the high density treatment reflects a doubling of the low density treatment, so the relative changes in density are equivalent and directly comparable. However, the changes in size structure reflected different relative alterations in each species, so we scaled the size structure and interaction effects of guppies to reflect the same relative change in

body length as killifish. For the size structure effects in each species, we calculated the change in median body size between small and large size structured treatments standardized by the pooled standard deviation. This value represents the relative treatment sizes for guppies and killifish. The ratio of the killifish to guppy treatment sizes acts as a multiplier to transform the guppy effect so that it reflects the same relative change in the median as imposed on killifish populations. We repeat this procedure for the interaction effects to determine the size structure contribution to the relative differences between small and large size structured populations at high and low density. We then take the average of the size structure effect and the 1:1 density effect to arrive at an overall interaction scaling of killifish to guppy treatments.

We calculated these contrasts for each of the bootstrap replicates to construct the posterior distribution of each of these quantities. We examined these distributions to assess how the density and size structure of each species impacted killifish population dynamics. To better understand how each of the vital rates contributed to the differences in λ among treatments or groups of treatments in the seven principal contrasts (Table 1.1), we performed a Life Table Response Experiment (LTRE) analysis (Caswell 1989, 2001). This analysis decomposes the observed differences in λ into the contributions from each vital rate. The first-order approximation for this decomposition for each contrast and vital rate is:

$$\sum \left[\left(vec\, \boldsymbol{V_i} - vec\, \boldsymbol{V_j} \right) \circ \frac{\mathrm{d}\lambda}{\mathrm{d}\, vec^T \overline{\boldsymbol{V}}} \right],$$

where *vec* $\boldsymbol{V_i}$ and *vec* $\boldsymbol{V_j}$ are the vector transformed demographic rate matrices for treatments *i* and *j* and $\frac{\mathrm{d}\lambda}{\mathrm{d}\, vec^T \overline{\boldsymbol{V}}}$ represents the sensitivity of the asymptotic population growth rate to the vector transformed mean demographic rate matrix. The ∘ operator indicates to take the Hadamard product between the differences in the vectorized vital rate matrices and sensitivity. When the contrasts compare more than 2 treatments, $\boldsymbol{V_i}$ and $\boldsymbol{V_j}$ represent the mean demographic rate matrices across treatments. The sensitivity of λ to a demographic rate can be expanded using the chain rule to:

$$\frac{\mathrm{d}\lambda}{\mathrm{d}\,\mathrm{vec}^T \boldsymbol{V}} = \frac{\mathrm{d}\lambda}{\mathrm{d}\,\mathrm{vec}^T \overline{\boldsymbol{A}}} \frac{\mathrm{d}\,\mathrm{vec}\,\overline{\boldsymbol{A}}}{\mathrm{d}\,\mathrm{vec}^T \boldsymbol{A}} \frac{\mathrm{d}\,\mathrm{vec}\,\boldsymbol{A}}{\mathrm{d}\,\mathrm{vec}^T \boldsymbol{V}}.$$

$\frac{\mathrm{d}\lambda}{\mathrm{d}\,\mathrm{vec}^T \overline{\boldsymbol{A}}}$ is the sensitivity of the asymptotic population growth rate to the matrix elements of $\bar{\boldsymbol{A}}$, $\frac{\mathrm{d}\,\mathrm{vec}\,\overline{\boldsymbol{A}}}{\mathrm{d}\,\mathrm{vec}^T \boldsymbol{A}}$ is the sensitivity of the elements in $\bar{\boldsymbol{A}}$ to the elements of $\boldsymbol{A}$, and $\frac{\mathrm{d}\,\mathrm{vec}\,\boldsymbol{A}}{\mathrm{d}\,\mathrm{vec}^T \boldsymbol{V}}$ is the sensitivity of the matrix elements of $\boldsymbol{A}$ to the elements of the elements of the vital rate matrix $\boldsymbol{V}$.

Perturbation analysis

Evolutionary comparisons of KO and KG communities suggest that guppy predation shapes killifish life histories by reducing the density of killifish (Walsh and Reznick 2009, 2010, Walsh et al. 2011, Furness et al. 2012), although these studies cannot exclude competition as a plausible explanation.

Similarly, predation trials conducted in experimental aquaria indicate that guppies can have a significant negative impact on the survival of neonate killifish (Fraser and Lamphere 2013, Furness and Reznick 2015), but these results may not capture the impacts of guppy predation in more realistic ecological settings. These trials do suggest, however, that only the smallest size classes of killifish (< 7 mm TL) are vulnerable to predation by wild-type guppies (Furness and Reznick 2015). Moreover, our experimental populations did not include any of these vulnerable neonates since they are rarely seen or captured in nature. Therefore, the observed treatment responses reflect the competitive, but not predatory, impact of guppies.

We used perturbation analyses to explore how guppy predation might influence the population dynamics of killifish. To do so, we imposed a constant reduced survival probability on individuals below a threshold size in all treatments. We determined this threshold size by examining the extremes (± 3 S.D.s) of the offspring size and growth kernels to find a value (11 mm TL) that would include nearly all neonates while excluding nearly all individuals that survived the initial 14-day time step after hatch. We take this approach to best match the likely window of vulnerability in nature. We explored a range of reduced survival probabilities (0.25, 0.4 and 0.5) for these size classes to bracket the potential impact of predation. For each of these neonate survival probabilities, we constructed and analyzed the IPM as before, excepting the

LTRE analysis since all differences between the original and perturbed kernel can be attributed to survival below the threshold size.

We considered a range of plausible scenarios in calculating the seven main contrasts with the perturbed IPMs (Table 1.1). For the guppy invasion contrast, we compared the unperturbed IPM estimates for the treatment that did not contain guppies (and hence that would not suffer guppy predation) with each of the three perturbed IPM estimates in the corresponding treatment with guppies. For the set of three guppy population structure comparisons, we calculated contrasts where all treatments received the same perturbation for each of the reduced survival probabilities (0.25, 0.4, and 0.5), as well as guppy density-dependent survival probabilities (survival = 0.5 for low guppy density, survival = 0.25 for high guppy density), guppy size structure-dependent survival probabilities (survival = 0.5 for small guppy size structure, survival = 0.25 for large guppy size structure), and guppy density- and size structure-dependent survival probabilities (survival = 0.5 for low density, small size structure guppies, survival = 0.4 for high density, small size structure and low density, large size structure guppies, and survival = 0.25 for high density, large size structure guppies). Likewise, for the three killifish population structure comparisons, we calculated contrasts where all treatments received the same perturbation for each of the reduced survival probabilities (0.25, 0.4, and 0.5), as well as killifish density-dependent survival probabilities (survival = 0.5 for high killifish density,

survival = 0.25 for low killifish density), killifish size structure-dependent survival probabilities (survival = 0.5 for large killifish size structure, survival = 0.25 for small killifish size structure), and killifish density- and size structure-dependent survival probabilities (survival = 0.5 for high density, large size structure killifish, survival = 0.4 for low density, large size structure or high density, small size structure killifish, and survival = 0.25 for low density, small size structure killifish). These contrasts among the perturbed IPM statistics allow us to capture the population dynamics of killifish under a range of plausible relationships between guppy predation and the population structure of each species. Since we have no information about the form of these relationships in nature and observed very little variation in the killifish response among the different guppy predation scenarios, we limit ourselves to considering comparisons among equal survival probability perturbations for the intra- vs. interspecific scaled contrasts.

Results

The two experimental replicates initially included 264 killifish of which 244 survived the 28-day treatment periods. We recorded usable growth increments from 240 of these individuals, excluding data from 4 survivors that escaped prompt capture at the end of the replicates. Of those 240 survivors, we determined that 170 individuals were either potentially breeding females or immature. We used the observed number of mature oocytes from these

individuals to inform the model of fecundity. From the potentially fecund females, we recorded the average mature egg dry mass (offspring size) from 49 killifish.

Our Bayesian model selection criteria revealed little uncertainty in the best model parameterization of each vital rate. For growth, survival and offspring size, additive models had lower PSIS LOO information criteria than models including a length $\times$ treatment interaction, and the standard errors of these differences indicated they were meaningful (Table 1.2). Likewise, the stacking weights provided no support for any interactions in these vital rate models (Table 1.2). Given these decisive criteria, we removed these interaction terms from further consideration. Fecundity presented the sole vital rate, where an interaction term received some support. In this model, the length $\times$ treatment interaction in the negative binomial conditional component of the model received some weight (0.15) and the difference in PSIS LOO and SEs (4.0 ± 3.6) suggested that this model did not suffer from significantly worse predictive ability, although both of these metrics did favor the additive model (Table 1.2). To admit this minor uncertainty in the fecundity model specification, we considered both parameterizations in the Bayesian bootstrap of the vital rate models to evaluate the IPM and the experimental contrasts. Since the predicted differences from these alternatives proved minor, we present only results from

IPMs built with the better supported additive models (see Table 1.3 for parameter estimates).

Guppy Invasion

We found limited evidence for a guppy competitive effect upon first invasion on killifish asymptotic population growth rate (λ) or the mean of the stable size distribution ($\vec{z}$). While adding a low density, small size-structure guppy population to a high density, small size structured killifish population decreased λ (median: -0.20, 95% quantile interval [QI]: -0.55-0.06) and increased $\bar{z}$ (contrast: 0.12 cm, 95% quantile interval [QI]: -0.39-1.03), neither of these changes proved significant (λ: $p = 0.136$; $\bar{z}$: $p = 0.477$; Figs 2). This moderate reduction in λ with the addition of guppies reflected complementary decreases in growth, fecundity and, especially, survival (Fig 1.3). Despite these effects on overall population growth rate, we found no significant differences in any of the vital rates between these two treatments at the mean body size (all $p > 0.05$, Table 1.4, Fig 1.1).

Guppy Population Structure

The guppy density, size structure and interaction contrasts provided weak evidence for these effects on killifish λ or $\bar{z}$. Increasing guppy density led to almost no change in λ (median: -0.01, 95% QI: -0.82 – 0.28, $p = 0.839$) or $\bar{z}$ (median: 0.03 cm, 95% QI: -0.85 – 0.81, $p = 0.953$; Fig 1.2). The minor decrease in population growth rate across guppy density treatments primarily reflected

the effects of reduced growth (Fig 1.3), although we found no significant differences in any of the vital rates (all $p > 0.05$, Table 1.4, Fig 1.1).

In contrast, moving from a small to a large size structured guppy population produced a moderate decrease in λ (median: -0.32, 95% QI: -1.39 – -0.01, $p = 0.058$) and a weak increase in $\bar{z}$ (median: 0.61 cm, 95% QI: 0.06 – 1.81, $p = 0.091$; Fig 1.2). This change in λ largely reflected complementary effects of reduced fecundity, and to a lesser extent, reduced growth (Fig 1.3). Killifish experienced significantly reduced growth rates (median: -0.05 cm per 14 days, 95% QI: -0.081 – -0.018, $p = 0.003$) and fecundity (median: -3.07, 95% QI: -5.98 – -1.148, $p = 0.017$) when paired with large size structured guppy populations as opposed to small size structured guppy populations (Table 1.4, Fig 1.1).

We also found little support for a guppy density $\times$ size structure interaction effect on either asymptotic population growth rate or mean of the stable size distribution of killifish. This contrast showed little change in λ (median: 0.08, 95% QI: -0.34 – 0.50, $p = 0.276$) or $\bar{z}$ (median: -0.04 cm, 95% QI: -0.84 – 0.82, $p = 0.892$; Fig 1.2). This increase in λ reflected the complementary contributions of increased survival, fecundity and growth (Fig 1.3), although none of the vital rates differed significantly for this contrast (all $p > 0.05$, Table 1.4, Fig 1.1).

Killifish Population Structure

The intraspecific killifish contrasts suggested some role of killifish density, but not size structure or density × size structure interaction, in determining λ and $\bar{z}$. Increasing killifish density led to a marked decrease in λ (median: -0.26, 95% QI: -1.98 – -0.03) and an increase in $\bar{z}$ (median: 0.43 cm, 95% QI: -0.15 – 2.45), although only the former difference carried significance (λ: p = 0.047; $\bar{z}$: p = 0.178; Fig 1.2). This decline in λ reflected the complementary contributions of reduced growth and fecundity (Fig 1.3), although only the difference in growth rates between high- and low-density treatments proved significant (median: -0.12 cm per 14 days, 95% QI: -0.149 – -0.097, $p < 0.001$, Table 1.4, Fig 1.1).

Conversely, altering the population size structure of killifish did not substantially alter the asymptotic population growth rate or mean of the stable size distribution of killifish. Moving from a small to a large killifish population size structure led to a negligible decrease in λ (median: -0.14, 95% QI: -0.54 – 0.12, p = 0.933) and a modest, but insignificant, increase in $\bar{z}$ (median: 0.51 cm, 95% QI: -0.09 – 2.38, p = 0.142; Fig 1.2). The minor decrease in λ largely depended upon diminished fecundity (Fig 1.3), although these differences in fecundity were not strong (median: -1.92, 95% QI: -11.80 – -0.10, p = 0.091, Table 1.4, Fig 1.1).

We found little support for an effect of the killifish density × size structure interaction on λ or $\bar{z}$. This contrast showed little evidence for appreciable changes in λ (median: -0.08, 95% QI: -0.40 – 0.24, p = 0.811) or $\bar{z}$ (median: -

0.27 cm, 95% QI: -2.16 – 0.37, p = 0.315; Fig 1.2). The minor differences in λ across treatments in this contrast largely derived from reduced survival (Fig 1.3), although none of the vital rates along showed significant differences across this contrast (all $p > 0.05$, Table 1.4, Fig 1.1).

Inter- vs. Intraspecific Effects

Comparing the magnitude of the killifish and guppy, density, size structure and interaction effects did not strongly distinguish the relative impacts of either species on killifish populations. Doubling the density of killifish had a larger impact on λ (median: 0.18, 95% QI: -0.17 – 1.22) and $\bar{z}$ (median: 0.21 cm, 95% QI: -0.76 – 2.25) than doubling the density of guppies, although not significantly so (λ: p = 0.130; $\bar{z}$: p = 0.454; Fig 1.2). Increasing killifish density did yield a significantly greater effect on killifish growth than increasing guppy density (median: -0.10 cm per 14 days, 95% QI: 0.059 – 0.131, $p < 0.001$, Table 1.4, Fig 1.1).

The impact of a standard deviation unit change in size structure of the killifish population relative to a comparable change in the guppy size structure differed for the killifish asymptotic population growth rate and the mean of the stable size distribution. For λ, the effect of guppy size structure exceeded those of killifish size structure (median: -0.04, 95% QI: -0.46 – 0.21), while the killifish size structure effect outweighed the corresponding guppy effect on $\bar{z}$ (median: 0.16 cm, 95% QI: -0.64 – 2.08; Fig 1.2). Neither of these effects were particularly

strong (λ: p = 0.674; $\bar{z}$: p = 0.527), nor were there significant differences in any vital rates for this comparison (all p > 0.05, Table 1.4, Fig 1.1).

The scaled density × size structure interaction effects of killifish exceeded those of guppies for λ (median: 0.01, 95% QI: -0.32 – 0.32) and $\bar{z}$ (median: 0.12 cm, 95% QI: -0.61 – 2.06; Fig 1.2). These minor differences were not significant (λ: p = 0.517; $\bar{z}$: p = 0.516). We found no significant differences in any of the vital rates for this contrast (all p > 0.05, Table 1.4, Fig 1.1).

Perturbation Analysis

The perturbation of neonate survival had some impact on the guppy invasion contrast. In this contrast, the perturbation of survival to simulate guppy predation reinforced the effects of guppy competition on λ and $\bar{z}$. The combination of guppy competitive and predatory effects led to a larger decrease in killifish λ between the treatment without guppies (or a survival perturbation) and that with the low density, small size structured guppy population (survival 0.5: -0.24; survival 0.4: -0.25; survival 0.25: -0.27) with corresponding gains in significance (survival 0.5: p = 0.078; survival 0.4: p = 0.066; survival 0.25: p = 0.049; Fig 1.4). The trend in the differences of $\bar{z}$ followed the same pattern (survival 0.5: 0.22 cm; survival 0.4: 0.26 cm; survival 0.25: 0.33 cm), although the significance of these differences remained questionable (survival 0.5: p = 0.310; survival 0.4: p = 0.254; survival 0.25: p = 0.181; Fig 1.4).

The hatchling survival perturbation had a more limited impact on the guppy population structure contrasts (Fig 1.4). For the guppy density contrast, the neonate survival perturbations produced trivial increases in the magnitude of the minor competitive effects on λ and $\bar{z}$. For the guppy population size structure contrast, the neonate survival perturbations produced small reductions in the magnitude and significance of the differences in λ and $\bar{z}$. Likewise, Perturbing the survival of neonates did not appreciably change the outcome of the density $\times$ size structure contrast for λ or $\bar{z}$.

The perturbation of neonate survival also had a small effect on the killifish population structure contrasts. For the killifish density contrast, the neonate survival perturbations produced small, conflicting effects on the magnitude of the density contrast for λ and $\bar{z}$ (Fig 1.4). Increasing levels of neonate mortality led to smaller differences in λ, but larger differences in $\bar{z}$. Similarly, the neonate survival perturbation had small, but opposing effects, on the killifish size structure contrasts of λ and $\bar{z}$ (Fig 1.4). Elevated hatchling mortality produced minor declines in the magnitude of the contrasts for λ and minor increases in magnitude of differences in $\bar{z}$ across killifish population size structures. For the killifish density $\times$ size structure contrast, the perturbation of neonate survival produced small declines in the magnitudes of the contrasts of asymptotic population growth rate and slight increases in the magnitudes contrasts for the mean of stable population size distribution (Fig 1.4). None of these minor

changes in magnitude altered the direction or significance of the killifish population structure effects.

Given the minor effect of the perturbation on either the guppy or killifish population structure effects, we found little evidence for the hatchling survival altering the relative impacts of the killifish and guppy density, size structure or interaction effects (Fig 1.4).

Discussion

Our results show that killifish should persist ($\lambda > 1$) across a range of densities and size structures of KO killifish and KGP guppies (Fig 1.2). Moreover, killifish population dynamics, particularly population growth rate, varied substantially with changes in the density and size structure of intra- and interspecific competitors. Killifish population growth rates significantly decreased with a doubling in killifish density, but only decreased weakly with a comparable increase in guppy density (Fig 1.4). In contrast, killifish population growth rates marginally decreased between small and large guppy population size structures but differed little in the corresponding contrast of killifish population size structures (Fig 1.4). When we scaled these effects to represent an equivalent standardized change in median size, we found that the guppy and killifish population size structure effects had similar magnitudes, with the guppy effects slightly exceeding those of killifish on average. This relatively strong interspecific frequency dependence may complicate the conditions required for

coexistence in KG communities. We further noted that the addition of a low density, small size structure guppy population to a high density, small size structure killifish population led to a weak decrease in killifish population growth rate through competitive interactions. Our perturbation of hatchling survival designed to mimic the effects of guppy predation reinforced the killifish response to guppy competition in this comparison, leading to a significant decline in population growth rate (Fig 1.4). Simulated guppy predation had little effect in any of the other contrasts, suggesting that competitive interactions may dominate the killifish response once guppies establish in KG communities.

Density-Dependence in KG killifish

The assembly of a KG community begins with the invasion of a KO killifish population by guppies. The pre-existing KO killifish population likely occurs at the high densities typical of KO communities (Gilliam et al. 1993, Fraser and Lamphere 2013, Furness and Reznick 2015). At these high densities, killifish likely face strong intraspecific competition that limits population growth rates. Against this backdrop of intense intraspecific interactions, the addition of interspecific competition from guppies may impose a relatively steep cost to killifish population growth rate. These strong competitive effects may frequently occur in nonequilibrium communities subject to colonizing competitors, environmental perturbations or experimentally manipulated competitor distributions (Kokkoris et al. 1999, Urban et al. 2012). Moreover, most of the

observed differences in population growth rate under these intense competitive interactions derived from minor differences in survival (Fig 1.3). Adding predation mortality compounded the competitive effects of guppies on survival, further reducing population growth rates (Fig 1.4). This finding aligns with previous work demonstrating importance of predation to invasion dynamics among species that have both competitive and predatory interactions (Montserrat et al. 2008, Schröder et al. 2009a, Montserrat et al. 2012, Reichstein et al. 2013).

As guppies become established in the community, killifish population densities decline in response to the combination of competitive and predatory interactions with guppies. This decline in killifish density reduces intraspecific population regulation, allowing for increased population growth rates largely due to significant increases in individual growth rates and fecundity (Fig 1.3). These observed differences in individual growth rates between low and high killifish density populations match the results of a field transplant experiment. In this experiment, individuals that moved from high density KO areas to low density KG communities accelerated growth to match the resident KG individuals (Walsh et al. 2011). Moreover, this response of killifish to the effects of guppy competition and/or predation echoes the effects of reduced survival across many taxa, where predation mortality reduces intraspecific competition and increases individual growth rates (Schoener 1983, Gascon and Travis 1992, Werner and Anholt 1996, Relyea 2002). However, the significant increase in

fecundity we observed in low vs high killifish density does not accord with the similar egg productivities of KO killifish recorded in laboratory common garden experiments at high and low food levels, which mimic the food available in KG and KO communities, respectively (Walsh and Reznick 2010, 2011). One explanation for this disagreement may derive from the increased individual growth rates of killifish at low density, which allows them to realize larger body sizes and hence greater reproductive output. Alternatively, the food treatments applied in laboratory experiments may not capture all of the relevant impacts of intraspecific density and underestimate the demographic response relative to what we observed.

At the same time as killifish densities decline, guppy densities also increase. However, these two changes do not have equivalent effects on killifish. The significant reduction in intraspecific killifish population regulation likely outweighs the minimal effects of guppy density on killifish population growth rates (Fig 1.4). The relative strengths of these density effects meet one of the necessary conditions for stable persistence: intraspecific population regulation must exceed interspecific population regulation (Chesson 2000, Adler et al. 2007). Although empirical support for this condition has historically been limited among pairs of apparently coexisting species (Silvertown 2004, Siepielski and McPeek 2010), recent work has begun to shed new light on this apparent mismatch between theory and observation. Several recent studies have found

evidence for stable coexistence based upon niche differences that concentrate intraspecific interaction relative to interspecific interactions (Levine and HilleRisLambers 2009, Adler et al. 2010, Chu and Adler 2015). Likewise, Adler et al. (2018) found that intraspecific effects far exceeded interspecific effects in meta-analysis of 39 studies of competitive plant communities. Thus, the killifish response to variation in interspecific and intraspecific density contributes to the growing consensus around this central tenet of coexistence theory.

Evolutionary studies of killifish further support a principal role of intraspecific density-dependence in killifish from KG communities. Surveys of killifish life history traits in natural streams show that KG killifish mature at smaller sizes, and produce more and smaller eggs than their KO counterparts (Walsh and Reznick 2009, Furness et al. 2012). Laboratory experiments using second generation individuals reared in a common garden environment further demonstrate that these life history traits have a genetic basis and depend upon food. When provisioned with food comparable to a low killifish density KG environment, KG killifish outperform KO killifish by exhibiting the differences in traits observed in natural streams, but these differences reverse under the low food conditions typical of a high density KO community (Walsh and Reznick 2010, 2011). These genetic differences match the predictions of life history theory that accounts for the indirect effects of interactions with guppies on killifish density and the less intense intraspecific interactions that follow (Abrams

and Rowe 1996). Intraspecific density-dependence likely contributes to both the short-term ecological and long-term evolutionary trajectory of killifish in KG communities.

Size-Structure Dependence in KG Killifish

During the formation of a KG community, both killifish and guppies exhibit changes in population size structures that effect and respond to competitive interactions within the community and manifest in the mean of the stable size distributions. In response to the initial guppy invasion, we observed a nonsignificant increase in the mean of the stable size distribution and increasing levels of guppy predation led to larger, but still statistically insignificant, changes in this population parameter (Fig 1.4). This pattern further implicates the importance of survival and guppy predation during the first phase of KG community assembly.

These initially small changes in the stable size distribution may form a positive feedback loop that reinforces the increase in mean size. We observed a larger, but also insignificant, positive change in the stable size distribution between the small and large size structured killifish size structure treatments (Fig 1.4). Over the longer term, the composition of the KG guppy population also shifts to contain more large individuals than the initial invaders from KGP habitats due to reduced predation pressure and the rapid evolution of life histories (Reznick 1982, Reznick and Bryga 1987, Rodd and Reznick 1997). Our

results predict that this change may facilitate an additional increase in the mean of the stable size distribution. These increases in mean size when moving from a small to a large size structure population in either species likely reflect more intense competition that yields reduced fecundity and, to a lesser extent, individual growth rates (Table 1.4, Fig 1.1). Since the effects of population size structure depend upon competition, guppy predation on hatchling killifish had relatively little impact on the size structure contrasts, perhaps, because reduced fecundity at large population size structures limited the number of vulnerable hatchling killifish.

The combination of the relatively small effects of predation and alterations in the competitive environment may explain the complex dynamics of killifish population size structures during KG community assembly. In the short term, guppy predation, and the upward shifts in intra- and interspecific population size structure may lead to the trend towards increasing killifish body sizes seen in replicated experimental introductions of guppies into previously KO environments in the first several years after introduction (Fraser and Lamphere 2013, Goldberg unpublished data). However, in the long-term, the countervailing effects of reduced killifish density (Fig 1.4) and/or evolutionary adaptations in either species may return the killifish population size structure to its initial state. To this end, comparisons of killifish population size structures from long extant KG communities do not suggest any enduring shift in average

body sizes (Gilliam et al. 1993, Furness and Reznick 2015, Goldberg unpublished data)

These changes in size structure and the underlying competitive interactions of killifish and guppy populations can have a measurable impact on killifish population growth rates. As the killifish population shifts to larger sizes, we observed a decrease in killifish population growth rate, although this effect was extremely weak at the size structures prescribed in the treatments. In contrast, the difference between the small and large size structure treatments in guppies yielded a marginally significant decrease in killifish population growth rate. Thus, the outcome of these ecological interactions depends upon both intra- and interspecific variation. Moreover, our standardization of the size structure effects revealed that killifish population growth rate was similarly sensitive to intra- and interspecific changes in the average body size. This finding contradicts the general principle that persistent populations should be more sensitive to intra- than interspecific interactions.

Recent theory shows that this pattern of intra- and interspecific frequency-dependence can occur among stably coexisting species under limited conditions. In particular, the species that is a superior competitor for shared resources must have less variability than the inferior competitor species, regardless of whether this variability comes from ontogenetically variable or stable traits (Hart et al. 2016, Bassar et al. 2017b). Thus, variation can act as

coexistence mechanism by opening ecological space for inferior competitors and moderating the intense interactions with competitively dominant species. This variation driven coexistence appears to operate in at least some natural communities (Clark et al. 2010, Pruitt and Ferrari 2011, Costa-Pereira et al. 2018, Hausch et al. 2018), although our analysis does not provide an account of how resource requirements and use vary among killifish and guppies of different body sizes.

Our factorial analysis summarizes how the population size structure treatments impact killifish populations but does not explicitly capture the competitive interactions among individuals that determine the population response. In contrast, the trait-based models of Bassar et al. (2017b) do represent the interactions between focal individuals and each of its intra- and interspecific competitors. These models offer dynamic characterizations of populations that jointly admit density- and frequency-dependence, as well as potential ontogenetic niche shifts, and thus allow calculation of equilibrium population densities and size structures. However, these methods also require auxiliary data (or assumptions) to specify some model parameters. Lacking information to define these values suitably, our approach yields a reasonable, phenomenological approximation of how changes in the size structures of killifish and guppies influence killifish population dynamics.

On a larger scale, our experiments do not consider spatial variation, which often play an important role in species persistence. Both theoretical and empirical work have recognized that spatial variation can shape species coexistence through a variety of mechanisms (MacArthur and Levins 1967, MacArthur 1972, Tilman 1982, Chesson 2000, Amarasekare 2003, Kneitel and Chase 2004), including intraguild predation relationships with mixed predatory and competitive interactions (Borer et al. 2004, Snyder et al. 2005, Amarasekare 2006, 2007a, Okuyama 2008). In our system, killifish and guppies occur and interact in a range of habitats, including pools, riffles, side pools and isolated pools, but the mesocosms likely capture a subset of these conditions. This simplification of the stream environment may mask important spatial variation in killifish-guppy interactions or performance that facilitate the assembly and persistence of KG communities, although the broad correspondence between our results and patterns in experimental guppy introduction streams suggests that we have captured the gross effects of the interaction. More broadly, individual variation may vary across populations, raising the possibility that the mechanisms generating coexistence between two species may vary across a landscape (Costa-Pereira et al. 2018, Potter et al. 2019). Expanding our design to include multiple drainages, each of which represent an independent origin of killifish-guppy interactions, would allow us to evaluate this hypothesis.

Similarly, our short experimental periods may exclude relevant temporal variation that modifies the persistence of the KG community. Temporal variation can alter coexistence outcomes by inducing correlations between environmental conditions and competition that concentrate intraspecific interactions relative to interspecific interactions (Chesson 2000, Amarasekare 2007b, 2008). The streams of Trinidad exhibit distinct wet and dry seasons that alter the abundance and distribution of resources, as well as those of each species (Rodd and Reznick 1997, Gilliam and Fraser 2001, Owens 2010, Kohler et al. 2012, Travis et al. 2014, Goldberg unpublished data). This raises the possibility that each species may have a preferred season that facilitates long-term persistence through unfavorable conditions that benefit the other.

At longer time scales, heritable individual variation in interaction traits may precipitate the evolution of novel community outcomes that would not emerge by ecological means alone (Lankau 2011, Rael et al. 2011, Hiltunen et al. 2014b, Patel and Schreiber 2015). This kind of selection may operate in KG communities, since guppies have lowest fitness when KGP guppies occur with KO killifish, intermediate fitness when KG guppies interact with KO killifish and greatest fitness when pairing sympatric KG guppies and killifish (Bassar et al. 2017a). Moreover, killifish did not show a corresponding pattern of increased fitness with the adaptation of community members in this experiment, suggesting that the evolutionary response of interaction traits may respond

indirectly or asymmetrically within a community (Bassar et al. 2017a). Future work may reveal how this evolutionary variation impacts coexistence outcomes in this and other natural communities.

Conclusions

We used manipulative experiments to reconstruct the invasion and assembly of a community of competitors with size-structured interactions. Our results illuminate how the resident species responds to variation in intra- and interspecific variation in density and size-frequency distribution. We show that populations of this species can persist across the range of imposed conditions, but that the asymptotic population growth rates depend strongly upon size-selective predation, intraspecific density, and similarly upon intra- and interspecific population size structure. Predation had the greatest effect during the initial invasion stage of the interactions but had reduced impact once the invader established. The significant effect of intraspecific density suggests that these species fulfill the universal condition for coexistence upon first contact, while the roughly equivalent effects of variation in population size structure in each species indicate that ontogenetic changes in competitive ability with body size may play a role in the equilibrium of the community. Thus, understanding community dynamics and coexistence requires knowing not only how many of each species, but also what traits they possess.

Tables

Table 1.1. Description of fractional factorial design and a priori contrasts of 2016 mesocosm experiments with number of fish and initial length (mean ± S.D.) measured in mm of each species. Length reflects the standard length of guppies and the total length of killifish. Dashes (-) represent treatments where a species is absent.

Treatment	Guppy		Killifish		Contrast						
	Density	Length	Density	Length	Guppy Invasion	Guppy Density	Guppy Size	Guppy Density × Size	Killifish Density	Killifish Size	Killifish Density × Size
1	-	-	12	41.3 ± 15.10	-1	0	0	0	0	0	0
2	8	13.8 ± 3.37	6	40.8 ± 14.12	0	-0.5	-0.5	-0.5	-0.5	-0.5	-0.5
3	8	15.4 ± 4.64	6	40.4 ± 15.10	0	-0.5	0.5	0.5	0	0	0
4	16	13.8 ± 3.36	6	41.3 ± 15.70	0	0.5	-0.5	0.5	0	0	0
5	16	15.6 ± 4.72	6	40.8 ± 15.88	0	0.5	0.5	-0.5	0	0	0
6	8	13.6 ± 3.40	6	43.8 ± 17.99	0	0	0	0	-0.5	0.5	0.5
7	8	13.8 ± 3.24	12	40.4 ± 12.86	1	0	0	0	0.5	-0.5	0.5
8	8	13.7 ± 3.30	12	44.5 ± 17.02	0	0	0	0	0.5	0.5	-0.5

Table 1.2. Bayesian model selection criteria for each vital rate model fit to data from artificial stream experiments conducted in 2016. ΔLOOIC represents the Pareto-smoothed importance sampling leave-one-out cross-validation information criteria comparison between the model with the minimum expected log-predictive density and a given model. SE reflects the standard error on this value. Weight represent the Bayesian stacking weight. Dashes (-) represent poorly specified models that did not converge on the posterior distribution.

Vital Rate	Model	ΔLOOIC	SE	Weight
Growth	Juvenile: length + treatment Adult: length + treatment	0.0	0.0	1.00
Growth	Juvenile: length × treatment Adult: length + treatment	6.4	2.3	0.00
Growth	Juvenile: length × treatment Adult: length × treatment	12.6	4.2	0.00
Growth	Juvenile: length + treatment Adult: length × treatment	-	-	-
Survival	length + treatment	0.0	0.0	1.00
Survival	length × treatment	3.4	2.5	0.00
Fecundity	Hurdle: length + treatment Conditional: length + treatment	0..0	0.0	0.85
Fecundity	Hurdle: length + treatment Conditional: length × treatment	4.0	3.6	0.15
Fecundity	Hurdle: length × treatment Conditional: length + treatment	9.3	3.1	0.00
Fecundity	Hurdle: length × treatment Conditional: length × treatment	13.6	4.9	0.00
Offspring Size	length + treatment	0.0	0.0	1.00
Offspring Size	length × treatment	14.7	6.3	0.00

Table 1.3. Parameter estimates of killifish vital rate models characterized by the posterior distribution of a nonparametric Bayesian bootstrap. Estimates presented as posterior median (95% quantile interval). β_0 is the intercept, which varies across treatments. β_z is the coefficient for initial length *z*, measured in cm and centered at the mean of all observations. β_{zj} and β_{za} are the coefficients of initial length *z* during the juvenile and adult phases of growth, respectively. β_Δ is the breakpoint where the slope of growth rate changes. σ_0 gives the residual standard deviation (at the mean body size in models where residual variance depends upon body size) and σ_z gives the covariate of initial length *z* on the residual variance (on the log link scale).

Parameter	Treatment	Growth ($\mu_G(z)$)	Survival ($S(z)$)	Breeding ($B(z)$)	Fecundity ($M(z)$)	Offspring Size ($\mu_D(z)$)
β_0	1	0.12 (0.057, 0.161)	3.77 (2.313, 6.274)	1.16 (-0.417, 3.209)	1.64 (1.182, 1.949)	0.79 (0.773, 0.811)
β_0	2	0.22 (0.149, 0.254)	3.06 (1.457, 5.575)	0.90 (-0.850, 2.894)	1.87 (1.458, 2.258)	0.80 (0.753, 0.835)
β_0	3	0.18 (0.106, 0.231)	4.18 (1.906, 8.635)	4.06 (1.910, 8.365)	1.77 (1.109, 2.204)	0.79 (0.776, 0.800)
β_0	4	0.20 (0.132, 0.261)	4.15 (1.909, 8.445)	0.08 (-1.776, 2.108)	1.51 (0.614, 2.089)	0.79 (0.761, 0.819)
β_0	5	0.14 (0.073, 0.181)	3.07 (1.539, 5.759)	3.68 (1.500, 7.571)	1.40 (0.271, 2.093)	0.81 (0.781, 0.834)
β_0	6	0.21 (0.146, 0.260)	2.32 (0.834, 4.752)	2.15 (0.206, 4.739)	1.29 (0.774, 1.710)	0.80 (0.766, 0.841)
β_0	7	0.11 (0.040, 0.144)	2.33 (0.880, 4.564)	1.04 (-0.583, 2.970)	1.02 (-0.375, 1.728)	0.80 (0.778, 0.822)
β_0	8	0.08 (0.016, 0.117)	3.67 (2.137, 6.276)	3.50 (1.744, 6.703)	1.09 (-18.199, 1.760)	0.79 (0.751, 0.819)
β_z	-	-	0.52 (0.018, 1.213)	-0.78 (-1.525, -0.286)	0.40 (0.251, 0.579)	0.02 (0.009, 0.029)
β_{zj}	-	- 0.13 (-0.159, -0.096)	-	-	-	-
β_{za}	-	-0.02 (-0.039, -0.002)	-	-	-	-
β_Δ	-	-0.01 (-0.329, 0.771)	-	-	-	-
σ_0	-	0.06 (0.051, 0.069)	-	-	-	0.03 (0.019, 0.041)
σ_z	-	-0.19 (-0.500, 0.105)	-	-	-	-

Table 1.4. *A priori* contrasts of killifish demographic rates from 2016 mesocosm experiments, characterized with the posterior median, 95% quantile interval (QI) and p-value from nonparametric Bayesian bootstrapping of vital rate models. All contrasts evaluated at the mean body size. For the fecundity model, the contrast is evaluated by taking the differences of the log-transformed products of the predicted probability of breeding and fecundity conditional on breeding. Significant contrasts ($p < 0.05$) highlighted in bold.

	Growth (cm 14-days^{-1})			Survival			Fecundity (Mature Eggs)			Offspring Size (cm)		
Contrast	Median	QI	p	Median	QI	p	Median	QI	p	Median	QI	p
Guppy Invasion	-0.02	-0.051, 0.016	0.260	-1.42	-4.264, 1.273	0.259	-0.54	-2.961, 1.577	0.502	0.01	-0.020, 0.035	0.611
Guppy Density	-0.03	-0.057, 0.006	0.105	0.00	-2.807, 2.705	0.991	0.04	-2.034, 2.361	0.940	0.01	-0.020, 0.034	0.536
Guppy Size	**-0.05**	**-0.081, -0.018**	**0.003**	0.04	-2.749, 2.895	0.965	**-3.07**	**-5.980, -1.148**	**0.017**	0.01	-0.020, 0.035	0.550
Guppy Density × Size	0.02	-0.016, 0.047	0.339	1.18	-1.295, 4.318	0.349	0.06	-2.305, 2.177	0.966	-0.01	-0.038, 0.015	0.328
Killifish Density	**-0.12**	**-0.149, -0.097**	**0.000**	0.32	-1.608, 2.282	0.721	-1.35	-11.094, 0.439	0.143	0.00	-0.036, 0.029	0.871
Killifish Size	-0.02	-0.040, 0.012	0.263	0.32	-1.631, 2.235	0.738	-1.92	-11.795, -0.099	0.091	0.00	-0.037, 0.029	0.831
Killifish Density × Size	0.01	-0.013, 0.038	0.355	-1.03	-2.997, 0. 267	0.829	0.33	-1.568, 9.933	0.491	0.01	-0.026, 0.040	0.728
|Killifish| - |Guppy| Density	**0.10**	**0.059, 0.131**	**0.000**	-0.20	-2.545, 1.675	0.756	0.60	-1.624, 10.216	0.405	0.00	-0.024, 0.029	0.929
|Killifish| - |Guppy| Size	0.01	-0.019, 0.034	0.670	-0.03	-1.860, 1.695	0.950	1.48	-0.441, 11.325	0.153	0.00	-0.013, 0.029	0.635
|Killifish| - |Guppy| Interaction	0.00	-0.027, 0.027	0.963	0.14	-2.739, 2.385	0.974	0.12	-1.558, 9.290	0.571	0.00	-0.023, 0.033	0.879

Figures

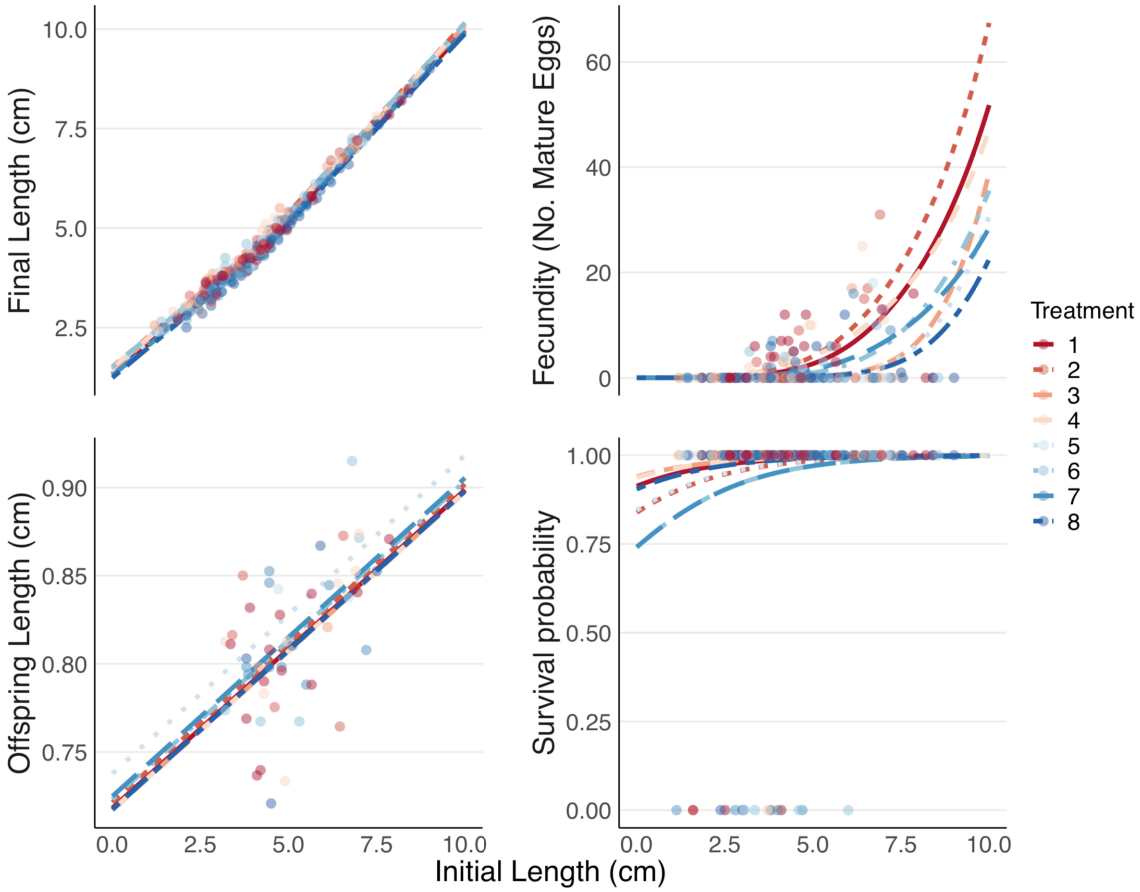

Figure 1.1. Observed (points) and predicted (lines) killifish demographic rates as a function of initial total length (in cm) for the 8 experimental treatments in artificial stream experiments from 2016. The lines represent predicted values at the posterior median parameter estimates from the Bayesian bootstrap of the vital rate models.

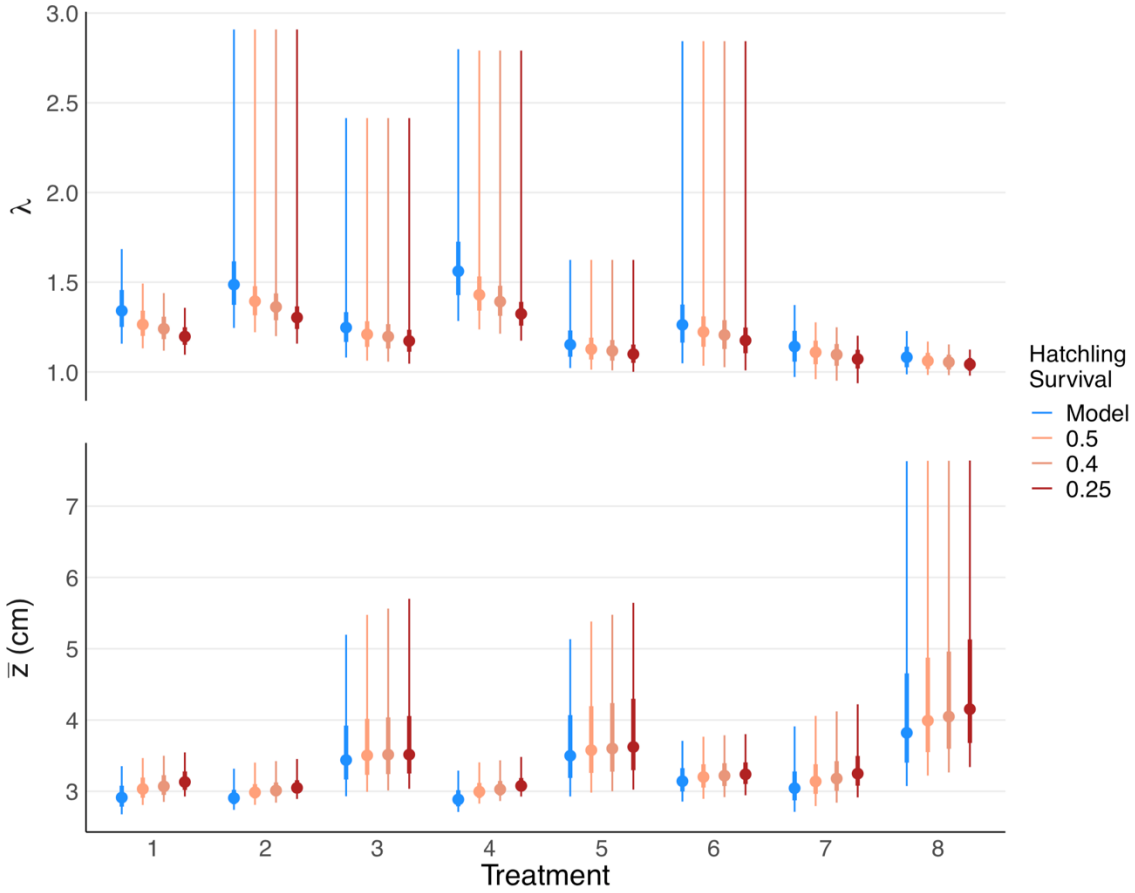

Figure 1.2. Asymptotic population growth rates (λ) and means of the stable size distributions ($\bar{z}$, measured in cm total length) for each experimental treatment in 2016 mesocosm experiments. Treatments described in Table 1.1. Points represent the posterior median of Bayesian bootstrap replicates, thick bars capture the 66% quantile intervals (QI) and thin bars the 95% QIs. Colors represent the different perturbations of hatchling survival: model estimated survival probabilities (blue); and survival probabilities of 0.5 (light salmon), 0.4 (dark salmon) and 0.25 (dark red).

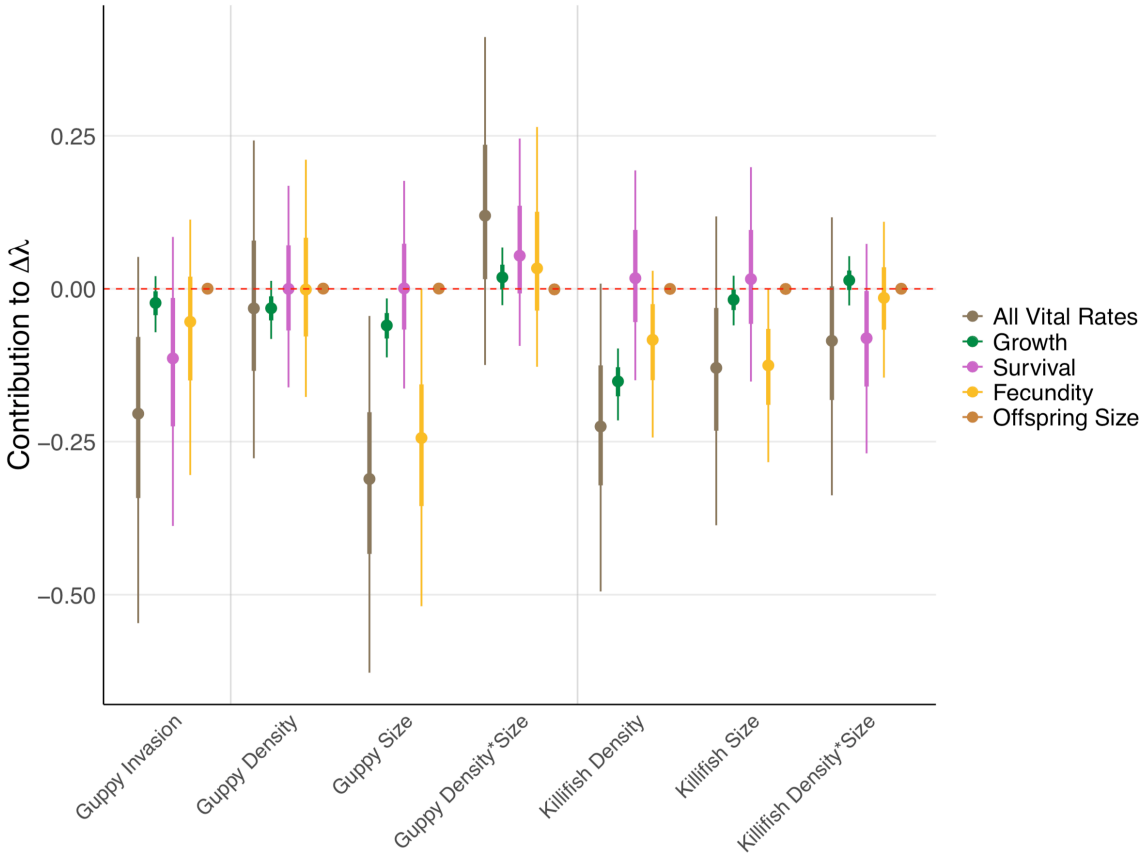

Figure 1.3. Overall differences in killifish asymptotic population growth rates (λ) and LTRE decomposition for the experimental contrasts into the component vital rates: growth (green), survival (violet), fecundity (yellow) and offspring size (brown). The sum of these vital rates provides a first-order approximation of the overall differences in the contrast (gray). Points represent posterior medians of Bayesian bootstrap replicates, thick lines capture the 66% quantile intervals (QI) and thin bars the 95% QIs.

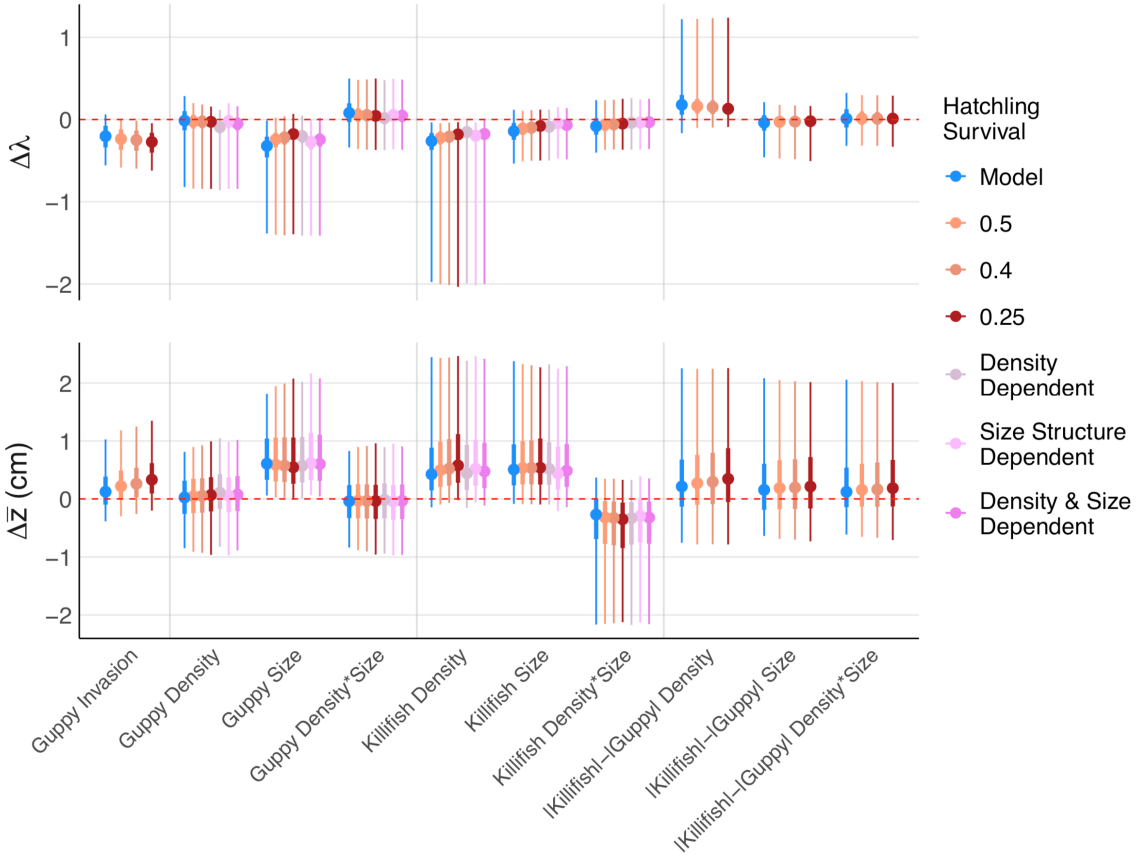

Figure 1.4. Differences in killifish asymptotic population growth rates (λ) and means of the stable size distributions ($\bar{z}$, measured in cm total length) for the experimental contrasts under varying scenarios of guppy predation through perturbed hatchling survival: model estimated survival probabilities for all treatments (blue); constant, reduced survival probabilities of 0.5 (light salmon), 0.4 (dark salmon) and 0.25 (dark red) for treatments including guppies; and hatchling survival that depends upon density (gray), size structure (pink) or both density and size structure (violet) of either species. Points represent posterior medians of Bayesian bootstrap replicates, thick lines capture the 66% quantile intervals (QI) and thin bars the 95% QIs.

Chapter 2: Differential habitat use mitigates the impact of invasion by an intraguild predator

Abstract

Theory predicts that species engaged in intraguild predation (IGP) can rarely coexist, yet IGP is often observed in nature. We propose that habitat-dependent, differential recruitment could facilitate the development of a persistent IGP relationship. We evaluated predictions of this hypothesis with a replicated experimental introduction of an IG predator/competitor to a natural stream community that previously contained only the other IG predator/competitor, followed by monthly mark-recapture sampling of both species. The density of the resident decreased as the introduced species successfully established. We tested whether the decline in the resident could be attributed to predation and/or competition with the introduced species and how differential use of the alternative habitats modified the demographic responses to these IGP interactions. Both species use pool and riffle habitats, but the introduced species used pools more than riffles, while the resident species had no bias in habitat use. The mean size of the resident increased over time in pools with abundant invaders, but not in other localities. This change was accompanied by a decrease in number of resident recruits in these same pools and could not be explained by a local increase in individual growth rates. Nor did local growth rates significantly decrease in the presence of abundant

invaders as predicted under intense interspecific competition, suggesting size-selective predation by the invader dominated the residents' demographic response. The continued recruitment of resident juveniles in riffles, habitat sparsely occupied by the introduced species, likely facilitates the persistence of the resident. Thus, differential reproductive success in alternative habitats can promote coexistence and set the stage for evolutionary changes during the long-term development of a stable IGP relationship.

Introduction

The introduction and initial establishment of an intraguild predator, a species that is both a predator and competitor, results in novel, complex interactions that influence the population dynamics of a resident intraguild prey species. Theory predicts that such intraguild predation (IGP) will destabilize coexistence, with one species driving the other to extinction under most conditions. Both species persist only at intermediate resource productivity and when the IG prey is a superior competitor for the common resource (Polis et al. 1989, Holt and Polis 1997, Morin 1999, Diehl and Feissel 2000, Mylius et al. 2001, HilleRisLambers and Dieckmann 2003). Moreover, bidirectional intraguild predation, where both species are predators on each other, makes the persistence of both IG predator and IG prey even less likely. For example, Schellekens and van Kooten (2012) found that coexistence under bidirectional IGP requires each species to have a different diet, so that one acts primarily as a

consumer and the other as a predator. Thus, bidirectional IGP demands a more precise balance of competition and predation for both species to coexist.

Contrary to these predictions, intraguild predation is common in nature (Arim and Marquet 2004, Janssen et al. 2007). Proposed explanations for coexistence include the availability of alternative resources (Heithaus 2001, Daugherty et al. 2007, Holt and Huxel 2007), size-structured intraguild predation (Abrams 2011, Hin et al. 2011, Henkanaththegedara and Stockwell 2014, Toscano et al. 2016), spatial structure of resources and interactions (Finke and Denno 2006, Okuyama 2008), cannibalism (Rudolf 2007, Amarasekare 2008), behavioral interactions (Holway and Suarez 1999, Thompson et al. 2012, Camacho-Cervantes et al. 2018) and niche dimensionality (Clark 2013). Of these potential coexistence mechanisms, spatial structure has received relatively more attention as a promising explanation for the persistence of IGP interactions in nature. A meta-analysis of 10 manipulative experiments and 38 observational studies revealed that habitat complexity tended to reduce the negative effects of IG predators on IG prey and thus facilitated the persistence of intraguild predation (Janssen et al. 2007). Similarly, Langellotto and Denno (2004) found that increased habitat structure increased the abundance of IG predators and prey in seven out of nine examined communities.

Habitat structure and complexity can provide a refuge that reduces encounter rates between IG predator and IG prey. Persson and Eklov (1995)

found that habitat complexity created partial or complete refuges from predation for the IG prey, but also increased competitive interactions between juvenile IG predators and IG prey in these same areas. This altered balance of stage-specific IGP interactions helped to explain the two species distributions in lakes with different levels of structural complexity. This view of habitat as creating refuges with altered IGP interactions agrees with behavioral observations of IG prey in the presence of IG predators (Finke and Denno 2006, Rudolf and Armstrong 2008). Vulnerable IG prey use some habitats to avoid encounter and capture by IG predators.

Here, we consider how differences among species in habitat use lead to less intense IGP interactions and promote a stable, bidirectional IGP relationship in natural streams in the Northern Range Mountains of Trinidad. These streams exhibit a longitudinal gradient of fish diversity (Haskins et al. 1961). In the higher order streams, killifish (*Rivulus hartii*) and guppies (*Poecilia reticulata*) co-occur with many predatory species (high predation). Barrier waterfalls block some species, yielding progressively simpler communities upstream. Killifish occur alone in the headwaters of these streams (killifish-only: KO). Guppies occasionally breach these barrier waterfalls to form killifish-guppy communities (killifish-guppy: KG; or low-predation). The latter communities are the focus of this study.

In KG communities, killifish prey on guppies, especially neonates and immatures (Seghers 1974, Mattingly and Butler IV 1994), but guppies prey on neonate killifish (Fraser and Lamphere 2013, Furness and Reznick 2015). Adult guppies and juvenile killifish also compete for resources (Gilliam et al. 1993, Fraser and Lamphere 2013). Thus, killifish and guppies have a bidirectional IGP relationship, which theory predicts should be unstable and unlikely to persist (HilleRisLambers and Dieckmann 2003, van de Wolfshaar et al. 2006, Schellekens and van Kooten 2012). Despite this prediction, KG communities are well-established across these mountain streams (Haskins et al. 1961, Endler 1978, Gilliam et al. 1993). What factors might bridge the gap between theory and observation and explain this apparent paradox?

Comparative studies and the experimental introduction of guppies from high predation communities into KO streams demonstrate that both species evolve different life histories in response to these introductions (Reznick and Bryga 1987, Reznick et al. 1990, Reznick et al. 1997, Walsh and Reznick 2011). The evolution of each species in response to the other thus represents a likely long-term solution to this paradox, but evolution cannot address how the two species persist after guppies first invade KO habitats. Understanding long-term coexistence requires examining the transient dynamics of the IGP relationship during the initial phases of guppy invasion of previously KO communities. These initial dynamics can have important consequences for coexistence and

community outcomes (Amarasekare 2008, Maciel and Kraenkel 2017, Hastings et al. 2018). During this time, ecological factors, such as habitat use and productivity, may facilitate coexistence and set the stage for longer-term persistence and coevolutionary interactions.

Most assessments of the role of habitat in stabilizing IGP interactions have treated alternative habitats as being used exclusively (or nearly so) by one of the protagonist species. However, more subtle differences in habitat use or preferences by IG predator and IG prey may facilitate coexistence (Snyder et al. 2005). Our experimental streams consist of two identifiable habitats, permanent pools and non-pool habitats (the latter hereafter “riffles”). Pools are portions of stream with discrete inlets and outlets but without directional flow within the pool. Pools are separated by riffles, which have a steeper gradient and directional flow. The riffle category includes riffles, small riffle pools, seepages and portions of stream that fill after periods of high rainfall. Killifish frequent all habitats. In contrast, guppies concentrate in the larger, permanent pools, although they do occur in low numbers in the other habitat types, especially during wet season.

We introduced guppies from a high predation community into four streams that previously contained only killifish, creating an opportunity to study the factors promoting the stability of an IGP relationship during the critical period of initial invasion as the community moves toward a new equilibrium.

Waterfalls prevented the upstream dispersal of guppies, thus creating a KO control site upstream of all four introductions. The introduced guppy populations exhibited initial exponential growth, then seasonal oscillations (Travis et al. 2014, De Bona et al. 2019). Killifish abundance declined, which corresponds to the lower population densities of killifish in natural KG vs. KO communities (Gilliam et al. 1993, Walsh et al. 2011, Furness and Reznick 2015).

The joint findings of skewed guppy habitat use and reduced killifish density in the presence of an expanding guppy population motivates our hypothesis that differential use of or recruitment from riffles enhances killifish persistence in the face of IGP interactions with guppies. We consider properties of killifish populations that test this hypothesis. First, if guppy predation on neonate killifish, rather than competition, dominates in its effect on killifish then we predict that the mean of the size frequency distribution of killifish in pool habitats should increase where guppies were introduced, relative to riffles in the introduction site or to either habitat in the upstream controls where guppies are absent. This prediction reflects the expectation that guppy predation restricts the recruitment of juvenile killifish, leading to a population dominated by larger size classes. We thus also predict the recruitment of fewer killifish in pools relative to riffles where guppies were introduced and also fewer than recruited into either pools or riffles in the KO control sites upstream. Alternatively, an increase in average killifish size could also reflect changes in intraspecific

competition with reduced killifish population density leading to enhanced individual killifish growth rates (Walsh et al. 2011). On the other hand, if the main effect of guppies is instead to compete with killifish, then we predict a decrease in killifish growth rates in pools where guppies were introduced relative to killifish that occupy riffles or the upstream control.

Methods

Preliminary site preparation procedure

We chose four KO headwater streams in the upper Guanapo River watershed (Heights of Guanapo) for guppy introduction. We selected Introduction and Control reaches based on their having relatively long stretches with good pool-riffle development and barrier waterfalls which constrained upstream movements of guppies within the Introduction reach. As part of the extended goals of this experiment (López-Sepulcre et al. 2013, Travis et al. 2014, Dick et al. 2018), we thinned the tree canopy in the Control and Introduction portions of two streams (UPL and TAY) and in that way increased primary productivity.

Transplant and sampling procedures

We transplanted guppies from downstream high predation communities into LOL and UPL in March 2008 and to CAI and TAY in March 2009. The Introduction reach of LOL and UPL received 78 guppies and that of CAI and TAY received 104 guppies with an even sex ratio in all four streams. Introduction

reaches varied from 65 to 150 m in length between streams. The killifish Control reaches were upstream of the guppy Introduction reaches, above barrier falls that prevented further upstream movement of introduced guppies. Control reaches varied from 26 to 62 m in length between streams.

We censused guppy populations every month during daylight hours. We sampled pools and riffles with dipnets of assorted sizes with the goal of capturing all guppies ≥14 mm standard length. Guppies from each pool or riffle were kept separate, as were males and females. All fish were measured, marked by subcutaneous injection of a colored elastomer (Northwest Marine Technologies, Shaw Island, Washington, USA) then released at the point of capture. Details of the guppy censuses can be found elsewhere (López-Sepulcre et al. 2013, Travis et al. 2014, Dick et al. 2018, De Bona et al. 2019).

We sampled killifish with aquarium dipnets after dark with headlamps because they are more easily seen and caught at night. We also used baited minnow traps in the deeper pools. Captured fish were separated by location of capture and transported to the laboratory where each fish was measured (total length), weighed, and marked in the same fashion as guppies, then returned to the point of capture. We classified the habitat type, pool or riffle, at the time and place of each individual capture. We standardized sampling procedures, e.g. times and personnel, to minimize variation in effort across habitats and samples, so that the number of captures and resulting size distributions could be

compared. We censused the killifish in each stream 6 times per year, beginning 1 year (6 samples) prior to guppy introduction in LOL and UPL and 3 months (3 samples) prior to guppy introduction in CAI and TAY. During the first two years of the study (2007-2008), we captured fish every other month. Beginning in 2009, we altered the sampling schedule to better resolve recruitment and growth of the smaller size classes of killifish. We sampled the streams once each month for three months, then skipped three months and sampled again, once each month. The three-month sampling periods were chosen to represent the dry and wet seasons. Logistical constraints near the end of our study limited sampling in late 2011 and 2012 to a single sample.

Estimating population sizes of killifish in Introduction vs Control Reaches

We used the POPAN formulation of the Jolly-Seber model in the R (R Core Team 2018) package RMark (Laake 2013) as an interface to program MARK (White and Burnham 1999) to estimate the population abundance of killifish in Control and Introduction reaches of each stream. We allowed both survival, ϕ, and probability of entry ("recruitment"), p_{ent}, to vary in each sampling interval and reach, i.e. reach $\times$ time. We considered a few parametrizations of encounter probability, p, including reach $\times$ time, time, reach and an intercept only model, since detection probability may have varied between reaches and/or across sampling events. We used a sine link function for ϕ and p to improve parameter estimation near the boundaries, and a multinomial logistic link for p_{ent}

(Cooch and White 2018). We fit the full POPAN model with each of these parameterizations of *p* to the data and evaluated the relative support of each model by ΔAIC_c (Burnham and Anderson 2002). Because our model selection approach showed little uncertainty ($\Delta AIC_c > 7$ for all streams, Table 2.1), we restricted our subsequent analysis to the top model for each stream. Using the top model, we derived the population abundance at each intermediate time point in our time series. We excluded the terminal population sizes because they depend on inestimable parameters. We then scaled these abundances and their covariances to density per meter length of the sampling area.

To assess the relative impact of guppies on killifish densities over time, we log-transformed the estimated densities and used the delta method to estimate the associated variance-covariance matrix. We then computed the difference in log-density (Introduction – Control) at each time point. Finally, to test the temporal trend in the difference in killifish densities between reaches, we employed a variance components analysis on the differences in log-transformed density including the estimated variance-covariance matrix. In this analysis, we began with a model considering fixed effects of stream pair (guppy introductions performed in 2008 or 2009), canopy treatment (intact or thinned canopy), and time since introduction (in months) and all interactions of these factors. We treated all samples prior to guppy introduction as occurring at time 0, so that the y-intercept reflected the average pre-introduction difference in

density. We briefly considered random intercepts for each stream and a random slope of time since introduction within each stream but found little support for these random effects parameterizations ($\Delta AIC_c > 18$), likely due to the limited number of streams sampled. After fitting the initial, fully parameterized model (stream pair $\times$ canopy $\times$ time since introduction) by maximum likelihood, we sequentially removed the highest-order interaction terms, and compared the full and reduced model using likelihood ratio tests. We removed non-significant terms and repeated this procedure until only significant effects remained in the model (i.e. backwards step-wise model selection). Finally, we re-fit the final reduced model with restricted maximum-likelihood to assess model adequacy and make inference on the temporal trend in killifish density in the guppy Introduction reaches relative to the upstream Controls.

Habitat use of guppies and killifish

As a necessary precondition for our hypothesis of habitat-dependent, differential recruitment, we assessed the relative habitat use of guppies and killifish. To do so, we examined the total number of individuals captured of each species in each habitat from the time of guppy introduction through March 2012. Our average probability of catching a guppy if alive exceeded 90%, so these counts very nearly represent population size in the pool and riffle habitats. Although our killifish sampling never approached this level of completeness (average encounter probabilities for killifish approx. 40%), we distributed our

sampling effort roughly in proportion to the abundance of detectable killifish and so the counts of killifish captured in each habitat should on average reflect gross differences in habitat use within each reach. The distribution of these counts for each species showed right-skewness and so we log-transformed these values prior to analysis to fulfill assumptions of a normally distributed residuals. We analyzed these log-transformed counts of captured individuals using a generalized least squares model fitted using restricted maximum likelihood (Pinheiro et al. 2017) in R (R Core Team 2018). We included four factors and all of their interactions as independent variables in this model: (i) stream pair (guppy introductions done in 2008 or 2009); (ii) canopy treatment (intact or thinned canopy); (iii) habitat (pool or riffle); and (iv) a composite variable of species and reach (Introduction Guppy, Introduction Killifish and Control Killifish). After fitting this full model, we incorporated a continuous autoregressive correlation structure that accounts for the non-independence of successive counts as well as the variable time intervals between samples in each time series. Finally, we examined remaining residual heteroscedasticity with variance terms that incorporated all possible interactions of the factor covariates (i-iv) alone, nested within and in combination with an exponential variance structure for time since introduction or the fitted values from the model. We evaluated the relative support for each of these variance structures using Akaike Information Criterion (AIC) (Burnham and Anderson 2002). After determining an appropriate variance

structure, we tested the significance of habitat × species-reach interaction to assess the relative differences in habitat use of killifish and guppies across all streams.

Size distributions in pool and riffle habitats

We tested whether the effect of guppies on killifish would be greater in pool than in riffle habitats by comparing the behavior of the mean body size of captured individuals over time in pools and riffles in both Introduction and Control reaches. If guppies prey on neonate killifish, we predict that the proportion of juveniles in the killifish population would decline over time, thereby shifting the size distribution to a larger mean total length. Since guppies and presumably guppy predation occur more frequently in pools, we expected an increase in mean size in Introduction pools relative to Introduction riffles or either habitat in the Control. Alternatively, if guppies compete with killifish, slowing killifish growth, we would expect an accumulation of killifish in the smaller size classes. Since guppies are most abundant in pools, we would predict guppy competitive effects to match their distribution and Introduction pool mean size would decrease over time relative to the Introduction riffle or Control means.

To evaluate these hypotheses, we used generalized least squares linear models to assess habitat-specific change over time in the mean of the killifish size distribution in each habitat type and reach (Pinheiro et al. 2017, R Core

Team 2018). We considered several variables and many of their interactions in the initial model: (i) stream pair (guppy introductions performed in 2008 or 2009); (ii) canopy treatment (hereafter “canopy”, intact or thinned canopy); (iii) reach (Control or guppy Introduction); (iv) habitat (pool or riffle); (v) season (wet or dry); and (vi) time since guppy introduction (in months). The initial model, fit with restricted maximum likelihood, contained two five-way interactions: stream pair × canopy × reach × habitat × season and stream pair × canopy × reach × habitat × time. As in the variance components analysis of killifish densities, we coded the time as 0 for all mark-recapture samples collected prior to guppy introduction, so that we considered the average pre-introduction differences in mean size without the potential for temporal variation in the samples leading up to introduction.

Having constructed a full model, we next moved to account for the temporal autocorrelation in successive samples using a continuous autoregressive correlation structure, which incorporates the variable time intervals between samples. We also examined remaining residual heteroscedasticity and assessed the relative support for each variance structure using AIC. We considered variance terms that incorporated all possible interactions of the factor covariates (i-v) alone, nested within and in combination with an exponential variance structure for time since introduction or the fitted values from the model. After determining an appropriate variance structure, we

tested the significance of explanatory variables (i.e. the fixed effects). To do so, we used backwards step-wise selection on models fit with maximum likelihood and assessed the significance of each term using likelihood ratio test(s). When all remaining model terms were significant, we re-fit the model with restricted maximum likelihood to perform checks of model adequacy and inference.

Differential recruitment in pool and riffle habitats

We also reasoned that the loss of hatchling killifish due to guppy predation or competitive effects of guppies on killifish reproductive output would cause a reduction in numbers of killifish recruits in pools vs riffle habitats over time. Thus, we compared counts of first-time captures of immature killifish, < 28 mm total length (fish in this range were almost always first-time captures), in the alternative habitats in the Introduction and Control reaches. We expected that Introduction pool numbers would decrease over time, a result of direct mortality on immatures or through competition with mature killifish reducing egg productivity. Either of these IGP interactions should slow recruitment into the adult population in pools, where guppies are most abundant. In contrast, if riffles provide a reduction in IGP interactions with guppies, we should expect recruitment in riffles to remain relatively unchanged, mimicking recruitment in Control reaches.

We evaluated these predictions using generalized linear models with a negative binomial error structure and a log link (Brooks et al. 2017). We tested

the effects of several variables, including: (i) stream pair (guppy introductions done in 2008 or 2009); (ii) canopy treatment (intact or thinned canopy); (iii) reach (Control or guppy Introduction); (iv) habitat (pool or riffle); (v) season (wet or dry); (vi) time since guppy introduction (in months); and (vii) number of mature (≥28 mm) individuals captured. Our full model structure contained three interaction terms: stream pair × canopy × season; reach × habitat × time; and stream pair × canopy × reach × habitat × adult captures. The stream pair × canopy × season term accounts for potential seasonal differences in recruitment that may differ among (but not within) streams. The reach × habitat × time term addresses potential changes in recruit numbers over time within each stream across habitats and reaches. Preliminary investigation provided no support for differences in temporal trends across streams and so we did not consider it further. As before, we coded the time as 0 for pre-introduction samples. The stream pair × canopy × reach × habitat × adult captures term incorporates potential differences in the relationship between the number of immature and mature individuals captured within and among streams. We included this term to account for potential differences in the distribution of habitat, sampling effort or individuals across the study populations.

We then considered potential over-dispersion of our negative binomial response. We fit the full fixed effects model structure with dispersion terms for all possible interactions of the seven variables (i-vii), as well as sampling period

(pre- or post-2009 change in sampling scheme). The dispersion model used a log link for all terms. We assessed the merit of these different dispersion structures using AIC. After determining an appropriate dispersion model, we performed backwards step-wise model selection on the fixed effects using the same routine as applied to the models of differences in killifish density and killifish mean size.

Differential growth in pool and riffle habitats

We examined the alternatives of increased growth rates as an indirect effect of guppy predation decreasing killifish density versus decreased growth rate in response to the competitive impacts of guppies on killifish by testing the differences in killifish growth rates between pool and riffle habitats in the control and introduction sites.

At small sizes, killifish grow rapidly, but growth rate decelerates markedly as juveniles develop to maturity. Upon reaching maturity, adult growth rates continue to decline with body size, but at a much slower rate than observed in juveniles. While many complex modeling approaches have been developed to describe this pattern of growth (Quince et al. 2008a, Quince et al. 2008b, Wilson et al. 2018), we use piecewise linear models to describe differences in killifish growth rate with body size across habitats and reaches. Thus, we specify a model in which the slope of growth rate with body size differs on either side of a breakpoint to account for the juvenile and adult phases of killifish growth.

To address these differences in growth rate between habitats and reaches across a range of body sizes, we applied necessary restrictions to our killifish mark-recapture data. First, to assess differences in growth rate with body size, we excluded recaptures of individuals that occurred 45 or more days apart. Second, we excluded any successive recaptures in which an individual switched habitat or reach, so that we could reasonably associate the growth response with a specific habitat-reach combination. Finally, we also eliminated any successive recaptures in which an individual moved ≥ 10 m and could have crossed alternative habitats.

Before proceeding to analyze these data, we noted that the distribution of monthly killifish growth increments contained many individuals with no growth or slightly negative growth, likely related to measurement error or possibly "shrinkage" (Wikelski and Thom 2000). These negative growth values (minimum observed growth rate = -2.5 mm/mo.) preclude a standard log-normal model, so we employed a log-plus-3.5 transformation of growth rates to satisfy the assumption of normality in model residuals. We modeled this response as a function of (i) stream pair (guppy introductions done in 2008 or 2009); (ii) canopy treatment (intact or thinned canopy); (iii) reach (Control or guppy Introduction); (iv) habitat (pool or riffle); and (v) total length (in mm) at the beginning of the growth interval, as well as their interactions in the model. We centered the total length at the mean of all observations, 47.5 mm, so that the intercept for each

habitat and reach represented growth rate at this body size. We used a single, common breakpoint for the slope of growth rate with total length for all streams, habitats and reaches since this shift in the relationship of growth with body size represents a physiological parameter that is unlikely to predictably differ across these factors. Initial models that included a random intercept of individual identity suggested no estimable variation in growth rates among individuals, so we dropped this term from the model, yielding a linear piecewise model. We fit this model in R (R Core Team 2018). After fitting this model, we checked model adequacy before proceeding to make inferences. Inspection of residuals revealed no undesirable structure in model error with time since introduction or across the explanatory variables. Having validated modeling assumptions, we proceeded to compute contrasts in growth rates across reaches, habitats and the reach $\times$ habitat interaction across all streams across a range of body sizes, although we only present comparisons at the mean body size as we found them representative of the overall pattern. We also compared the juvenile and adult slopes of the growth increments with body size in a similar fashion. For one stream-reach-habitat combination, we had insufficient data to obtain a reliable estimate of the juvenile slope of growth rate and so we excluded this stream from comparisons of this parameter.

Results

Killifish population sizes

Here we show that the introduction and establishment of guppies is associated with a decline in the abundance of killifish in the introduction sites relative to the control sites in all four streams. We captured 8,327 killifish a total of 21,112 times between May 2007 and March 2012 across the four headwater streams. The median number of captures per individual was 2 (range: 1-18). We fit mark-recapture models to data from each stream with four different parameterizations of encounter probability, *p*. Models that allowed *p* to vary in each sample in each reach (time × reach) generally provided the most parsimonious description of the data, as measured by AIC_c, except in CAI, where the best model included only time-varying encounter probabilities (Table 2.1). The final variance components model of these population estimates included significant effects of stream pair × canopy ($\chi^2_1 = 23.43$, $p < 0.001$) and time since introduction ($\chi^2_1 = 16.63$, $p < 0.001$) on the relative killifish densities in guppy Introduction relative to Control reaches.

We first quantify the abundance of killifish in the introduction sites relative to the controls before guppies were introduced. The stream pair × canopy effect captures variation in the average density difference between reaches in each stream. In one stream pair, the intact canopy stream (LOL) had a greater initial

ratio of introduction to control killifish density (at time = 0, Introduction/Control = 1.8, 95% confidence interval [CI]: 1.42 – 2.24) than the thinned canopy stream (UPL; at time = 0, Introduction/Control = 1.0, 95% CI: 0.74 – 1.38). In the other pair, the estimated relationship was the opposite, with the thinned canopy stream (TAY) having a greater ratio of introduction to control killifish density (at time = 0, Introduction/Control = 1.3, 95% CI: 1.10 – 1.56) than the intact canopy stream (CAI; at time = 0, Introduction/Control = 0.8, 95% CI: 0.64 – 0.92).

We then consider how abundance in the introduction site changes relative to the control after the guppies were introduced. The time since introduction effect reflected a significant negative trend in the killifish density of guppy Introduction reaches relative to Control reaches ($\hat{\beta}$ = -0.01 $\pm$ 0.004; Fig 2.1) in all four streams. Thus, by the end of the study, the estimated ratio of killifish density in the introduction relative to the control significantly declined to 1.0 (95% CI: 0.81 – 1.20) in LOL, 0.6 (95% CI: 0.42-0.75) in UPL, 0.5 (95% CI: 0.41 – 0.61) in CAI, and 0.9 (95% CI: 0.70 – 1.04) in TAY. Killifish density is thus declining in Introduction sites relative to upstream controls, although these relative declines reflected different patterns of abundance across streams. In LOL and UPL, the density in Introduction reaches declined, while the Control reaches had relatively constant density. In CAI, the density in the Control reach increased over the course of the study, while the density in the Introduction reach remained relatively constant. In TAY, density in both the Control and

Introduction reaches fluctuated over time, although density in the Introduction did decrease relative to the Control over the course of the study.

Habitat use of killifish and guppies

Guppies and killifish used both pools and riffles, but guppies used pool more than riffle habitats than did killifish from either the Control reach or the Introduction reach.

Our model of the guppy and killifish counts in the alternative habitats included terms to account for temporal autocorrelation and residual heteroscedasticity. We found a significant temporal autocorrelation within each time-series ($\chi^2_1 = 389.08$, $p < .001$) with a strong correlation across samples, autocorrelation (ρ) = 0.87. Our variance structure selection showed little uncertainty (min. ΔAIC = 10.0) and included a combination of separate variance weights for each stream, habitat and species/reach combination and an exponential variance covariate of time since introduction. This variance structure represented a substantial improvement over the model without variance covariates (ΔAIC = 335.29). After accounting for the sources of autocorrelation and heteroscedasticity, we found no strong deviations from model assumptions and proceeded to interpret the relative habitat use of each species.

Mark-recapture sampling documented both species in pools and riffles across all four experimental streams (Fig 2.2; Table 2.2). On average, we captured 316.9 guppies (95% CI: 231.26 – 434.36) in pools and 37.1 guppies

(95% CI: 12.58 – 109.57) in riffles. For killifish, we captured an average of 36.9 individuals (95% CI: 22.96 – 59.38) and 68.9 individuals (95% CI: 50.43 – 94.06) in Control and Introduction pools, respectively, and 44.8 individuals (95% CI: 27.42 – 73.34) and 52.0 individuals (95% CI: 33.33 – 81.28) in Control and Introduction riffles, respectively. The estimated marginal means for each species/reach and habitat show that guppies used pools more than riffles as compared to Control killifish (linear contrast: $t_{580} = 3.48$, $p = 0.001$) or Introduction killifish (linear contrast: $t_{580} = 2.93$, $p = 0.004$), while Control and Introduction killifish did not differ in habitat use (linear contrast: $t_{580} = -1.07$, $p = 0.287$). On average, the proportion of pool habitat exceeded that of riffle habitat by a factor of 2 (ratios riffle/pool; CAI: 1/2.13, LOL: 1/2.33, UPL: 1/1.56, TAY: 1/1.63). Therefore, we can infer that guppies use pools relatively more than riffles, while killifish show no such bias in habitat use.

Size distributions

We found that mean sizes of killifish increased in Introduction pools (average model estimated percent change from introduction to end of study: 24.2 $\pm$ 3.15% S.E.) relative to Introduction riffles (2.2 $\pm$ 3.16%), Control pools (10.8 $\pm$ 3.16%) and Control riffles (4.4 $\pm$ 3.19%), as predicted if the dominant IGP interaction is guppy predation on neonate killifish, resulting in the reduced recruitment of smaller size classes of killifish in the Introduction pools.

Our final model for the mean of the killifish size distribution incorporated a continuous time autocorrelation structure and separate variance weights for wet and dry season in each stream. The temporal autocorrelation structure was highly significant ($\chi^2_1 = 12.05$, $p < .001$) and estimated a moderately strong correlation across monthly samples, $\rho = 0.53$. While our variance structure selection showed some uncertainty (Table 2.3), we note that the top 4 models all included separate weights for each season and stream (stream pair x canopy x season), and we therefore chose the simplest (and best supported by AIC) variance structure. Incorporating independent variance estimates for each season in each stream represented a substantial improvement over a model with no variance covariates ($\Delta AIC = 43.1$; Table 2.3). Estimated residual standard error varied between 0.27 mm and 9.05 mm in each stream, season combination. After accounting for these factors, the remaining residual variation was approximately normal and contained no strong sources of heteroscedasticity. Our model validation also found limited residual correlations across reaches and habitats within each stream. These checks allow us to use the final model for inference.

The final model contained fixed effects terms for season ($\chi^2_1 = 4.97$, $p = 0.026$), stream pair $\times$ canopy $\times$ habitat $\times$ reach ($\chi^2_1 = 4.80$, $p = 0.028$) and habitat $\times$ reach $\times$ time ($\chi^2_1 = 7.83$, $p = 0.005$; Table 2.4). The estimated season effect indicated that the mean of the size-frequency distribution increased by 0.80 $\pm$

0.408 mm in the wet season as compared to dry season. The stream pair × canopy × habitat × reach interaction terms accounts for the average differences in the mean of the size distribution in each stream, reach, habitat time-series (Table 2.4, compare y-intercept terms for further detail on how the mean differed across these factors). The habitat × reach × time term reflects how the trend in the mean of the killifish size distribution, estimated as the mean change in killifish body size (in mm) per month, varies among streams and habitats. This term implies significantly faster increase in the mean of killifish size distributions in Introduction pools (0.26 ± 0.033 mm/mo.) relative to (1) Introduction riffles (0.02 ± 0.033 mm/mo.; linear contrast: $t_{336} = 4.96$, $p < 0.001$), (2) Control pools (0.11 ± 0.033 mm/mo.; linear contrast: $t_{336} = 3.02$, $p = 0.014$) and (3) Control riffles (0.05 ± 0.034 mm/mo.; linear contrast: $t_{336} = 4.42$, $p < 0.001$; Fig 2.3). The trends in Introduction riffles, Control pools and Control riffles did not differ (Control pools – Control riffles: $t_{336} = 1.43$, $p = 0.485$; Control pools – Introduction riffles: $t_{336} = 1.94$, $p = 0.212$; Control riffles – Introduction riffles: $t_{336} = 0.50$, $p = 0.958$). The question is why we see such an increase in the size of Rivulus in introduction site pools relative to introduction site riffles or either habitat type in the control reach? One possibility is that it is caused by a reduction in recruitment of killifish in Introduction pools.

Recruitment

We found a reduction in killifish recruitment in Introduction pools (average model estimated percent change from introduction to end of study: -90.6%, 95% CI: -95.58 – -79.96) relative to Introduction riffles (54.0%, 95% CI: -23.48 – 209.84), Control pools (-49.6%, 95% CI: -80.00 – 27.01), or Control riffles (-0.5%, 95% CI: -57.23 – 131.28), as predicted if guppies prey on killifish neonates and/or if interspecific competition leads to increased juvenile mortality or decreased egg production.

The number of new juvenile recruits exhibited residual heteroscedasticity. We therefore incorporated negative binomial dispersion terms into our model. The best model of dispersion included a three-way interaction of canopy × mature captures × sampling period. The AIC values of alternative dispersion models revealed little model selection uncertainty (minimum ΔAIC = 5.0, w_i = 0.79; Table 2.5). Incorporating these dispersion terms substantially improved upon the standard negative binomial model (ΔAIC = 12.5). After accounting for these factors, the residual error showed no strong sources of heteroscedasticity and we proceeded to evaluate the importance of the fixed effects in the model.

The final model contained significant terms for stream pair × canopy × season (χ^2_1 = 5.64, p = 0.018), canopy × reach × mature captures (χ^2_1 = 13.81, p < 0.001), and habitat × reach × time (χ^2_1 = 7.15, p = 0.007; Table 2.6, Fig 2.4). The stream pair × canopy × season term accounts for differences in recruitment

that varied seasonally in each stream, such that recruitment was generally lower during wet season ($\hat{\beta} < 0$), except in LOL, which showed no significant seasonal differences in recruitment ($\hat{\beta} = 0.05 \pm 0.182$; Table 2.6). The canopy × reach × mature captures term shows that the number of new recruits depended upon the number of mature individuals captured in each reach and canopy treatment, such that under thinned canopies, the number of new recruits had a stronger positive relationship with the number of adult captures in the Control ($\hat{\beta} = 0.04 \pm 0.007$) than in the Introduction reach ($\hat{\beta} = 0.00 \pm 0.004$; Table 2.6). The habitat × reach × time term describes how the number of new killifish recruits changed in the 3-4 years following guppy introduction. New killifish recruits declined in Introduction pools ($\hat{\beta} = -0.06 \pm 0.009$) relative to (1) Introduction riffles ($\hat{\beta} = 0.01 \pm 0.008$; linear contrast: $t_{329} = -5.39$, $p < 0.001$), (2) Control pools ($\hat{\beta} = -0.02 \pm 0.011$; linear contrast: $t_{329} = 2.74$, $p = 0.032$), and (3) Control riffles ($\hat{\beta} = 0.00 \pm 0.010$; linear contrast: $t_{329} = -4.10$, $p < 0.001$; Table 2.6, Fig 2.4). The trends in Introduction riffles, Control pools and Control riffles did not differ (Control pools – Control riffles: $t_{329} = -1.16$, $p = 0.654$; Control pools – Introduction riffles: $t_{329} = -1.88$, $p = 0.237$; Control riffles – Introduction riffles: $t_{329} = -0.78$, $p = 0.864$). There is thus the predicted reduction in recruitment in the Introduction pools relative to the other three habitats if IGP interactions with guppies impact killifish recruitment.

Growth

If the primary impact of guppies on killifish is to compete for resources, we predicted a deceleration in killifish growth rates in Introduction Pools relative to Introduction riffles or either habitat in the Control without guppies. The differences in growth rates at the mean body size across reaches and habitats varied among streams (Fig 2.5, Table 2.7). On balance, we failed to find evidence of an average reduction in killifish growth rates in Introduction pools (growth rate at mean body size: 0.65 mm/mo., 95% CI: 0.577 – 0.726) relative to Introduction riffles (0.68 mm/mo., 95% CI: 0.482 – 0.881; linear contrast: t_{3003} = -0.24, p = 0.388) or Control pools (0.70 mm/mo., 95% CI: 0.611 – 0.795; linear contrast: t_{3003} = 0.86, p = 0.276). Growth rates in Introduction pools did decrease relative to Control riffles (1.02 mm/mo., 95% CI: 0.841 – 1.196; linear contrast: t_{3003} = 3.00, p = 0.004; Fig 2.5, Table 2.7). Thus, the pattern of growth rates across habitats and reaches do not match those predicted if competition with guppies strongly impacts killifish in Introduction pools where guppies are most abundant.

The shape of the killifish growth curve did not vary significantly across reaches or habitats. The model estimated breakpoint in the relationship between growth rate and body size occurred at 38.1 mm (95% CI: 36.23 – 40.76). At smaller sizes, during the steep decline in growth rates with increasing body sizes, the rate of decline did not significantly depend upon reach (t_{3003} = 0.59, p

= 0.668), habitat (t_{3003} = -0.06, p = 0.796) or their interaction (t_{3003} = 0.72, p = 0.616; Table 2.7). Similarly, at larger sizes, when growth rates decrease more gradually with increasing body size, the slope of this relationship did not vary significantly across reaches (t_{3003} = -0.06, p = 0.796), habitats (t_{3003} = 1.52, p = 0.249) or their interaction (t_{3003} = -0.63, p = 0.656; Fig 2.5, Table 2.7). Thus, differences in growth rate largely reflected overall differences between reaches and habitats as captured by the estimated growth rate at the mean body size (y-intercept). At this size, differences in killifish growth rates do not correspond to the relative distribution of guppies (and presumably their competitive effects) across habitats or changes in the mean of the killifish size distribution. Furthermore, these results show that the increase in killifish body size in Introduction site pools relative to other habitat types (Intro Riffles, Control pools, Control riffles) is not caused by accelerated growth.

Discussion

Our results support the hypothesis that the persistence of killifish in a bidirectional, asymmetric IGP relationship with guppies, is enabled by the joint phenomena of differential habitat-use and habitat-dependent recruitment. Introduced guppies caused killifish population densities to decline towards those typical of KG communities (Fig 2.1), as recorded in earlier studies of natural KG communities or decades old introduction experiments (Gilliam et al. 1993, Walsh et al. 2011, Furness and Reznick 2015). As guppies establish and

killifish decline, guppies exhibit a strong bias towards using pools over riffles, while killifish show no strong difference in habitat use (Fig 2.2). This differential habitat use is associated with an increase in the mean of the killifish size distribution in Introduction site pools in comparison to those in Introduction site riffles and in pools or riffles in the guppy-free Control site (Fig 2.3). This upward shift in mean size was accompanied by a decrease in the number of killifish recruits in Introduction site pools with abundant guppies (Fig 2.4). The growth rates of killifish in Introduction pools did not increase relative to those in riffles or in either habitat in the Control (Fig 2.5), so growth cannot account for the increase in mean of the killifish size distribution in Introduction site pools. We conclude that the increase in mean killifish size in Introduction site pools in comparison to other localities is caused by reduced recruitment. In independent experiments, we found that guppies prey upon newborn killifish (Fraser and Lamphere 2013, Furness and Reznick 2015). Taken together, these results support the hypothesis that guppies function as an IG predator of IG prey killifish. Furthermore, our results suggest that the killifish persist in the face of the guppy invasion because guppies selectively use pools, which allows killifish to maintain recruitment in riffles. Thus, the scarcity of guppies in riffle habitats promotes the persistence of the IG predator and prey in spite of theory that predicts that the two species are unlikely to stably coexist (Polis et al. 1989, Holt and Polis 1997, Mylius et al. 2001).

In comparison to predation, guppy competition appears to play a minor role in the impact of IGP interactions on killifish. We found no evidence of decreased individual growth rates in Introduction pools relative to other areas as predicted by guppy competition. Similarly, Fraser and Lamphere (2013) showed experimentally that the growth of guppies was more strongly affected by an equivalent mass of the killifish than by an equivalent mass of their own species. Traditional models of coexistence established the universal criterion for successful coexistence: each species should have a stronger impact on its conspecifics than other species (Chesson 2000, Adler et al. 2007). The failure of this criterion suggests that guppies should not be able to successfully invade KO environments, yet they do.

The importance of killifish-guppy competition was further challenged by the lower killifish abundance in KG communities relative to KO communities plus the observation that killifish grow faster in KG communities than in KO communities, implying higher per-capita resource availability for killifish when guppies are present (Gilliam et al. 1993, Walsh et al. 2011, Furness and Reznick 2015). Walsh et al. (2011) reinforced this interpretation by transplanting individual marked killifish from a KO site into the KG site downstream. The growth rates of the transplanted fish accelerated to match those of the residents (Walsh et al. 2011). Thus, competition may play a subordinate role to predation

in the effect of guppies and killifish as IGP interaction occur across the alternative habitats.

The importance of habitat use

Fraser and Lamphere (2013), and Furness and Reznick (2015) established that guppies can only consume recently hatched killifish. The probability of a guppy encountering a near-term egg with a moving embryo or a newly hatched killifish may vary across habitat types. In pools, killifish typically deposit sticky eggs in overhanging rootlets, woody debris or, if those are unavailable, on the substrate, where they can be readily seen and the hatchling captured before escaping into the substrate (Fraser and Lamphere 2013). In contrast, in riffles, killifish spawn and deposit eggs among the complex, rocky substrate and leafy debris and do so in a habitat type with much lower densities of guppies. Goldberg (unpublished) recently found that, controlling for density, killifish behaviorally modified their egg deposition sites in response to guppies. Killifish placed more eggs in riffles than pools when guppies were present than when absent in both artificial stream experiments and in these same experimental introduction streams. These differences in egg density and detectability may combine with the strong pool-bias of guppy distributions (Fig 2.2) to yield a lower IG predator attack rate in riffles.

The differential habitat use of guppies and killifish differs from numerous cases in which predation risk promotes size-specific habitat shifts (e.g., Savino

and Stein 1982, Werner and Hall 1988, Eklöv and Persson 1995, Persson and Eklov 1995, Byström et al. 2003). In our system, the survival and persistence of IG prey killifish depends upon the differential, but not exclusive, use of alternative habitats, rather than size-specific use or ontogenetic niche shifts (HilleRisLambers et al. 2006, Abrams 2011, Hin et al. 2011). Riffles serve as a habitat in which killifish can be more successful in reproduction and recruitment because guppies are far less abundant in riffles than in pools. Thus, lower killifish recruitment in pools with abundant guppies likely causes the overall reduction of killifish density in KG habitats (Fig 2.1), and differential habitat use acts to stabilize the killifish population at a new, lower average density. This conclusion generally agrees with prior results demonstrating that habitat structure reduces antagonistic IGP interactions and promotes coexistence (Finke and Denno 2006, Janssen et al. 2007) and theory that evaluates differential habitat use or preferences under IGP (Snyder et al. 2005).

Our findings accord with a habitat-specific impact of guppy predation upon neonate killifish driving a decline in killifish density. A limitation of our approach is that we cannot produce a well-calibrated map of the competitive and predatory interactions in this IGP system. The mean of the killifish size distribution represents the outcome of many interacting demographic processes, including growth, survival and reproductive output across a range of body sizes. Changes in any of these vital rates can lead to differences in the size

structure of a population. Similarly, reduced recruitment could represent the product of guppy predation on hatchling killifish and/or guppy competition with breeding killifish reducing egg productivity; however, the observed differences in growth rates across habitats and the relative competitive superiority of adult killifish to guppies suggests that predation is a more probable explanation. Despite these limitations, we have described several results that support the predictions of our hypothesis.

Other factors that affect the stability of IGP interactions

Classic IGP models predict that coexistence is limited to intermediate productivities, such that increased productivity will favor the IG predator at the expense of the IG prey (e.g., Polis et al. 1989, Holt and Polis 1997, Mylius et al. 2001). Despite the differences between canopy treatments in productivity, we did not find consistent effects of canopy thinning on killifish density in the two stream pairs. Rather, in one stream pair (CAI/TAY), the thinned canopy had generally higher population densities in the Introduction as compared to the Control, while in the other stream pair (LOL/UPL), the thinned canopy had lower population densities in the Introduction as compared to the Control (Fig 2.1). Novak (2013) reported results of a study involving predatory whelks that similarly contradicted theory, such that the abundance of the IG prey increased with productivity. We also found no significant effects of our canopy treatment on mean body size of the killifish population. Thus, we find no reason to suggest

that differences in productivity can account for the observed dynamics of the killifish population. Our results may most closely echo those of Borer et al. (2003), who showed that the IG predator positively responded to an increase in productivity, while the IG prey density did not vary in a system of two parasitoid insects. As in our system, these parasitoid insects show distinct patterns of habitat use, which likely contribute to their coexistence (Borer et al. 2004).

Age-, size- or stage-structured trophic interactions, where one stage is invulnerable to predation, can provide another path to invasion success and coexistence (Mylius et al. 2001, van de Wolfshaar et al. 2006, Hin et al. 2011, Reichstein et al. 2013). Montserrat et al. (2012) demonstrated empirically that invasion success depended upon the stage-structure of the resident and invader populations of a reciprocal IGP system. IG prey populations with adults always resisted invasion by the IG predator. However, when they removed all IG prey adults who could prey on the IG predator's juveniles, all invasion attempts were successful. Likewise, our IGP relationship depends on size-structured predation and competition between both species. Size-structured predation takes the form of invading adult guppies preying on hatchling killifish and adult killifish preying on juvenile guppies (Seghers 1974, Mattingly and Butler IV 1994, Fraser and Lamphere 2013, Furness and Reznick 2015). These interactions can produce recruitment bottlenecks as demonstrated in other IGP systems (Schröder et al. 2009b, Toscano et al. 2016) and may contribute to habitat

dependent recruitment and the persistence of both species in this IGP system. Similarly, competitive interactions depend upon the size of the interacting individuals within and between both species. Indeed, on-going work examining the size-structured interactions between these two species indicates that all but the smallest size classes of killifish (< 12 mm) out-compete all size classes of guppies in aquaria without any potential habitat structure (Potter, pers comm). These findings suggest that the population size-structure of the interacting species plays a critical role in this IGP.

These structured IGP interactions may further vary seasonally and influence the persistence of the community. Theory and empirical work show that species with differential responses to temporal variation (i.e., phenology) may have improved odds of coexistence (Amarasekare 2007b, 2008). In these systems, seasonality acts to temporally partition resources, creating a temporal refuge of sorts that reduces the overall strength of interspecific interactions relative to intraspecific interactions. Similar mechanisms may operate in KG communities as each species responds to the wet and dry seasons. Wet season flooding reduces resource availability and displaces some guppies downstream, leading to reduced guppy densities and recruitment, and a shift towards larger body sizes (Rodd and Reznick 1997). Similarly, the killifish population size structure and recruitment also differed between seasons, such that killifish were on average larger during the wet season and had generally greater recruitment

during dry season (Table 2.4, Table 2.6). These patterns strongly suggest that both the numbers and size distributions of each species, and thus, the intensity of IGP interactions, will depend upon seasonality as the KG community develops. This seasonal variation may play a key role in the persistence of both species.

A community in transition

The current study spans the relatively short time scale of 3-4 years. The characteristics of the killifish populations in the guppy introduction sites do not yet match those typical of natural KG communities or older introduction experiments. The differences in the size structure of killifish populations in these new experiments, with reduced recruitment causing a shift to larger mean of the killifish size distribution in pools, is different from what we see in natural KG communities. The killifish populations in KG communities have similar or even smaller mean sizes than in the KO communities upstream (Gilliam et al. 1993, Furness and Reznick 2015, Goldberg unpublished data). Furthermore, killifish from natural KG communities have substantially higher growth rates than their counterparts upstream, above the barrier waterfalls that exclude guppies (Walsh et al. 2011). We observed the opposite trends: killifish in the guppy Introduction sites tend to grow more slowly than those in the upstream Controls without guppies.

A key difference between the current study and previous comparisons of growth rates in natural KO and KG communities is that we are documenting the ecological and evolutionary transition from a KO to a KG community. The population densities of killifish remains higher than those in natural KG communities, which means that the level of intraspecific competition experienced by killifish in the Introduction also remains higher than it would be in a well-established KG community. Moreover, the niche overlap between guppies and killifish will change as guppies adapt to the KG environment and shift from eating a diet rich in invertebrates to mostly algae and detritus (Bassar et al. 2010, Zandonà et al. 2011, Simon et al. 2017). Experiments in artificial streams reveal that niche divergence between guppies and killifish increases with the evolution of each species. KG guppies paired with KG killifish have improved fitness relative to KG guppies paired with KO killifish, and KG guppies have higher fitness than high predation guppies when both are paired with KO killifish (Bassar et al. 2017a).

The time window of the current study allows for the evolution of some aspects of the life histories and phenotypes of male guppies but not of female guppies (Endler 1980, Reznick and Bryga 1987, Reznick et al. 1990, Reznick et al. 1997, Kemp et al. 2018, Reznick et al. *in press*). Killifish have a much longer generation time and likely require longer periods to evolve in response to guppies and the associated changes in ecology in KG habitats. Nonetheless,

these short-term transient phenomena set the stage for adaptive evolution that will ultimately lead to stable, long-term dynamics within this IGP system. Although the evolutionary dynamics of killifish have not been studied in the same detail as guppies, Walsh and Reznick (2011) showed that killifish life history evolution happened within 30 and 35 years after the introduction of guppies in two experiments, presumably leading to IGP relationships comparable to natural KG communities.

Our large-scale field study has revealed how the transient dynamics of an IGP relationship can contribute to the persistence of IG prey species. We have demonstrated that guppies' differential use of pools enables killifish to sustain recruitment in riffles, which should in turn enhance their ability to persist in the face of invading guppies. More generally, these results argue that differences in habitat use among IGP species can facilitate short-term persistence that may create sufficient time for the two species to evolve in ways that mitigate antagonistic interactions and establish stable, long-term coexistence.

Tables

Table 2.1. Model selection criteria for different parameterizations of encounter probability, p, in POPAN mark-recapture models of population dynamics in four headwaters streams of the Guanapo drainage from 2007-2012. AIC_c gives the Akaike Information Criteria with small sample correction ΔAIC_c gives the difference between a given model and the minimum AIC_c in the set. All models use a time × reach parameterization for survival, ϕ, and probability of entry, p_{ent}.

CAI			TAY			LOL			UPL		
Model	AIC_c	ΔAIC_c	Model	AIC_c	ΔAIC_c	Model	AIC_c	ΔAIC_c	Model	AIC_c	ΔAIC_c
time	9942.1	0	time × reach	11718.2	0	time × reach	24116.4	0	time × reach	15374.4	0
time × reach	9950.5	8.34	time	11743.9	25.69	time	24270.5	154.10	time	15381.6	7.21
intercept	9978.2	36.09	reach	11805.5	87.26	reach	25011.4	895.04	intercept	15620.6	246.21
reach	9981.0	38.87	intercept	11834.2	116.00	intercept	25063.5	947.14	reach	15624.7	250.39

Table 2.2. Marginal mean estimates for model of number of captured individuals of killifish and guppies in Control (C) and guppy Introduction (I) reaches in pool (P) and riffle (R) habitat in four headwaters streams of the Guanapo drainage from 2007-2012. Estimates and standard errors (SE) given for the log-transformed count of individuals.

Species	Stream	Reach	Habitat	$\hat{\beta}$	SE
Guppy	CAI	I	P	5.3	0.22
Guppy	CAI	I	R	2.3	1.22
Killifish	CAI	C	P	3.1	0.59
Killifish	CAI	C	R	3.8	0.42
Killifish	CAI	I	P	4.3	0.20
Killifish	CAI	I	R	3.3	0.74
Guppy	TAY	I	P	5.4	0.47
Guppy	TAY	I	R	3.4	1.41
Killifish	TAY	C	P	3.9	0.38
Killifish	TAY	C	R	3.4	0.77
Killifish	TAY	I	P	3.9	0.38
Killifish	TAY	I	R	4.4	0.33
Guppy	LOL	I	P	6.0	0.26
Guppy	LOL	I	R	4.1	0.83
Killifish	LOL	C	P	3.6	0.60
Killifish	LOL	C	R	4.2	0.26
Killifish	LOL	I	P	4.5	0.24
Killifish	LOL	I	R	4.4	0.28
Guppy	UPL	I	P	6.3	0.28
Guppy	UPL	I	R	4.6	0.84
Killifish	UPL	C	P	3.9	0.27
Kiliifish	UPL	C	R	3.7	0.41
Killifish	UPL	I	P	4.2	0.23
Killifish	UPL	I	R	3.7	0.30

Table 2.3. Selection criteria for variance structure of the generalized least squares model of temporal trends in mean total length (mm) of killifish in Control and guppy Introduction reaches in pool and riffle habitat in four headwaters streams of the Guanapo drainage from 2007-2012. Variance structures that combine factor covariates with continuous covariates are indicated with '+' and while those that condition the continuous covariate on the factors are indicated with '|'. AIC gives the Akaike Information Criteria ΔAIC gives the difference between a given model and the minimum AIC in the set and w_i gives the model weight, $\exp(-\Delta AIC_i)/\sum_i \exp(-\Delta AIC_i)$. Only dispersion models with ΔAIC < 8 (and the intercept-only model) shown for brevity. All models include a continuous autoregressive correlation structure.

Variance Structure	AIC	ΔAIC	w_i
year pair × canopy × season	1916.3	0	0.35
year pair × canopy × season + time since introduction	1917.2	0.9	0.22
year pair × canopy × season + fitted values	1918.0	1.6	0.16
fitted value | year pair × canopy × season	1919.4	3.1	0.08
year pair × season + time since introduction	1921.6	5.3	0.03
year pair × season	1923.0	6.7	0.01
season + time since introduction	1923.4	7.1	0.01
fitted values | year pair × season	1923.4	7.1	0.01
fitted values | reach × season	1923.5	7.2	0.01
year pair × season + fitted values	1923.6	7.3	0.01
year pair × habitat × season + time since introduction	1924.3	7.9	0.01
Intercept-only	1959.4	43.1	<0.01

Table 2.4. Parameter estimates for model of temporal trends in mean total length (mm) of killifish in Control (C) and guppy Introduction (I) reaches in pool (P) and riffle (R) habitat in four headwaters streams of the Guanapo drainage from 2007-2012. Y-intercept parameters indicate the mean length at the time of guppy Introduction during the dry season. Dashes indicate parameters apply to all streams, reaches and/or habitats.

Parameter	Stream	Reach	Habitat	$\hat{\beta}$	SE
y-intercept	CAI	C	P	50.9	1.51
y-intercept	CAI	C	R	48.0	1.59
y-intercept	CAI	I	P	51.9	1.51
y-intercept	CAI	I	R	50.4	1.51
y-intercept	TAY	C	P	41.4	1.13
y-intercept	TAY	C	R	45.3	1.14
y-intercept	TAY	I	P	41.8	1.13
y-intercept	TAY	I	R	41.6	1.13
y-intercept	LOL	C	P	41.3	1.06
y-intercept	LOL	C	R	43.0	1.06
y-intercept	LOL	I	P	40.7	1.06
y-intercept	LOL	I	R	41.5	1.06
y-intercept	UPL	C	P	43.5	1.06
y-intercept	UPL	C	R	41.0	1.08
y-intercept	UPL	I	P	43.7	1.06
y-intercept	UPL	I	R	43.0	1.06
Season - wet	-	-	-	0.80	0.408
Time	-	C	P	0.11	0.033
Time	-	C	R	0.05	0.034
Time	-	I	P	0.26	0.033
Time	-	I	R	0.02	0.033

Table 2.5. Selection criteria for negative binomial dispersion model of the number of new killifish recruits in Control and guppy Introduction reaches in pool and riffle habitat in four headwaters streams of the Guanapo drainage from 2007-2012. AIC gives the Akaike Information Criteria ΔAIC gives the difference between a given model and the minimum AIC in the set and w_i gives the model weight, $\exp(-\Delta AIC_i)/\sum_i \exp(-\Delta AIC_i)$. Only dispersion models with ΔAIC < 10 (and the intercept-only model) shown for brevity.

Dispersion terms	AIC	ΔAIC	w_i
canopy × mature captures × sampling period	1578.8	0	0.79
canopy × sampling period	1583.8	5.0	0.07
pair × mature captures × sampling period	1586.2	7.3	0.02
sampling period	1587.2	8.4	0.01
habitat × sampling period	1587.5	8.6	0.01
pair × canopy × mature captures × sampling period	1587.6	8.7	0.01
mature captures	1587.9	9.1	0.01
habitat × mature captures × sampling period	1588.0	9.2	0.01
habitat × canopy × sampling period	1588.2	9.3	0.01
Intercept-only	1591.3	12.5	< 0.01

Table 2.6. Parameter estimates for model of temporal trends in new killifish recruits in Control (C) and guppy Introduction (I) reaches in pool (P) and riffle (R) habitat in four headwaters streams of the Guanapo drainage from 2007-2012. Y-intercept parameters indicate the number of recruits at the time of guppy introduction during the dry season given the mean number of adult captures in a stream × reach × habitat. Dashes indicate parameters apply to all streams, reaches and/or habitats. All parameter estimates given on the log-scale.

Parameter	Stream	Reach	Habitat	$\hat{\beta}$	SE
y-intercept	CAI	C	P	1.31	0.297
y-intercept	CAI	C	R	1.44	0.303
y-intercept	CAI	I	P	1.27	0.234
y-intercept	CAI	I	R	1.00	0.256
y-intercept	TAY	C	P	2.20	0.282
y-intercept	TAY	C	R	2.33	0.314
y-intercept	TAY	I	P	2.17	0.201
y-intercept	TAY	I	R	1.90	0.231
y-intercept	LOL	C	P	1.30	0.290
y-intercept	LOL	C	R	1.42	0.286
y-intercept	LOL	I	P	1.25	0.220
y-intercept	LOL	I	R	0.99	0.235
y-intercept	UPL	C	P	1.91	0.291
y-intercept	UPL	C	R	2.03	0.321
y-intercept	UPL	I	P	1.87	0.216
y-intercept	UPL	I	R	1.61	0.239
Season – wet	CAI	-	-	-0.60	0.255
Season – wet	TAY	-	-	-0.54	0.253
Season – wet	LOL	-	-	0.05	0.182
Season – wet	UPL	-	-	-0.98	0.226
Mature captures	CAI/LOL	C	-	0.02	0.005
Mature captures	CAI/LOL	I	-	0.02	0.003
Mature captures	TAY/UPL	C	-	0.04	0.007
Mature captures	TAY/UPL	I	-	0.00	0.004
Time	-	C	P	-0.02	0.011
Time	-	C	R	0.00	0.010
Time	-	I	P	-0.06	0.009
Time	-	I	R	0.01	0.008

Table 2.7. Parameter estimates for piecewise linear mixed model of killifish growth rates in Control (C) and guppy Introduction (I) reaches in pool (P) and riffle (R) habitat in four headwaters streams of the Guanapo drainage from 2007-2012. Y-intercept parameters indicate the monthly growth rates of killifish at the population average body size, 47.5 mm total length. Dashes indicate parameters apply to all streams, reaches and/or habitats. All parameter estimates given on the log plus 3.5 scale, except for the slope breakpoint. Juvenile slope represents the slope of growth rate with body size at body sizes less than the breakpoint, while adult slope indicates the same slope at body sizes greater than the breakpoint. NAs represent inestimable parameters.

Parameter	Stream	Reach	Habitat	$\hat{\beta}$	SE
Slope Breakpoint	-	-	-	38.13	0.646
y-intercept	CAI	C	P	1.47	0.026
y-intercept	CAI	C	R	1.71	0.030
y-intercept	CAI	I	P	1.51	0.020
y-intercept	CAI	I	R	1.62	0.086
y-intercept	LOL	C	P	1.51	0.016
y-intercept	LOL	C	R	1.46	0.022
y-intercept	LOL	I	P	1.39	0.013
y-intercept	LOL	I	R	1.35	0.021
y-intercept	TAY	C	P	1.37	0.023
y-intercept	TAY	C	R	1.43	0.036
y-intercept	TAY	I	P	1.42	0.018
y-intercept	TAY	I	R	1.31	0.028
y-intercept	UPL	C	P	1.38	0.023
y-intercept	UPL	C	R	1.30	0.030
y-intercept	UPL	I	P	1.38	0.021
y-intercept	UPL	I	R	1.43	0.031
Juvenile Slope	CAI	C	P	-0.0317	0.00833
Juvenile Slope	CAI	C	R	-0.0177	0.01030
Juvenile Slope	CAI	I	P	-0.0443	0.00947
Juvenile Slope	CAI	I	R	NA	NA
Juvenile Slope	LOL	C	P	-0.0210	0.00541
Juvenile Slope	LOL	C	R	-0.0230	0.00480
Juvenile Slope	LOL	I	P	-0.0157	0.00488
Juvenile Slope	LOL	I	R	-0.0239	0.00331
Juvenile Slope	TAY	C	P	-0.0389	0.00387
Juvenile Slope	TAY	C	R	-0.0299	0.00811
Juvenile Slope	TAY	I	P	-0.0295	0.00536
Juvenile Slope	TAY	I	R	-0.0338	0.00568
Juvenile Slope	UPL	C	P	-0.0419	0.00523
Juvenile Slope	UPL	C	R	-0.0418	0.00686
Juvenile Slope	UPL	I	P	-0.0426	0.01049
Juvenile Slope	UPL	I	R	-0.0383	0.00620
Adult Slope	CAI	C	P	-0.0044	0.00191
Adult Slope	CAI	C	R	-0.0095	0.00234

Adult Slope	CAI	I	P	-0.0069	0.00112
Adult Slope	CAI	I	R	-0.0140	0.00429
Adult Slope	LOL	C	P	-0.0035	0.00151
Adult Slope	LOL	C	R	-0.0064	0.00243
Adult Slope	LOL	I	P	-0.0023	0.00117
Adult Slope	LOL	I	R	-0.0061	0.00266
Adult Slope	TAY	C	P	-0.0032	0.00214
Adult Slope	TAY	C	R	-0.0031	0.00320
Adult Slope	TAY	I	P	-0.0041	0.00185
Adult Slope	TAY	I	R	-0.0035	0.00341
Adult Slope	UPL	C	P	-0.0083	0.00248
Adult Slope	UPL	C	R	-0.0051	0.00402
Adult Slope	UPL	I	P	-0.0023	0.00147
Adult Slope	UPL	I	R	-0.0034	0.00345

Figures

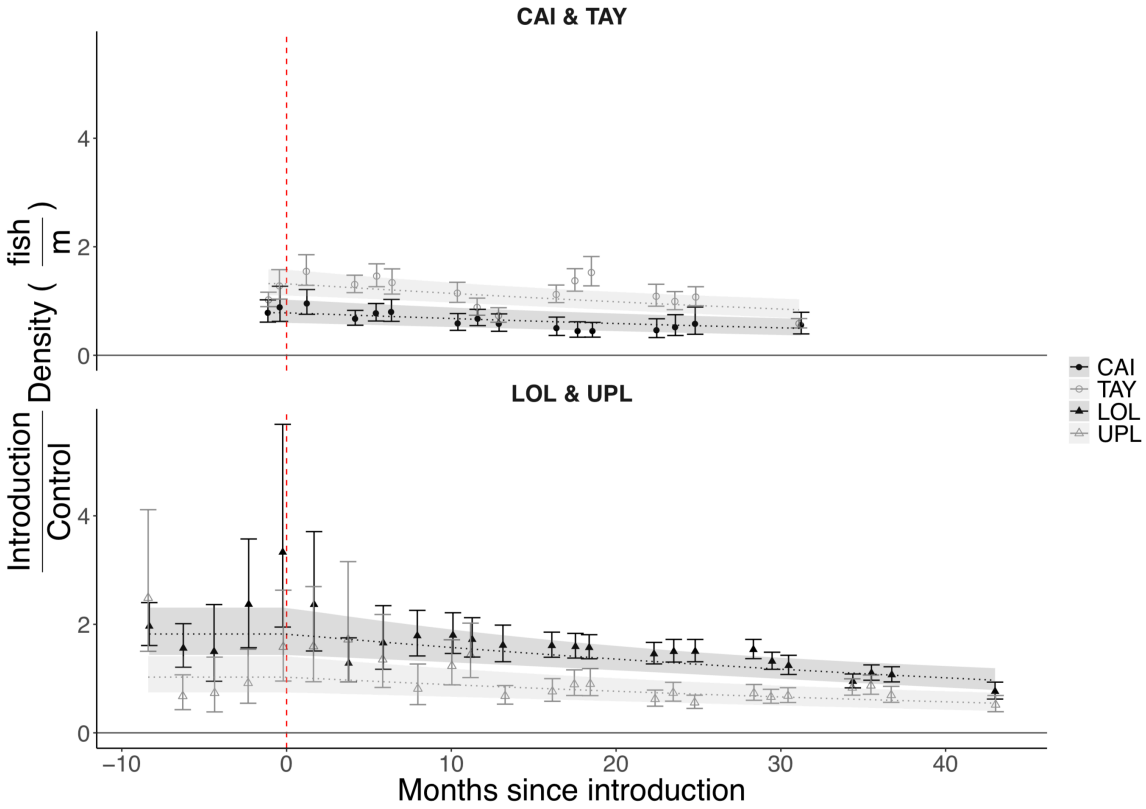

Figure 2.1. Difference in density (fish/m ± 1 SE) between Control and guppy Introduction reaches in four headwaters streams (CAI: black circles; TAY: gray circles; LOL: black triangles; UPL: gray triangles) of the Guanapo River between 2007-2012. Densities in each reach estimated using the POPAN formulation of the Jolly-Seber mark-recapture model. Lines represent the estimated difference in density from the final model of the variance components analysis of temporal trend and shaded regions capture the CI of this estimate.

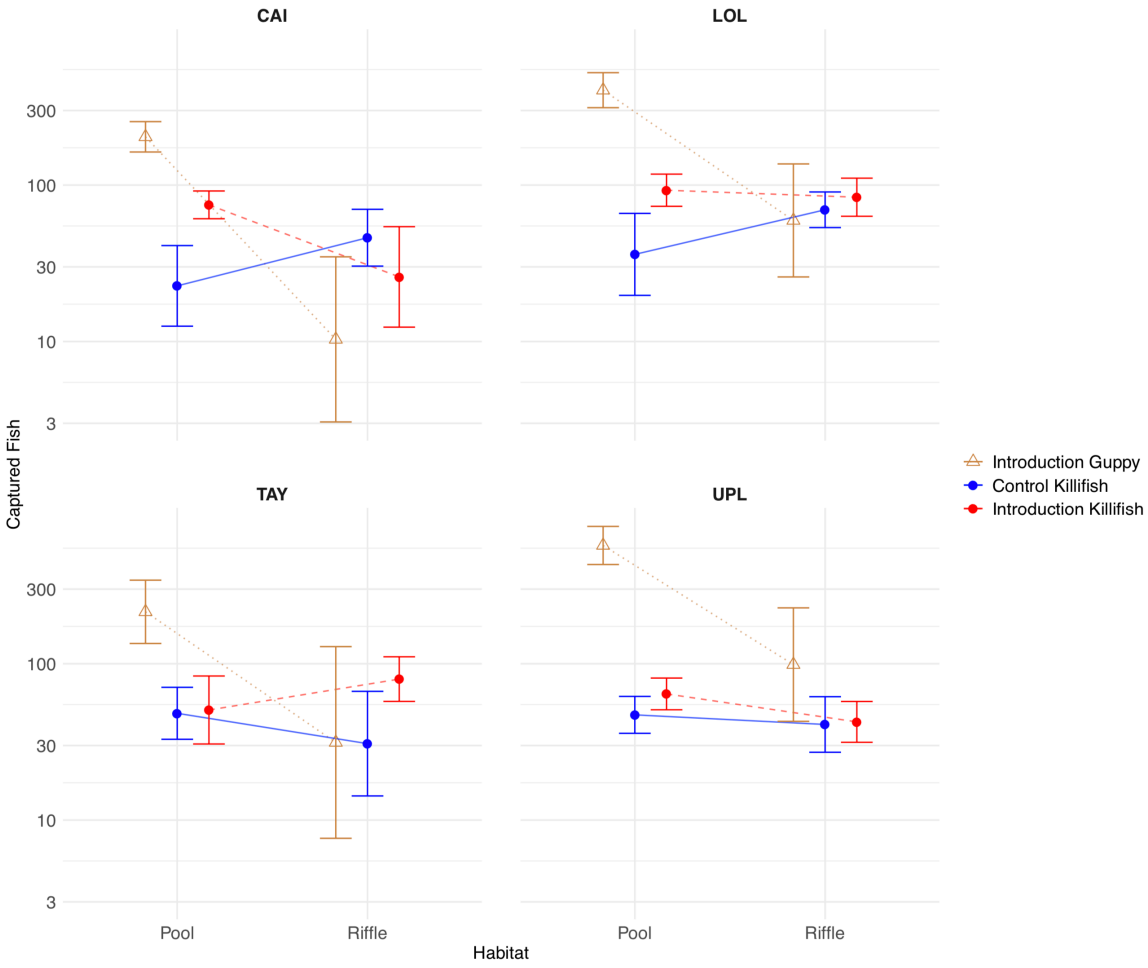

Figure 2.2. Pool and riffle habitat use of guppies (brown triangles) captured in the Introduction reach, and killifish captured in the Control (blue circles) and Introduction (red circles) reaches of four headwaters streams of the Guanapo River between 2008-2012. Points represent marginal means and error bars capture ± 1 SE from a generalized least squares model. Note that these means do not account for the relative availability of habitat or capture probabilities.

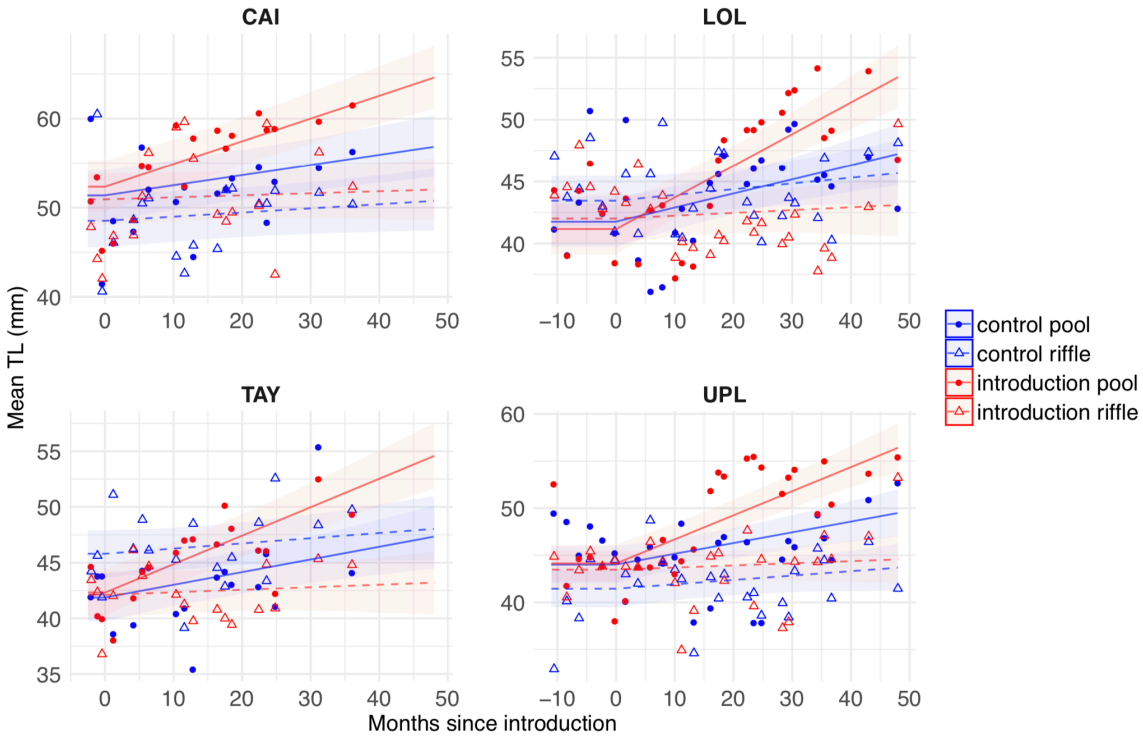

Figure 2.3. Temporal trends in mean of the killifish size distribution, measured in total length (TL, mm) in Control (blue) and guppy Introduction (red) reaches in pool (filled circles and solid lines) and riffle (open triangles and dashed lines) habitats in four headwaters streams in the Guanapo watershed from 2007-2012. Data shown with points, generalized least squares model estimates shown with lines and shaded regions represent CIs of model estimates. Model estimates are plotted at an average seasonality for our sampling period.

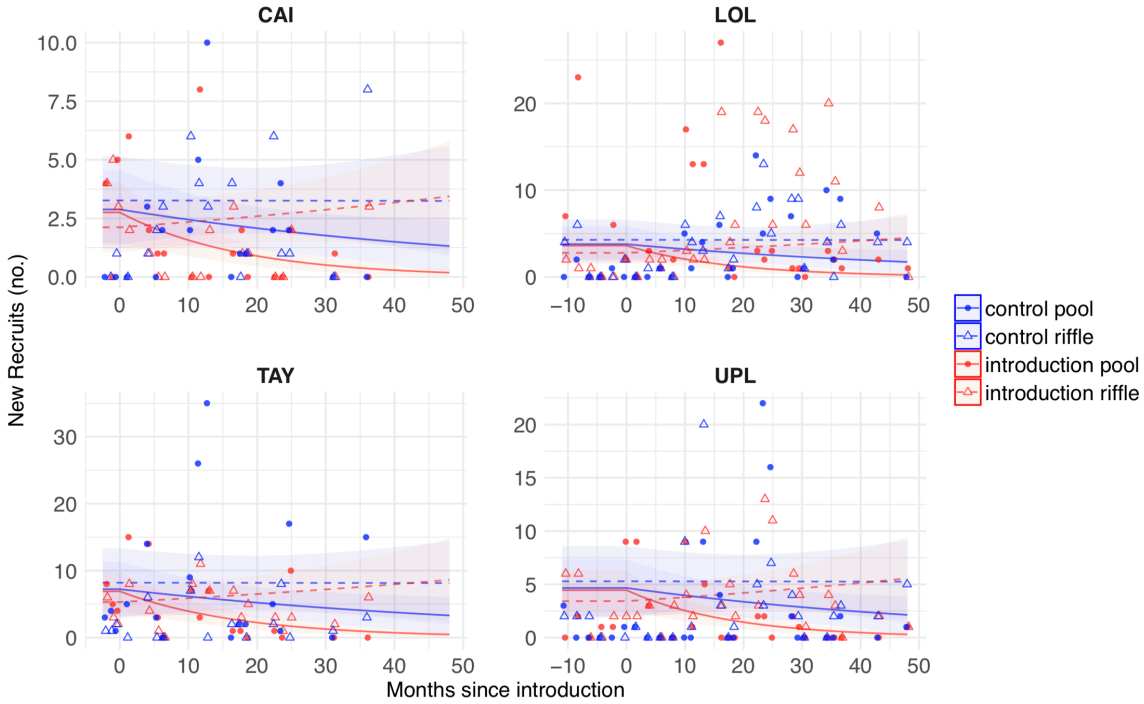

Figure 2.4. Temporal trends in the number of unmarked, immature killifish (<28 mm) in Control (blue) and guppy Introduction (red) reaches in pool (filled circles and solid lines) and riffle (open triangles and dashed lines) habitats in four headwaters streams in the Guanapo watershed from 2007-2012. Data shown with points, generalized linear model estimates shown with lines and shaded regions represent CIs of model estimates. Model estimates are plotted at an average seasonality and with an average number of adult captures for our sampling period.

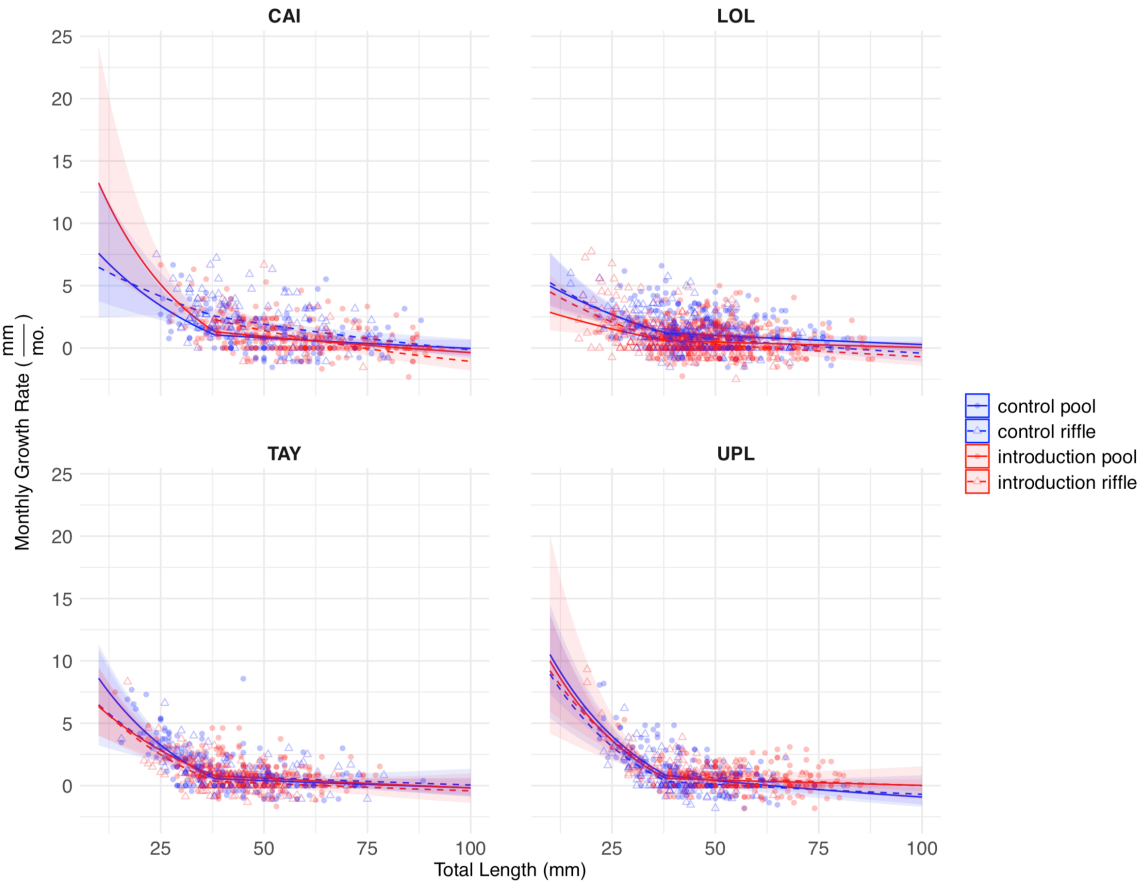

Figure 2.5. Monthly growth rates (mm total length/mo.) of killifish in Control (blue) and guppy Introduction (red) reaches in pool (filled circles and solid lines) and riffle (open triangles and dashed lines) in four headwaters streams in the Guanapo watershed from 2009-2011. Data shown with points, piecewise linear model estimates shown with lines and shaded regions represent 95% CIs of model estimates.

Chapter 3: Evolution modifies habitat selection, diel activity patterns and population persistence under intraguild predation

Abstract

In intraguild predation, two consumer species compete for a shared resource and also prey upon each other. Theory predicts that these interactions should rarely occur, yet they are frequently found in nature. Although many mechanisms have been proposed to explain this pattern, the potential for evolutionary change to modify intraguild predation relationships have rarely been considered. If evolution alters these interactions, then key interaction traits should change as each species adapts to the ecological context created by joint competition and predation. We test this prediction by examining stage-specific patterns of habitat selection and diel activity across an evolutionary gradient of intraguild prey killifish (*Rivulus hartii*) experience with intraguild predator guppies (*Poecilia reticulata*). Using artificial stream experiments and observations in natural streams, we show that guppies preferentially use pools, leading to differential responses in the distribution of killifish adults and eggs depending upon prior experience with guppies. Naïve adult killifish show no change or decrease in abundance in marginal habitats with guppies, while the number of killifish eggs spawned in these same marginal areas increases with guppies. Conversely, experienced adult killifish increase in abundance in marginal habitat with guppies, but show no differences in the egg distribution with guppies. In

contrast to these dynamic patterns, killifish and guppy diel activity patterns remained stable regardless of evolutionary experience with guppies primarily active during the daytime and adult, but not juvenile, killifish shifting to nocturnal activity patterns in the presence of guppies. These differing responses suggest that killifish habitat preferences and diel activity likely represent evolutionary and ecological reactions to intraguild predation that enhance coexistence between the species. Coexistence under intraguild predation may rely upon the dynamics of multiple ecological and evolutionary mechanisms that facilitate the persistence of each species.

Introduction

Intraguild predation (IGP) occurs where two species compete for a shared resource and one species (IG predator) also consumes the other (IG prey) (Polis et al. 1989, Holt and Polis 1997). IGP interactions take place frequently in nature and have been documented across a broad array of taxa and ecological conditions (Persson et al. 1991, Arim and Marquet 2004). Despite their prevalence, however, theory predicts that IGP should be unstable with one or both consumer species becoming extinct in most settings. In classic models of IGP, both consumer species coexist only at intermediate resource productivity and when the IG prey has an advantage over the IG predator in exploiting the shared resource (Polis et al. 1989, Holt and Polis 1997, Mylius et al. 2001); predictions which have not been consistently borne out in the laboratory or

nature (Borer et al. 2003, Montserrat et al. 2008, Novak 2013). Traditional ecological theory does not match empirical observations.

Resolving the discord between IGP theory and observations has attracted considerable interest as these interactions can have important consequences for the distribution and dynamics of ecological communities (Murdoch et al. 2002, Schmitz et al. 2017, Costa-Pereira et al. 2018). Theorists have proposed a variety of mechanisms that may enhance coexistence, including stage-structure (Mylius et al. 2001, van de Wolfshaar et al. 2006, Hin et al. 2011), cannibalism (Rudolf 2007, Amarasekare 2008), alternative resources (Briggs and Borer 2005, Daugherty et al. 2007, Holt and Huxel 2007), shared predators (Hall 2011), differences in predator foraging or life history (Krivan 2000, Krivan and Diehl 2005, HilleRisLambers et al. 2006), spatial structure (Amarasekare 2006, 2007a, Okuyama 2008), and IG prey refuges (HilleRisLambers et al. 2006, Amarasekare 2007b, 2008). These mechanisms act to reduce or partition interspecific interactions and concentrate intraspecific interactions, which can expand the conditions that allow both species to persist, but still restrict coexistence to intermediate productivities. Collectively, these results raise the question as to whether adding ecological detail alone can bring theory into alignment with observation (Borer 2006).

An alternative approach recognizes that evolutionary feedbacks may play an important role in ecological dynamics and coexistence in IGP systems.

Theory tested by replicated microcosm experiments demonstrate an expanded realm of potential population dynamics when the basal resource of IG predator and IG prey can evolve rapidly (Ellner and Becks 2011, Hiltunen et al. 2014a). These dynamics, however, do not necessarily promote stable coexistence nor do they address the evolution of the consumer species. Recent theory has shown that evolution of IG predator and IG prey foraging traits can yield novel coexistence outcomes (Patel and Schreiber 2015, Wang et al. 2016). Empirical work comparing IG prey traits from populations occurring with and without IG predators further implicates evolutionary adaptation in stabilizing communities with IGP (Ingram et al. 2012, Urban 2013, Miller et al. 2015, Anderson and Lawler 2016, Granados et al. 2017). These results generally show that evolution operates in a fashion consistent with reducing the strength of interspecific interactions through similar mechanisms as proposed in ecological theory (e.g., spatial refuges, stage-structured interactions, cannibalism and/or adaptive foraging). However, these comparative studies only examine traits after IG predators and IG prey have co-occurred for many generations and do not capture the potentially important transient stages of IGP interactions that may influence coexistence and long-term community outcomes (Amarasekare 2008, Maciel and Kraenkel 2017, Hastings et al. 2018). Short-term ecological responses may dominate during the initial phase of IGP before the development of longer-term evolutionary coexistence mechanisms. As IGP interactions

develop, evolutionary adaptation may weaken, reinforce or develop new coexistence mechanisms that stabilize these communities.

We assess this hypothesis by examining an evolving, persistent IGP community in the freshwater streams of Trinidad. In the headwaters of these streams, the killifish *Rivulus hartii* occurs alone without competitors or predators (killifish-only: KO), but shares downstream reaches with guppies (*Poecilia reticulata*) and large predators (killifish-guppy-predator: KGP) (Gilliam et al. 1993). Barrier waterfalls separate these locations into discrete communities, but guppies occasionally breach these waterfalls to form killifish-guppy (KG) communities. In these newly formed KG communities, killifish and guppies have complex size-structured IGP interactions. Adult guppies prey upon newborn killifish, killifish prey upon guppies, predominantly of small size classes, and juvenile killifish compete with guppies of all sizes (Seghers 1973, Mattingly and Butler IV 1994, Fraser and Lamphere 2013, Furness and Reznick 2015). Theory predicts this sort of bidirectional IGP interaction should be difficult to sustain (HilleRisLambers and Dieckmann 2003, van de Wolfshaar et al. 2006, Schellekens and van Kooten 2012), yet KG communities can be found throughout the Northern Range Mountains and have persisted for at least 40 years (Endler 1978, Gilliam et al. 1993). In addition to these natural KG communities, guppies have been introduced and successfully established in previously KO reaches in historical (30-40 years ago) and contemporary (~10

years ago) experiments (Endler 1980, Reznick and Bryga 1987, Fraser and Lamphere 2013, Dick et al. 2018). Despite the prevalence and persistence of KG communities, the coexistence mechanisms underlying these IGP interactions have not been well-described.

Understanding IGP interactions in KG communities likely requires an evolutionary view. KG guppy populations rapidly evolve distinct life histories, morphology and behavior in KG environments (Reznick 1982, Reznick and Bryga 1996, Travis et al. 2014). Similarly, KG killifish show a suite of life history differences that develop within 25 years and depend upon per-capita food availability, which varies predictably between KO and KG environments due to reduced killifish density in KG communities (Walsh and Reznick 2009, 2010, 2011). Moreover, evolutionary adaptation in each of these species affects IGP interactions. KG guppies perform better than KGP guppies in the presence of killifish, and better still with co-adapted killifish from KG communities as compared to killifish from KO localities (Bassar et al. 2017a). These results suggest that the evolution of each species modifies IGP interactions and may reflect changes in the strength or form of coexistence mechanisms at work during different evolutionary phases of the KG community. During the initial establishment of KG communities, ecological factors may drive short-term dynamics, facilitating persistence until longer-term (co)evolutionary-mediated coexistence dominates.

We address this idea by examining size-structured spatial and temporal activity of killifish across KG communities of varying age. In particular, we evaluate the spatial distribution of killifish eggs and diel activity patterns in killifish from KO and KG communities. Guppies tend to aggregate in large pool habitats and show diurnal activity patterns (Fraser et al. 1999, Fraser et al. 2004, Marshall et al. 2012). The spatial distribution of guppies predicts that KG killifish (relative to KO killifish) may alter their distribution or deposit more eggs in marginal habitats (i.e., side pools, riffles and isolated pools) to reduce competitive or predatory interactions with guppies. Similarly, killifish, particularly juveniles, may become more nocturnal to minimize competition with guppies. Our prior work suggests that each of these mechanisms present a plausible means of minimizing IGP interactions with guppies, since the effect of guppies on killifish recruitment varied across habitats and killifish became more nocturnal in KG sites relative to KO sites in one river (Marshall et al. 2012). Furthermore, if evolution strengthens or generates these coexistence mechanisms, we should expect their strength and/or prevalence to increase in old (natural streams and/or historical experiments) relative to young (contemporary experiments) KG communities. Conversely, if these coexistence mechanisms represent an immediate, ecological response to IGP interactions, then their strength and/or prevalence should remain unchanged or even

decrease over time, if evolution plays no role or derives alternative coexistence mechanisms.

We test these ideas using a series of experiments and observations to determine how the distribution of adult killifish and egg distributions across habitats and diel activity patterns vary as killifish adapt to IGP interactions in KG communities. First, we use artificial stream experiments with multiple habitat types to assess how killifish from KO and KG communities distribute eggs with guppies present or absent, as well as the habitat use of each species. We then examine the distribution of killifish adults and eggs between pool and marginal habitats in KO and KG sites of varying ages, including contemporary and historical guppy introductions, and natural KG localities. Second, we perform stage-specific activity observations of killifish during the day and night in KO and KG sites of varying ages (modern and historical experiments, as well as natural KG reaches). We then make use of on-going mark-recapture studies of guppies in the contemporary experimental streams to test how patterns of killifish activity respond to reduced guppy density. Taken together, these results allow us to evaluate how each of these coexistence mechanisms contributes to the persistence of this IGP interaction as the community transitions towards a long-term evolutionary equilibrium.

Methods

Artificial stream experiments

We evaluated how evolution shapes the response of killifish from long-established KO and KG communities to guppies in artificial streams (mesocosms) using a factorial design in which we crossed guppy presence (present or absent) with killifish origin (KO or KG). We employed an additive design for the guppy treatment to hold intraspecific interactions of killifish constant and assess the impact of an IG predator (guppies) on killifish egg production and distribution (Sih et al. 1998). Each channel contained 7 mature killifish from the appropriate site, and guppy treatment channels received an additional 9 mature KG guppies. We parameterized density, size structure and sex ratio of each species based upon our knowledge of natural populations and experience with previous mesocosm experiments (Gilliam et al. 1993, Bassar et al. 2013, Bassar et al. 2017a). Each channel received 2 male killifish (total length mean ± standard deviation, 1 small: 37.8 ± 3.08 mm; 1 large: 63.6 ± 11.57 mm) and 5 female killifish (total length mean ± standard deviation, 2 small: 36.8 ± 3.55 mm; 2 medium: 44.7 ± 2.37 mm ; 1 large: 70.4 ± 10.56 mm). Each channel with guppies contained 3 male (standard length mean ± standard deviation: 16.7 ± 2.67 mm), and 6 female (standard length mean ± standard deviation: 20.3 ± 4.89 mm) guppies. We repeated the experiment with fishes from a historical guppy introduction in the Aripo drainage (Reznick et al. 1990, Reznick et al.

1997) and a natural KG community in the Quare drainage (Endler 1978), as well as the upstream paired KO sites in these tributaries. These drainages represent independent ecological and evolutionary origins of killifish-guppy interactions and allow us to draw inference about the generality of the observed response.

We constructed 8 mesocosms total with each mesocosm formed by joining three 1 m x 0.5 m plastic troughs (Rotoplastics Trinidad Limited, Trinidad) into a single flow-through channel in the Arima Valley, Trinidad. Each trough of a channel was designed to mimic a natural habitat. The first compartment of each channel (hereafter side pool) had high structural complexity (gravel and 5 clay bricks), shallow average depth (approx. 5 cm) and little flow. The second compartment (riffle) had intermediate average depth (approx. 10 cm) and structural complexity (gravel and 2 clay bricks) and the most turbulent flow due to water entering each channel near the front of this compartment. The last compartment (pool) had little structural complexity (only gravel), greatest depth (approx. 15 cm) and regular flow as water moved smoothly towards the outflow. We stocked each segment with one bundle of unbraided nylon rope joined by a short (10-15 cm) section of PVC pipe and two 10 cm x 10 cm squares of artificial turf as spawning substrate (Fraser and Gilliam 1992). Water from the 8 channels flowed into a common sump tank, where it was recirculated to a head tank and back to each channel. We used a ball valve at the inflow to each channel to maintain target flow rates (~ 200 L/hr) in each channel.

We captured experimental fishes from KO (killifish) and KG (killifish and guppies) sites 10-14 days prior to the start of the experiment. We transported the fishes to our laboratory facility in the Arima Valley, Trinidad, where we housed them in 19 L glass aquaria separated by species and site. While in the lab, we fed *ad libitum* brine shrimp *naupli* and fish flake to guppies, and canned flaked tuna and fish flake to killifish. We performed water changes as necessary and visually inspected the health of all fishes during this time. Two or three days prior to the start of the experiment, we took the additional step of separating killifish by sex to prevent spawning and increase the likelihood that females would have mature oocytes. Immediately before beginning the experiment, we anesthetized all fishes in a buffered MS-222 solution, and measured total length and wet mass. For killifish, we also marked each individual with two subcutaneous injections of colored elastomer (Northwest Marine Technologies, Shaw Island, Wa.) that uniquely identified each individual in a channel. After all individuals had recovered from anesthesia, we placed them in the appropriate channel to begin the experiment.

During the course of the experiment, we distributed approx. 100 mg of flake food equally across each habitat of each channel each day and checked daily for dead or diseased fish, which we immediately replaced with fish of the same sex and similar size. In two guppy treatment channels in the Aripo river replicate, we replaced all guppies after 4 days when we observed apparent

signs of disease. In addition to these health checks, we also performed habitat use observations of guppies and killifish during the day and at night to assess how each species distributed themselves across habitats in the channels. For killifish, we searched channels for all observable individuals, noting the habitat compartment in which it was initially found and attempting to identify an individual's unique marks using a violet light, which causes the elastomer to fluoresce. For guppies, we recorded the number of individuals observed in each habitat of each channel where they occurred. We made habitat use observations prior to feeding so that they would not be influenced by this external stimulus and used a red light to make night time observations to minimize disturbance to the fishes. To assess the distribution of killifish eggs, we collected the egg deposition substrates (unbraided rope bundles and artificial turf swatches) weekly and counted all eggs for each habitat for each channel. After 14 days, we collected all fishes and euthanized them in an overdose of MS-222. For killifish, we identified, and measured total length and wet mass at this time.

We used generalized linear mixed models, cumulative logit mixed models and generalized linear models to evaluate the distribution of guppies, adult killifish and killifish eggs, respectively, across habitats in response to the treatment levels. We took a Bayesian approach to fitting these models using STAN (Carpenter et al. 2017) via the brms package (Bürkner 2017) in R (R Core Team 2018). For each model, we fit a full model incorporating the interactions of

all experimental factors (i.e., drainage, killifish origin, guppy presence and habitat) where relevant, accounting for variation across mesocosms using a random intercept. We specified weakly informative prior distributions of $t_3(1, 10^2)$, or $t_3(0, 10^2)$ in the killifish abundance model, for the model intercepts (which corresponded to the average value across all experimental groups) and $\Gamma(0.01, 0.01)$ prior distributions on the shape parameter in negative binomial models. For group-level variance terms, we used somewhat more informative $t_3^+(0, 1^2)$ prior distributions, which reflect a statistically conservative view of minor differences between channels. For the population-level parameters, we use $N(0, 1^2)$ prior distributions to capture our belief that many of the experimental factors have a small effect on the measured response, which acts to regularize unrealistically large estimates in the posterior distribution (Gelman et al. 2017). For each model, we ran 12 chains with 4,000 iterations per chain, discarding the first 1,000 iterations from each chain, to yield a posterior sample of 36,000.

After fitting the model, we ensured sampling convergence on the posterior by inspecting parameter trace plots and calculating the Gelman-Rubin convergence diagnostic, $\hat{R}$ (Gelman et al. 2013). We also monitored other sampling diagnostics specific to the Hamiltonian Monte Carlo methods used by STAN (i.e., divergent transitions, tree depth and kinetic energy) and tuned our sampling accordingly. For converged models, we used posterior predictive checks to assess discrepancies between the model and observed data. To

assess treatment responses, we performed post-hoc contrasts on the posterior population-level marginal effects of interest (killifish origin, guppy presence, habitat and their interactions), working from higher to lower order interactions so as to minimize the number of comparisons by excluding nested interactions and main effects (although we do note main effects where helpful to understanding interactions). For any significant contrasts, we checked to ensure that these effects did not depend upon drainage. While this approach can lead to many comparisons and potentially inflate Type I or family-wise error rates, these concerns may be mitigated by the hierarchical structure of the models and the shrinkage of the parameter estimates (Gelman et al. 2012, but see Ogle et al. 2019). Given these concerns, we present posterior modes with 99% highest posterior density intervals (HDI), as well as Bayesian p-values that represent the proportion of posterior contrast estimates that take the opposite sign from the modal value and represent the uncertainty in the direction of an effect.

For the analysis of guppy distribution, we quantified the response of guppies in terms of the number of guppies observed in each habitat in each channel during each observation. We assessed the relative descriptive power of zero-inflated Poisson and negative binomial models, using log link functions for the count models and logit links for the zero-inflation models. Our initial investigation indicated that the additional shape parameter of the negative binomial model did not improve model fit, so we proceeded to use the simpler

zero-inflated Poisson model to test the significance of model terms. Our full model included population-level effects for the three-way interaction of drainage × killifish origin × habitat with a random intercept for channel in both the conditional and zero-inflation components of the model. To test the significance of the explanatory variables, we integrated the Poisson count and zero-inflation posterior estimates to generate the model fitted guppy abundance (on the real scale). We then back-transformed these values to the log scale to compute contrasts that reflected the proportional change in guppy abundance across the specified experimental factor(s). This two-step approach allowed us to consider the full model in a single set of contrasts, rather than considering the count and zero-inflation models separately.

For the analysis of adult killifish distribution, we noted that in many observation periods we could not account for all adult killifish in a channel, since they frequently hid underneath the bricks and concealed themselves in the substrate. Since the data showed signs of underdispersion (relative to a Poisson model), we employed cumulative logit regression to best capture the distribution of detected adult killifish without making any assumptions about the unobserved individuals. Cumulative logit regression represents a flexible approach to modeling count data that do not meet the assumptions of other discrete response models (Min and Agresti 2005, Hostetler et al. 2012). In these models, we estimate the probability that an observation will be less than or equal to each

observed count value on the logit scale. The linear predictor in cumulative logit models consists of a vector of intercepts that correspond to the cumulative probability of observing each count value (except the highest count value since the probability of being less than or equal to the greatest count is one) plus any population or group-level model terms, which are independent of the count. Our model of detected killifish abundance included population-level effects of drainage × killifish origin × guppy presence × habitat and a random intercept for channel identity. To perform inference, we compute the probability of a count taking a particular value by subtracting the estimated sequential cumulative probabilities (i.e., $P(y_i = k) = P(y_i \leq k) - P(y_i \leq k-1)$) and then calculate the expected value of an observation by multiplying the value of the count by its probability and summing over all possible counts for each set of parameter estimates in the posterior distribution. We then compare posterior expected counts across the experimental factors on the log scale to examine proportional differences in killifish abundance.

For the analysis of killifish egg distribution, we first summed across the weekly egg counts to determine the total number of eggs laid in each habitat compartment in each channel. We then compared Poisson and negative binomial models with log link functions to estimates the number of eggs laid in each channel as a function of the four-way interaction of killifish origin × guppy presence × drainage × habitat. Comparisons between the two models provided

some evidence that negative binomial model better accommodated the mean-variance relationship of the data, although this model also predicted counts much larger than observed in the experiment. Despite this discrepancy, we opted to proceed with inference using the more conservative negative binomial model.

Natural Stream Killifish Distributions

We examined the impact of evolution on the relative distribution of killifish between pool and marginal habitats in KO and KG communities in streams with contemporary guppy introductions, historical guppy introductions and naturally colonized guppy populations. To quantify killifish density, we performed mark-recapture sampling in short (25-71 m) sections of each community with both habitat types in several streams during April-July 2017 and 2018. We sampled four streams with contemporary guppy introductions (Fraser and Lamphere 2013, Travis et al. 2014, Dick et al. 2018), and one stream each with historical guppy introductions (Reznick et al. 1990, Reznick et al. 1997) and naturally colonized guppy populations (Endler 1978) and collected 3 monthly samples at each site. To sample killifish, we visited sites after dark, when killifish are most easily seen and captured with small, aquarium dipnets. We also set minnow traps in large, deep pools. We classified the microhabitat (pool or marginal) of captured individuals in the field. After completing a standardized sampling effort (based upon time and personnel), we returned to the lab with all captured fish,

where we measured the total length and mass of each individual. At this time, we marked any previously unmarked individuals with a subcutaneous injection of a colored elastomer (Northwest Marine Technologies, Shaw Island, WA, USA) so that all captured individuals at a site would be individually identifiable.

To estimate killifish population abundance, we employed a closed population capture-recapture model. The closed population framework assumes that no individuals enter (through birth or immigration) or exit (through death or emigration) each population. This assumption further excludes movement between each habitat $\times$ reach $\times$ stream population. Although our data, strictly speaking, do not meet these assumptions, our previous knowledge indicates that these assumptions are approximately valid: killifish have high monthly survival in these sites (~90%, Furness and Reznick 2015, Goldberg unpublished data) and we rarely capture new recruits that would have been born within each 3-month sampling period. Additionally, we observed relatively low rates of movement between sites (mean $\pm$ standard error: 9.2 $\pm$ 7.37%), consistent with the high-degree of philopatry we have observed in our long-term studies of killifish populations. Additionally, we considered models of total killifish abundance, as well as that of mature, adult ($\geq$ 30 mm) individuals, since these killifish contribute to egg production and match our artificial stream populations.

We used the Huggins' parameterization of a closed population capture-recapture model with individual-level random effects in capture probability using

the R package RMark (Laake 2013) as an interface to program MARK (White and Burnham 1999). This parametrization incorporates three parameters: p, capture probability; c, recapture probability; and σ_p, the population-level standard deviation in capture probability. We took a two-step approach to model fitting: first, we explored a limited set of parametrizations of p and c with a common σ_p; second, we considered simplified parametrizations of σ_p within the best-fitting parameterization of p and c as determined by Akaike Information Criterion with small sample size correction (AIC_c). In the first step, we considered four models, each with σ_p(habitat × reach × stream): p(time × habitat × reach × stream)c(·), p(habitat × reach × stream)c(·), p(time × habitat × reach × stream)c(habitat × reach × stream) and p(habitat × reach × stream)c(habitat × reach × stream). Comparison of these models provided strong support for the p(time × habitat × reach × stream)c(·) parameterization of p and c (minimum $\Delta AIC_c = 94.75$ for total density and 17.04 for adult individuals, Table 3.1). We then considered all possible nested parameterizations of σ_p(habitat × reach × stream), given the best-fit parameterization of p and c. Comparison among the parameterizations of σ_p revealed some model selection uncertainty and so we used model averaging, excluding models receiving $w_i < 0.01$, to construct estimated population abundances at each site (Burnham and Anderson 2002). We then scaled the estimated population abundances and the variance-covariance matrix to density by dividing by the thalweg length of the sampled area within

each habitat of each reach of each stream. Finally, we log-transformed density and estimated the associated variance-covariance matrix using the delta method. We computed the habitat $\times$ reach contrasts on these values to assess the proportional differences in killifish density between habitats in KO and KG reaches and evaluated significance using Wald χ^2-tests.

Natural Stream Egg Distributions

We assessed how evolution impacts the distribution of killifish eggs across pool and marginal habitats in KO and KG communities in streams with contemporary guppy introductions, historical guppy introductions and naturally colonized guppy populations. As an index of *in situ* egg deposition rates, we placed 3 artificial egg substrates (unbraided rope bundles as used in the mesocosm experiments) in each habitat in both communities of several streams during February-April 2017 and March-April 2018. After placement, we left egg substrates in position for 9-13 days before returning to collect them. We chose this sampling period to be shorter than the time between egg deposition and hatch (at least 14.31 $\pm$. 0.9 days) in previous laboratory trials (Walsh and Reznick 2010). The placement and collection of all rope bundles in both reaches and habitats of each stream occurred at the same time to minimize potential environmental variation in egg productivity between habitats or reaches within each stream. After collecting substrates, we returned to our laboratory facilities, searched for deposited eggs and recorded the number found in each rope

bundle along with the corresponding stream, reach and habitat. We successfully surveyed 4 streams with contemporary guppy introductions, 1 stream with historically introduced guppies and 2 streams with naturally colonized guppies. Although we did attempt to survey additional streams, we observed a sharp decline in egg production in May that precluded further sampling.

We took a similar approach to analyzing these data as applied to the mesocosm experiments, using Bayesian generalized linear mixed models. We used a zero-inflated Poisson model with log link for the count model and logit link for the zero-inflation model to assess differences in egg deposition rates between habitats and reaches across the sampled streams. In the zero-inflation model, we included a population-level intercept with random variation across streams. In the count model, we included an offset variable of log-transformed sampling times to account for the different sampling durations of each stream, a population-level interaction for stream type $\times$ habitat $\times$ reach, as well as random effects of habitat $\times$ reach for each stream (i.e. a random intercept, and random slopes for habitat, reach and their interaction). This random effects structure allows for differences between habitats and reaches across streams, as well as correlations between these differences within streams, but makes the conservative assumption that these differences originate from a common distribution of effects without any differences between stream types.

In developing the model, we placed weakly informative priors on the count and zero inflation model intercepts (which represents the average egg production over all groups) of $t_3(1, 10^2)$ and logistic$(0, 1^2)$, respectively. For population level coefficients, we used $N(0, 2.5^2)$ priors to provide some information about the likely scale of possible effects and regularize unrealistic parameter estimates. We placed somewhat more informative $N^+(0, 1^2)$ priors on all of the random effects to constrain estimates of variance among streams and take a conservative view of observed differences, given the small number of streams surveyed. Finally, we specified a non-informative LKJ(1) prior on the Cholesky factorization of the random effects correlation matrix. We fit the model with 12 chains run for 4,000 iterations, discarding the first 1,000 iterations as warm-up to produce a sample of 36,000 from the posterior distribution. After fitting, we performed model validation as described for the mesocosm analysis, before calculating model contrasts to test the stream type $\times$ habitat $\times$ reach interaction, as well as the habitat $\times$ reach interaction overall and within each stream type. We calculated these contrasts with the Poisson count model (on the link scale), ignoring the estimated zero-inflation, as this component likely reflects an imperfect observation process due to sampling variation (e.g. substrate location or timing of samples) rather than true egg productivity.

Diel Activity Patterns

We examined how evolution shapes the diel activity patterns of guppies and killifish in KO and KG communities in streams with contemporary guppy introductions, historical guppy introductions and naturally colonized guppy populations. We quantified day and night guppy and killifish activity in April-July 2015-2018 across the KO and KG reaches of 8 streams: 4 streams with contemporary guppy introductions, 2 streams with historically introduced guppies and 2 streams with naturally colonized guppies. Additionally, mark-recapture sampling reduces guppy density for a period of 1-3 days per month in contemporary experimental streams, allowing us to compare activity at normal and low guppy density. We made additional observations in these 4 streams to examine the plasticity of killifish activity patterns in response to reduced guppy density in these streams. Mean guppy recapture probabilities during the relevant sample times were at least 80%, suggesting a large reduction in guppy populations during these observations (Bassar et al. unpublished data).

To measure activity in both species, we followed Marshall et al. (2012), conducting standardized observations in 10 locations with two observers working in parallel in each reach during daylight (10:00-16:00) and nighttime (19:00-04:00) hours. Upon arriving at a sampling location, an observer would place a 20 cm x 30 cm PVC quadrat in the water and wait during a 5-min. acclimation period. After this wait, we counted the number of guppies, and juvenile and adult killifish seen within the quadrat during a 10-sec. interval and

repeated this count at the beginning of each successive minute for a total of 10 observations per location. We repeated this process until all locations had been surveyed. We marked locations with pin flags on the bank of the stream to ensure that we sampled the same areas when repeating observations in subsequent sampling periods. While making night observations, we used either white (2015) or red (2016-2018) light during the 10-sec. observation periods, but otherwise left lights off. We did not notice any substantial difference in the way fishes responded to red versus white light and so pooled all data for analysis.

To analyze the activity observations, we partitioned our data and analysis between observations with normal guppy density across all streams, and observations in contemporary experimental streams with normal or reduced guppy density. We employed Bayesian generalized linear mixed models for guppies and cumulative logit mixed models for killifish to best capture the distribution of counts for each species. For the models including observations made across streams with normal guppy density, we structured our linear predictor for activity in a similar fashion as our analysis of the stream egg distributions. We specified a population-level interaction of stream type $\times$ reach $\times$ time (day/night), as well as random effects of time $\times$ reach for each stream (i.e. a random intercept, and random slopes for time, reach and their interaction), as well as a random intercept for observation location. In models of guppy activity

counts, we excluded reach as a model covariate in both the fixed and random effects, since guppies only occurred in KG reaches.

For the models comparing killifish activity during periods with normal or reduced guppy density in contemporary experiments, we include a population-level interaction for guppy density × reach × time, as well as random effects of guppy density × time × reach for each stream (i.e. a random intercept, and random slopes for guppy density, time, reach and their interactions), as well as a random intercept for observation location. We included guppy density in the random effects to account for potential variation in the effect of reduced guppy density across streams, e.g. due to a different proportion of the guppy population being removed by mark-recapture sampling.

We fit these models to data from guppies, and juveniles and adults separately to reduce model complexity and facilitate interpretability of results. For each model, we placed weakly informative priors on the model intercepts and population level coefficients of $t_3(0, 10^2)$ and $N(0, 2.5^2)$, respectively. The population-level priors provide some information about the expected scale of observed effects and guard against unrealistically large parameter estimates. For location-level random intercepts, we applied a $t_3^+(0, 1^2)$ prior distribution, but we used a somewhat more informative $N^+(0, 1^2)$ prior on all of the stream-level random effects to constrain estimates of variance and take a conservative view of observed differences among streams, given the small number of streams

surveyed. We specified a non-informative LKJ(1) prior on the Cholesky factorization of the random effects correlation matrix. For the model of guppy activity patterns, we additionally specified a $\Gamma(0.01, 0.01)$ prior on the shape parameter of the negative binomial distribution, since the data showed signs of over-dispersion relative to Poisson expectations. As before, we fit each model with 12 chains run for 4,000 iterations, discarding the first 1,000 iterations as warm-up to produce a sample of 36,000 from the posterior distribution and performed posterior model validation checks. As described for the model of artificial stream killifish abundance, we perform inference by computing posterior expected counts and making comparisons of proportional differences on the log-scale.

Results

Artificial Stream Experiments

We observed the 72 experimental guppies 1,210 times across 47 observation periods of the eight mesocosms in which we placed them. The model for guppy abundance predicted strong differences across habitats that depended to a lesser extent on drainage and killifish origin (i.e. a habitat $\times$ drainage $\times$ killifish origin interaction; Table 3.2, Fig 3.1). The model estimated a significant pattern of decreasing guppy abundance moving from the pool (2.0 guppies/observation, 99% HDI: 1.36-2.91) to the riffle (0.9 guppies/observation, 99% HDI: 0.57-1.36) to the side pool (0.3 guppies/observation, 99% HDI: 0.17-

0.49; pool-riffle contrast: 0.9, 99% HDI: 0.59-1.15, p = 0; pool-side pool contrast: 2.0, 99% HDI: 1.56-2.39, p = 0; riffle-side pool contrast: 1.1, 99% HDI: 0.66-1.56, p = 0). The habitat × drainage × killifish origin interaction reflected weak differences in how guppies from the Aripo and Quare used the riffle when paired with KG killifish (Fig 3.1). Quare guppies showed significantly higher abundance (1.5 guppies/observation, 99% HDI: 0.59-2.83) than Aripo guppies (0.6 guppies/observation, 99% HDI: 0.23-1.11) with KG killifish in this habitat (Quare-Aripo contrast: 0.9, 99% HDI: -0.04-1.89, p =0.006). These differences in the presence of KG killifish led Aripo guppies to have similar abundances in the riffle and side pool (riffle-side pool contrast: 0.4, 99% HDI:-0.33-1.18, p = 0.077) and Quare guppies to have similar numbers in the pool and riffle (pool-riffle contrast: 0.1, 99% HDI: -0.40-0.60, p = 0.328).

Across the 47 observations periods of all 16 mesocosms, we observed 112 individual killifish 1,513 times. The model for the abundance of detected killifish contained significant contrasts for killifish origin × guppy presence × habitat, which did not depend upon drainage (Table 3.3). This interaction reflected differences in how KG and KO killifish abundance responded to guppies across habitats, particularly in the side pool (Fig 3.2). In the side pool habitat, KO killifish without guppies had an estimated detectable abundance of 1.7 fish/observation (99% HDI: 1.36-2.14), this abundance decreased to 1.4 fish/observation (99% HDI: 1.14-1.70) in the presence of guppies. In contrast,

KG killifish showed similar estimated detectable abundance with guppies (1.6 fish/observation, 99% HDI: 1.34-2.03) and without guppies (1.6 fish/observation, 99% HDI: 1.30-1.95) in side pools. The response to guppies by killifish from different origins differed within the side pool habitat (contrast: 0.3, 99% HDI: -0.13-0.62, $p = 0.040$) and also distinguished the side pool from the pool (contrast: 0.2, 99% HDI: -0.11-0.51, $p = 0.050$) or riffle (contrast: 0.3, 99% HDI: -0.05-0.68, $p = 0.014$) in terms of how KO and KG killifish responded to guppies.

We collected 226 eggs across the two 2-week replicates of the mesocosm experiments. The model of killifish egg distribution found marginal evidence for a killifish origin × guppy presence × habitat interaction, which did not depend upon drainage, and strong main effects of habitat and guppy presence (Table 3.4, Fig 3.3). The model estimated that killifish deposited more eggs in the riffle habitat (6.5 eggs, 99% HDI 4.46-9.72) than in either the pool (2.8 eggs, 99% HDI: 1.72-4.59; pool – riffle contrast: -0.8, 99% HDI: -1.46- -0.23, $p < 0.001$) or the side pool (3.0 eggs, 99% HDI: 1.87-4.89; riffle – side pool contrast: 0.8, 99% HDI: 0.15-1.36, $p < 0.001$), which did not differ (pool – side pool contrast: -0.1, 99% HDI: -0.75-0.56, $p = 0.38$). Similarly, killifish egg production decreased significantly in presence of guppies (3.1 eggs, 99% HDI 2.01-4.53) as compared to when guppies were absent (4.9 eggs, 99% HDI 3.50-6.92; absent-present contrast: 0.4, 99% HDI: -0.05-0.98, $p = 0.009$). The killifish origin × guppy presence × habitat interaction captured moderate differences in

the way that killifish from KO and KG sites respond to guppies in the distribution of eggs across habitats (Fig 3.3). In the presence of guppies, the number of eggs deposited by KO killifish significantly decreased in the pool (present: 1.2 eggs, 99% HDI: 0.33-3.48; absent: 4.0 eggs, 95% CI: 1.79-8.17; contrast: 1.1, 99% HDI: -0.02-2.38, p = 0.006), weakly decreased in the riffle (present: 4.8 eggs, 99% HDI: 2.13-10.98; absent: 8.5 eggs, 99% HDI: 3.95-16.86; contrast: 0.6, 99% HDI:-0.51-1.54, p = 0.085), but did not change in the side pool (present: 2.9 eggs, 99% HDI: 1.11-7.11; absent: 3.4 eggs, 99% HDI: 1.27-7.79; contrast: 0.1, 99% HDI: -1.07-1.30, p = 0.416). In contrast, estimated KG killifish egg production declined marginally in the presence of guppies in the pool (present: 2.5 eggs, 99% HDI: 1.09-5.73; absent: 4.3 eggs, 99% HDI: 2.22-8.63; contrast: 0.5, 99% HDI: -0.37-1.44, p = 0.062) and side pool (present: 1.9 eggs, 99% HDI: 0.62-5.09; absent: 3.8 eggs, 99% HDI: 1.65-8.01; contrast: 0.7, 99% HDI: -0.51-1.78, p = 0.066), but did not differ in the riffle (present: 6.7 eggs, 99% HDI: 3.02-13.54; absent: 5.7 eggs, 99% HDI: 2.76-12.23; contrast: -0.1, 99% HDI: -1.03-0.88, p = 0.378). These varying responses to guppies by KO and KG killifish provided some evidence for differences between pools and side pools (contrast: -1.1, 99% HDI: -2.83-0.52, p = 0.039) and to a lesser extent riffles and side pools (contrast: -1.3, 99% HDI: -3.01-0.78, p = 0.056), but not pools and riffles (contrast: 0.1, 99% HDI: -1.57-1.59, p = 0.483).

Natural Stream Killifish Distributions

We captured 4,055 killifish (3,405 adult individuals) a total of 6,233 times (5,254 adult captures) in the course of our mark-recapture sampling in natural streams. The stream with naturally colonized guppies displayed a significant difference in total and adult killifish density between habitats and reaches (total density: $\chi^2_1 = 25.35$, $p < 0.001$; adult: $\chi^2_1 = 17.36$, $p < 0.001$; Fig 3.4), such that density in KG marginal habitat (52.6 $\pm$ 20.26 individuals/m; 44.9 $\pm$ 15.81 adults/m) increased relative to KO marginal habitat (8.5 $\pm$ 1.99 individuals/m; 9.6 $\pm$ 2.74 adults/m), as compared KG pools (39.9 $\pm$ 6.43 individuals/m; 35.0 $\pm$ 5.35 adults/m) versus KO pools (52.8 $\pm$ 5.00 individuals/m; 38.5 $\pm$ 3.87 adults/m). We found no evidence for similar differences in contemporary guppy introduction streams (total density: $\chi^2_1 = 0.51$, $p = 0.474$; adults: $\chi^2_1 = 1.41$, $p = 0.234$), the historical guppy introduction stream (total density: $\chi^2_1 = 0.33$, $p = 0.565$; adult: $\chi^2_1 = 0.06$, $p = 0.808$) or overall (total density: $\chi^2_1 = 0.26$, $p = 0.610$; adult: $\chi^2_1 = 0.03$, $p = 0.869$). The pattern of killifish density across habitats and reaches in the naturally colonized stream differed significantly from the contemporary guppy introduction streams (total density: $\chi^2_1 = 25.00$, $p < 0.001$, adult: $\chi^2_1 = 18.42$, $p < 0.001$) and the historical guppy introduction stream (total density: $\chi^2_1 = 9.20$, $p = 0.002$, adult: $\chi^2_1 = 5.74$, $p = 0.017$). The contemporary introduction streams did not differ significantly from the historical guppy introduction stream (total density: $\chi^2_1 = 1.02$, $p = 0.313$, adult: $\chi^2_1 = 1.02$, $p = 0.314$).

Natural Stream Egg Distributions

We collected 385 eggs across the 7 streams we sampled effectively. The killifish egg distribution model did not yield evidence for differences in the numbers of eggs laid in pool vs. marginal habitats in KO and KG reaches across streams with recently or historically introduced guppy populations or naturally colonized guppies (Table 3.5, Fig 3.5). We found no significant contrasts for stream type × reach × habitat interaction (Contemporary – Historical: 1.7, 99% HDI: -2.23-4.85, p = 0.118; Contemporary – Natural: 0.2, 99% HDI: -2.83-3.30, p = 0.394; Historical – Natural: -1.5, 99% HDI: -5.29-3.23, p = 0.193). The model did provide some evidence for a reach × habitat interaction within the contemporary experiment stream type (contrast: 1.4, 99% HDI: -0.79-3.06, p = 0.044; Fig 3.5). In these streams, KO killifish laid eggs at a rate of 1.6 eggs/10 days (99% HDI: 0.14-6.76) in pools and 0.4 eggs/10 days (99% HDI: 0.01-5.51) in marginal areas, while KG killifish laid eggs at a rate of 0.9 eggs/10 days (99% HDI: 0.16-3.00) in pools and 1.3 eggs/10 days (99% HDI: 0.05-5.13) in marginal habitats. We did not find similar differences between habitats in reaches in streams with historical experiments (contrast: -0.4, 99% HDI: -3.37-3.27, p = 0.372), naturally colonized guppies (contrast: 0.9, 99% HDI: -1.83-3.70, p = 0.164), or overall (contrast: 0.6, 99% HDI: -1.06-2.37, p = 0.142).

Diel Activity Patterns

Across over 3,000 observations in 8 streams during the day and night in KO and KG reaches, we counted 2,580, 987 and 1,420 instances of guppies, juvenile killifish and adult killifish, respectively. The guppy activity pattern model provided strong evidence that guppies decreased activity at night (contrast: 1.1, 99% HDI: 0.01-2.13, p = 0.006; Table 3.6, Fig 3.6). During the day, guppies had estimated activity rates of 1.1 fish/observation (99% HDI: 0.40-2.62), whereas activity rates decreased to 0.4 fish/observation (99% HDI: 0.07-1.89) at night. This diurnal pattern did not vary across stream types (contemporary – historical: -1.0, 99% HDI: -3.22-1.24, p = 0.096, contemporary – natural: 0.1, 99% HDI: -2.13-2.28, p = 0.484, historical – natural: 1.0, 99% HDI: -1.68-3.71, p = 0.129).

The models of killifish diel activity patterns suggested that juveniles and adults showed some differences in how they responded to guppies. The model of juvenile killifish activity across streams with different KG community ages produced little evidence that juveniles in KG reaches changed their activity patterns relative to those in KO communities overall (contrast: 0.8, 99% HDI: -0.71-2.42, p = 0.087) or within any stream type (contemporary experiments: 0.5, 99% HDI: -1.25-2.46, p = 0.220; historical experiments: 0.9, 99% HDI: -1.66-4.04, p = 0.177; natural colonization: 0.6, 99% HDI: -1.36-3.36, p = 0.183; Table 3.7, Fig 3.6). In contrast, the model of adult killifish revealed that KG killifish did alter diel activity patterns relative to KO killifish overall (contrast: 0.7, 99% HDI: -

0.43-1.80, p = 0.038; Table 3.8, Fig 3.6). Across all streams, adult KG killifish had estimated activity rates of 0.1 fish/observation (99% HDI: 0.01-0.325) during the day and 0.4 fish/observation (99% HDI: 0.12-1.03) at night, while adult KO killifish had corresponding rates of 0.3 fish/observation (99% HDI: 0.04-0.88) and 0.7 fish/observation (99% HDI: 0.19-1.64). This overall pattern reflected differences in streams with naturally colonized guppies (contrast: 0.9, 99% HDI: -0.74-2.40, p = 0.045) and to a lesser extent streams with recent guppy introductions (contrast: 0.8, 99% HDI: -0.61-2.03, p = 0.070), but not those with historical introductions (contrast: 0.7, 99% HDI: -1.73-2.75, p =0.222), although the change in adult activity patterns did not differ between any of the stream types (contemporary – historical: 0.0, 99% HDI: -2.24-2.50, p = 0.458, contemporary – natural: -0.1, 99% HDI: -2.11-1.63, p = 0.391, historical – natural: -0.2, 99% HDI: -2.98-2.28, p = 0.382).

In the four contemporary guppy introduction streams with guppies at normal and low density during the day and night, we counted 661 and 1,162 instances of juvenile and adult killifish, respectively, over our more than 3,000 observations. The response of killifish diel activity patterns to changes in guppy density depended upon stage. The model of juvenile killifish activity found no significant changes in overall activity levels with reduced guppy density between KO and KG sites (guppy density × reach contrast: 0.1, 99% HDI: -1.42-1.52, p = 0.373), nor did reduced guppy density lead to changes diel activity patterns

between sites (guppy density × reach × time contrast: 0.0, 99% HDI: -1.85-1.74, p = 0.484; Table 3.9, Fig 3.7). The model for adult killifish activity provided marginal support for a guppy density × reach × time interaction (contrast: 0.6, 99% HDI: -0.53-1.61, p = 0.079; Table 3.10, Fig 3.7). KO adult killifish had estimated daytime activity rates of 0.2 fish/observation (99% HDI: 0.02-0.72) and nighttime activity rates of 0.4 fish/observation (99% HDI: 0.01-1.96) with guppies at normal density. This disparity in KO adult activity rates increased somewhat with reduced guppy density in the KG site, such that the model estimated daytime activity rates of 0.1 fish/observation (99% HDI: 0.04-0.40) and nighttime activity rates of 0.5 fish/observation (99% HDI: 0.06-1.50). Adult KG killifish showed an even stronger response to reduced guppy densities (Fig 3.7). With guppies at normal densities, the model estimated KG adult daytime activity rates of 0.1 fish/observation (99% HDI: 0.01-0.22) and nighttime activity rates of 0.2 fish/observation (99% HDI: 0.01-1.12), as compared to 0.0 fish/observation (99% HDI: 0.01-0.11) during the day and 0.5 fish/observation (99% HDI: 0.11-1.12) at night when guppies had reduced density. These estimates reflect strong differences in adult activity between KO and KG reaches with reduced guppy density at night (contrast: 0.5, 99% HDI: -0.41-1.44, p = 0.034), but not during daylight (contrast: 0.0, 99% HDI: -1.05-1.00, p = 0.479). We also note that these estimates provided additional evidence for an

overall shift towards increased nighttime activity in KG killifish relative to KO killifish (contrast: 0.9, 99% HDI: -0.36-2.14, p = 0.023).

Discussion

We show that the distribution of killifish adults and eggs across habitats and diel activity patterns vary in response to guppies and that these responses can change over time as the killifish-guppy IGP interaction develops. Upon colonizing previously KO areas of stream, IG predator guppies show a preference for pool habitats (Fig 3.1) and a diurnal activity pattern (Fig 3.6), which remains stable over time (Fraser et al. 1999, Fraser et al. 2004, Marshall et al. 2012). In these same areas, naïve, IG prey killifish respond by placing a greater proportion of eggs outside of pools in more marginal habitat relative to their upstream, KO counterparts (Figs 3.3, 3.5). Over time, however, this shift attenuates and experienced killifish from long established KG communities do not alter the distribution of their eggs across habitats in response to guppies (Figs 3.3, 3.5). Moreover, these changes in egg distribution do not match and can run counter to the underlying distribution of potentially spawning adults (Figs 3.2, 3.4) and suggests that adult killifish may actively choose oviposition habitats. These adult killifish do, however, alter their diel activity patterns in the presence of guppies, generally becoming more nocturnal in KG reaches relative to KO areas, regardless of the time since guppy establishment (Fig 3.6). The contrasting dynamics of these traits paint a complex picture of IGP interactions

in this system and suggest a role for short-term, ecological and long-term evolutionary mechanisms in facilitating coexistence through spatial and temporal structure.

Spatial Structure under IGP

The range of habitats available to guppies and killifish in headwater streams may add spatial structure to their IGP interactions and lead to contrasting dynamics in different habitats. Ecological theory of spatially structured IGPs often conceptualizes the problem in terms of habitat patches of varying resource productivity connected by dispersal of the IG predator and/or IG prey. Although dispersal across habitats can facilitate the persistence of both species at the landscape scale across many patches, it does not generally enhance the local persistence of IG predator and IG prey within any given patch (Heithaus 2001, Amarasekare 2006, 2007a, but see Okuyama 2008). As in classic treatments of IGP (Polis et al. 1989, Holt and Polis 1997, Mylius et al. 2001), IG prey dominate in low productivity patches and IG predators dominate in high productivity patches. Predictions from these spatial dispersal models do not match the patterns of abundance we observed across habitats in guppies and killifish, nor can this theory explain similar results from other systems, in which both species occupy a range of habitats and productivities (Amarasekare 2000, Borer et al. 2003, Novak 2013).

This disagreement between theory and observation implies that other factors must explain these patterns. Heithaus (2001) noted that species distributions might also represent an evolutionary game, in which IG predator and IG prey densities equilibrated with resource productivity over many generations. We find some support for this evolutionary view of species distributions under IGP, although the patterns we observe may not reflect true genetic differences, since we used wild caught individuals. While guppies consistently show greatest abundance in pools (Fig 3.1), killifish distributions depend upon habitat and evolutionary experience with guppies. In artificial streams, we found that while KO killifish reduced abundance in the side pool in the presence of guppies, KG killifish increased in number in this habitat with guppies (Fig 3.2). This trend in our experiments matches the differences between streams with experimentally introduced guppies and naturally colonized guppy populations in nature. In the surveyed natural stream, KG killifish significantly increased in abundance in marginal habitats relative to pool habitats in KG reaches as compared to upstream KO populations (Fig 3.4). We must caution, however, that differences in the naturally colonized stream may reflect the peculiarities of that sampling site, which occurs adjacent to agricultural gardens and has other human disturbances that may alter the ecology of killifish-guppy interactions. We did not find significant differences between streams with recently introduced guppies and historically introduced

guppies (Fig 3.4), although the historical guppy introduction stream now harbors a recently introduced parasite (*Camallanus cotti*) that may alter killifish-guppy interactions or dynamics. Despite these limitations, the overall concordance between the pattern in artificial and natural streams suggests a role for an evolutionary response to guppies in the distribution of adult killifish.

These differences in killifish distributions may reflect the evolution of distinct habitat preferences in the presence of guppies, which enhance coexistence between the two species. Many lines of evidence suggest that habitat selection can and does respond to selection in many ecological scenarios (Jaenike and Holt 1991, Martin 1998, Morris 2003). Recent empirical work indicates that habitat preferences may evolve in response to IGP. Threespine stickleback from lakes with and without prickly sculpin, an IG predator, exhibit divergent morphologies, diets and positions in the water column associated with a shift from benthic to pelagic habitat (Ingram et al. 2012, Miller et al. 2015). These differences between stickleback from lakes with and without sculpin have a genetic basis, strongly suggesting that they represent an evolved response in habitat selection of the IG prey to the IG predator (Miller et al. 2015). Moreover, theory incorporating habitat preferences into IGP suggests that differences between IG predators and IG prey can act to promote coexistence regardless of if the protagonists share or differ in their habitat preferences (Snyder et al. 2005). Thus, the observed shift in habitat

selection of experienced KG killifish with guppies may reduce interspecific competitive or predatory interactions and stabilize coexistence between these two species. The evolution of habitat preferences in response to IGP interactions shows promise as a potential coexistence mechanism in other systems (Borer et al. 2004) and deserves further investigation.

Existing spatially structured IGP theory does not address age, stage or size structured interactions, although these factors play a role in many IGP systems (Werner and Gilliam 1984, Werner 1988). Non-spatial stage-structured IGP theory offers no consensus as to how these more nuanced interactions impact coexistence: in some cases expanding prospects for coexistence (Rudolf 2007, Abrams 2011, Hin et al. 2011), but not in others (Mylius et al. 2001, van de Wolfshaar et al. 2006, Yamaguchi et al. 2007). Despite this theoretical disagreement, empirical investigation shows that considering this additional structure can improve our understanding of observed dynamics (Rudolf and Armstrong 2008, Montserrat et al. 2012, Toscano et al. 2016). Habitat preferences in killifish depended upon life stage, as we found contrasting distributional patterns between adult killifish and eggs. The egg production of inexperienced, KO killifish or those in KG reaches of contemporary experimental streams increased in marginal habitats in the presence of guppies (Figs. 3, 5), even as adult distribution showed little response or decreased in this habitat. In contrast, experienced KG killifish from streams with long-standing guppy

populations showed no substantial differences in the distribution of their eggs across habitats (Figs. 3, 5), even as adults shifted to greater relative abundance in marginal habitats. These findings strongly suggest stage-specific evolution of habitat preferences in response to IGP.

The initial shift in egg distribution may reflect a response to competitive or predatory interactions with guppies. Adult KO killifish may suffer from intense competition with guppies in pools, leading to relatively greater per capita resource availability and killifish egg production in marginal habitats. While plausible this mechanism seems an unlikely explanation, since adult killifish dominate in competition with guppies of similar or smaller sizes (Fraser and Lamphere 2013). Moreover, the effects of guppy competition on killifish cannot explain the patterns of egg production in the mesocosms, where killifish readily crossed between habitats and each habitat had food provisioned equally. Alternatively, this change in egg distribution may reflect a facultative shift in spawning habitat in response to guppies. Many taxa select oviposition sites to reduce predation and improve the survival of offspring (Martin 1998, Blaustein et al. 2004, Rieger et al. 2004, Fontaine and Martin 2006). When first encountering guppies, naïve female killifish may reduce the exposure of offspring to predation by placing eggs in marginal habitats with fewer guppies. Hatchling killifish are most vulnerable to guppy predation immediately after hatch (Furness and Reznick 2015), so the additional structural complexity of marginal habitats may

further limit guppy predation, as has been documented in other IGP systems (Finke and Denno 2006, Reichstein et al. 2013). This spatial segregation of killifish eggs, and therefore hatchlings, from high guppy densities offers the added advantage of reducing competition with guppies. Competition experiments indicate that guppies (especially those of large size) have a competitive advantage over small KO killifish (< ~14 mm; Potter pers comm). Thus, the immediate shift after guppy colonization in the distribution of killifish eggs across habitats may reduce the deleterious competitive and predatory impacts of guppies during the most vulnerable killifish life stages and enhance coexistence in this system.

Despite the advantages of placing eggs in marginal habitats with complex structure away from high guppy densities, this oviposition habitat preference did not manifest among experienced KG killifish in the presence of guppies. This response (or lack thereof) may reflect other adaptations in the dynamic interplay between ecology and evolution in KG communities. Upon colonizing previously KO sites, guppies eat primarily invertebrates with relatively little algae or detritus in their diet (Zandonà et al. 2011, Sullam et al. 2015, Zandonà et al. 2015). As a result, invertebrate density declines, while algal biomass increases (Bassar et al. 2010, Bassar et al. 2012, Simon et al. 2017) and so the initial competitive impact of guppies on primarily insectivorous killifish, especially of small sizes, may be relatively strong, leading to reduced overall egg productivity and/or greater

advantages of shifts in egg deposition habitat as seen in the artificial streams. These changes to the ecosystem, however, alter the selective environment and precipitate evolutionary changes in a suite of features in both species. Adaptation to the KG environment modifies the killifish-guppy interaction, such that evolution in each species improves guppy fitness significantly, even though killifish show no corresponding significant changes in overall fitness (Bassar et al. 2017a). Locally adapted KG guppies eat a diet rich in algae and detritus with few invertebrates, reversing the initial decline and increase in invertebrate abundance and algal biomass, respectively (Bassar et al. 2010, Zandonà et al. 2011, Simon et al. 2017). These dietary patterns suggest a reduced interspecific competitive impact of guppies on killifish with the potential for increased egg productivity and a discounted benefit of altered oviposition habitat selection. The net effect of evolution in these and other, yet unknown, IGP interaction traits may reduce the costs associated with spawning eggs in pools with high guppy density. Evolution likely provides alternative mechanisms for facilitating the coexistence of the IG predator and IG prey.

As a result of this evolution, killifish oviposition habitat may respond to intraspecific density more strongly than interspecific density at evolutionary equilibrium. For example, Eurasian pygmy owls, an IG prey species, select nest sites based upon local density of conspecifics and resources, as well as vegetation structure, but do not avoid their IG predator, Tengmalm's owls,

despite decreased survival rates of pygmy owl young near IG predator nests (Morosinotto et al. 2017). Thus, the observed shift in adult killifish distributions towards marginal habitats in established KG reaches may lead to increased egg productivity and/or spawning in other habitats to reduce the intraspecific competition (or cannibalism) experienced by offspring. These intraspecific, stage-structured interactions have proved to be influential in theory and empirical work in other IGP systems (Rudolf 2007, Rudolf and Armstrong 2008, De Roos and Persson 2013, Toscano et al. 2016).

This increased importance of intraspecific interactions relative to interspecific IGP interactions matches our understanding of killifish evolution in KG communities. Adaptation to the KG environment alters killifish life histories, such that they mature earlier and at smaller sizes, and produce more and smaller eggs (Walsh and Reznick 2009, 2010, 2011). The direction of change in these traits agrees with theory that includes the indirect effects of increased per-capita resource availability to survivors (Michod 1979, Abrams and Rowe 1996). Thus, the ecology and evolution of killifish depends upon both intraspecific interactions and interspecific IGP interactions (Walsh and Reznick 2009, 2010, Walsh et al. 2011). Although we cannot produce a well calibrated map of these factors, continuing to explore the balance between inter- and intraspecific interactions in shaping the ecological evolutionary outcomes will provides fertile ground for exploring coexistence in IGP systems.

Temporal Structure under IGP

In addition to the apparent spatial structure provided by stream habitats, the different daily activity patterns of killifish and guppies add temporal structure to their interactions. Guppies had higher daytime activity rates during the day, while adult, but not juvenile, KG killifish showed greater nighttime activity than upstream KO killifish. IGP theory that considers temporal structure has done so in the form of long-term (e.g. seasonal) refuges for the IG prey species (Amarasekare 2007b, 2008). In these models, time periods without IGP interactions promoted coexistence of both species by allowing the IG prey to persist at higher levels of basal resource productivity than possible without these temporal refuges. Furthermore, experimental manipulations in an insect host-parasitoid IGP system matched the predictions of this theory, suggesting that temporal structure influences IGP in nature (Amarasekare 2007b). While this long-term temporal structure shows promise as a potential coexistence mechanism, the more specific, daily time scales of our observations of killifish and guppies make extrapolating these predictions difficult.

Adjustments in diel activity patterns create short-term temporal refuges that reduce competitive or predatory interactions. These short-term refuges thus act as a form of behavioral defense. Theory incorporating IG prey defense predicts similar outcomes as seen with long-term IG prey temporal refuges (Kimbrell et al. 2007, Urbani and Ramos-Jiliberto 2010, but see Wang et al.

2016). These predictions have largely borne out in laboratory chemostat experiments (Kratina et al. 2010). Similarly, the coexisting large carnivores of Africa show complex daily patterns of activity that minimize interactions with dominant, IG predator species (Hayward and Slotow 2009). Adding temporal structure at a variety of time scales presents as a plausible coexistence mechanism.

As with the spatial distribution of killifish adults and eggs, the temporal patterns of activity we observed depended upon life stage or body size. Although we anticipated juveniles would reduce daytime activity with guppies since they suffer more from competition with guppies than do adult killifish, KG juveniles did not significantly alter their diel activity patterns relative to KO individuals. Adult killifish, however, showed a significant shift towards nocturnal activity with guppies as compared to those without guppies (Fig 3.6). This difference may, in part, reflect reduced power in our tests of juvenile activity patterns, since we recorded juveniles less frequently than adults overall leading to more variable estimates of activity. Juvenile activity patterns did show a nonsignificant trend towards increased nocturnal activity with guppies. Alternatively, the difference between adults and juveniles may provide another indicator of intraspecific interactions. Killifish aggressively displace each other from foraging locations (J.F.G. pers obs) and large, adult killifish may dominate nocturnal foraging opportunities, limiting the ability of small, juvenile killifish to

feed effectively at these preferred times with less guppy activity. Thus, the diel activity patterns of juvenile killifish may reflect a balance between limiting interspecific IGP interactions with guppies and restricting competitive or cannibalistic intraspecific interactions with larger, adults. Understanding the balance of these factors will likely have important consequences for understanding how the size-specific shift towards increased nocturnal behavior impacts coexistence in this system.

Guppy and killifish diel activity patterns showed no signs of evolutionary change. Across streams with contemporary and historical guppy introduction and with naturally colonizing guppies, guppies maintained a primarily diurnal activity pattern. Similarly, the nocturnal shift in diel activity patterns in killifish from KG reaches from those from KO reaches had a similar magnitude across all streams. Thus, these killifish behavioral responses to guppies likely represent an immediate ecological response to the presence of diurnal, IG predator guppies that emerges shortly after guppies colonize previously KO areas. Previous studies offer no consensus as to how frequently evolutionary changes in diel activity patterns result from species interactions. These changes in daily cycles have been reported in response to competition or predation in many taxa (Kronfeld-Schor and Dayan 2003, Hut et al. 2012), yet they remain highly conserved on a macroevolutionary level (Anderson and Wiens 2017). This lack of evolutionary response may reflect strong physiological constraints within

lineages of nocturnal or diurnal organisms (Kronfeld-Schor and Dayan 2003). Evolution of diel activity patterns may not provide a common means of stabilizing IGP interactions.

Despite this evolutionary conservatism, diel activity patterns show considerable plasticity in response to many ecological stimuli, including resources, competition and predation (De Meester et al. 1999, Reebs 2002, Monterroso et al. 2014). We found some evidence for this kind of plasticity in our comparison of killifish activities at normal and reduced guppy densities. When monthly mark-recapture samples temporarily reduce guppy densities for 1-2 days, adult killifish became marginally more nocturnal than when guppies occurred at normal density. Puzzlingly, this plasticity took the opposite direction from our predictions, suggesting increased activity overlap and presumably competition with guppies when guppies were present at normal density. This modest plasticity in killifish diel activity patterns may reflect the disturbance created by the mark-recapture sampling of guppies, or some other environmental factor, but could also signal some level of killifish predation on guppies. If sufficiently prevalent, the IGP impacts of adult killifish on guppies could impose population bottlenecks on guppies by limiting recruitment so as to enhance coexistence (Schröder et al. 2009b, Montserrat et al. 2012, Schellekens and van Kooten 2012, Toscano et al. 2016). While plausible, this hypothesis seems unlikely, since survival estimates from guppy mark-recapture models do

not indicate that killifish predation has a large impact on guppy populations (Bassar unpublished data). Further investigation may reveal how plasticity in temporal activity patterns contributes to coexistence under IGP.

Conclusions

Through paired experiments and field observations, we have assessed how spatial, temporal and population structured IGP interactions vary across an evolutionary gradient. We show that the spatial structure of adult IG prey and their eggs depends upon experience with the IG predator, suggesting that evolution modifies this potential coexistence mechanism as each species continues to persist. In contrast, the temporal structure of the IG prey and IG predator did not depend upon evolutionary history, acting as an immediate, ecological response to the initiation of IGP interactions. Thus, coexistence under IGP may represent a dynamic interplay between multiple ecological and evolutionary mechanisms. Placing coexistence in this context may help resolve the apparent paradox of IGP. While no single mechanism may yield coexistence, the sum of many, smaller components, changing over time, may facilitate the persistence of each species. This view presents new challenges to understanding IGP systems, as it requires identifying and assessing the relative contributions of each of these small parts to overall coexistence as the IGP interactions unfold over time.

Tables

Table 3.1. Model selection criteria for closed population models fit to mark-recapture data from all killifish or adults during April-July 2017 and 2018 in pool and marginal habitat of killifish-only (KO) and killifish-guppy (KG) reaches across six headwaters streams in Trinidad. *K* gives the parameter count for each model, AIC_c gives the Akaike Information Criteria with small sample correction, ΔAIC_c gives the difference between a given model and the minimum AIC_c in the set, and w_i gives the relative model weight.

Model	*K*	AIC_c	ΔAIC_c	w_i
All Killifish				
p(time × habitat × reach × stream)$c(\cdot)\sigma_p$(habitat)	74	15,555.28	0.00	0.392
p(time × habitat × reach × stream)$c(\cdot)\sigma_p$(habitat × reach)	76	15,555.77	0.49	0.307
p(time × habitat × reach × stream)$c(\cdot)\sigma_p$(reach)	74	15,555.90	0.62	0.288
p(time × habitat × reach × stream)$c(\cdot)\sigma_p$(habitat × stream)	84	15,563.86	8.58	0.005
p(time × habitat × reach × stream)$c(\cdot)\sigma_p$(reach × stream)	84	15,564.13	8.85	0.005
p(time × habitat × reach × stream)$c(\cdot)\sigma_p$(stream)	78	15,564.94	9.66	0.003
p(time × habitat × reach × stream)$c(\cdot)\sigma_p$(habitat × reach × stream)	96	15,573.76	18.48	0.000
p(time × habitat × reach × stream)c(habitat × reach × stream) σ_p(habitat × reach × stream)	120	15,668.51	113.23	0.000
p(habitat × reach × stream)c(habitat × reach × stream) σ_p(habitat × reach × stream)	72	15,785.95	230.67	0.000
p(habitat × reach × stream)$c(\cdot)\sigma_p$(habitat × reach × stream)	48	15,866.93	311.65	0.000
Adult Killifish				
p(time × habitat × reach × stream)$c(\cdot)\sigma_p$(habitat)	74	13,152.89	0.00	0.517
p(time × habitat × reach × stream)$c(\cdot)\sigma_p$(reach)	74	13,154.22	1.33	0.265
p(time × habitat × reach × stream)$c(\cdot)\sigma_p$(habitat × reach)	76	13,154.66	1.77	0.213
p(time × habitat × reach × stream)$c(\cdot)\sigma_p$(habitat × stream)	84	13,164.83	11.94	0.001
p(time × habitat × reach × stream)$c(\cdot)\sigma_p$(stream)	78	13,164.83	11.95	0.001
p(time × habitat × reach × stream)$c(\cdot)\sigma_p$(reach × stream)	84	13,165.02	12.13	0.001
p(time × habitat × reach × stream)$c(\cdot)\sigma_p$(habitat × reach × stream)	96	13,178.57	25.69	0.000
p(time × habitat × reach × stream)c(habitat × reach × stream) σ_p(habitat × reach × stream)	120	13,195.61	42.72	0.000
p(habitat × reach × stream)c(habitat × reach × stream) σ_p(habitat × reach × stream)	72	13,305.62	152.73	0.000
p(habitat × reach × stream)$c(\cdot)\sigma_p$(habitat × reach × stream)	48	13,397.09	244.20	0.000

Table 3.2. Parameter estimates and diagnostics for model of guppy abundance in artificial stream experiments during June-July 2017. Estimates presented as mode and 99% highest density interval (HDI). $\hat{R}$ and N_{eff} give the Gelman-Rubin convergence diagnostic and the effective posterior sample size, respectively. β terms refer to population-level effects and σ terms represent the standard deviation of inter-mesocosm variation. Reference categories taken as pool habitat, Aripo drainage and KG killifish origin. The 'zi' prefix indicates parameters from the zero-inflation component of the model.

Parameter	Mode	99% HDI	$\hat{R}$	N_{eff}
β_Intercept	1.46	0.884, 1.963	1.00	21,117
β_zi_Intercept	0.04	-0.772, 0.794	1.00	27,145
β_locationR	-1.06	-1.595, -0.615	1.00	22,428
β_locationSP	-1.01	-1.614, -0.508	1.00	32,567
β_drainageQuare	-0.13	-0.813, 0.618	1.00	21,677
β_originKO	0.10	-0.588, 0.826	1.00	20,849
β_locationR:drainageQuare	1.06	0.497, 1.628	1.00	22,633
β_locationSP:drainageQuare	-0.16	-1.018, 0.563	1.00	33,704
β_locationR:originKO	-0.35	-0.986, 0.288	1.00	23,120
β_locationSP:originKO	-0.46	-1.437, 0.503	1.00	30,876
β_drainageQuare:originKO	0.03	-0.904, 1.021	1.00	21,680
β_locationR:drainageQuare:originKO	-0.18	-0.938, 0.619	1.00	24,944
β_locationSP:drainageQuare:originKO	0.68	-0.592, 1.887	1.00	31,910
β_zi_locationR	0.32	-0.498, 1.11	1.00	26,789
β_zi_locationSP	1.01	0.189, 1.829	1.00	34,030
β_zi_drainageQuare	0.19	-0.813, 1.173	1.00	25,169
β_zi_originKO	-0.20	-1.139, 0.84	1.00	26,839
β_zi_locationR:drainageQuare	-0.21	-1.187, 0.807	1.00	27,046
β_zi_locationSP:drainageQuare	-0.46	-1.619, 0.642	1.00	34,425
β_zi_locationR:originKO	-0.47	-1.687, 0.583	1.00	27,929
β_zi_locationSP:originKO	0.72	-0.553, 1.885	1.00	34,191
β_zi_drainageQuare:originKO	0.19	-1.055, 1.518	1.00	25,924
β_zi_locationR:drainageQuare:originKO	0.89	-0.483, 2.257	1.00	28,617
β_zi_locationSP:drainageQuare:originKO	0.08	-1.409, 1.632	1.00	34,859
σ_channel__Intercept	0.15	0.000, 0.652	1.00	11,130
σ_channel__zi_Intercept	0.21	0.000, 0.888	1.00	11,811

Table 3.3. Parameter estimates and diagnostics for model of killifish abundance in artificial stream experiments during June-July 2017. Estimates presented as mode and 99% highest density interval (HDI). $\hat{R}$ and N_{eff} give the Gelman-Rubin convergence diagnostic and the effective posterior sample size, respectively. β terms refer to population-level effects and σ terms represent the standard deviation of inter-mesocosm variation. Reference categories taken as pool habitat, Aripo drainage KG killifish origin and guppies absent.

Parameter	Mode	99% HDI	$\hat{R}$	N_{eff}
β_Intercept[1]	-0.57	-1.602, 0.302	1.00	23,331
β_Intercept[2]	1.17	0.167, 2.074	1.00	24,131
β_Intercept[3]	2.59	1.593, 3.579	1.00	25,845
β_Intercept[4]	4.06	2.885, 5.215	1.00	30,948
β_Intercept[5]	6.90	4.701, 11.238	1.00	46,550
β_drainageQuare	0.16	-1.095, 1.259	1.00	24,373
β_originKO	1.27	-0.048, 2.324	1.00	23,045
β_guppiesPresent	-0.39	-1.544, 0.757	1.00	25,713
β_locationR	-1.57	-2.536, -0.57	1.00	28,699
β_locationSP	-0.70	-1.453, 0.113	1.00	28,237
β_drainageQuare:originKO	-0.38	-1.75, 1.167	1.00	25,074
β_drainageQuare:guppiesPresent	-0.47	-1.935, 0.964	1.00	26,761
β_originKO:guppiesPresent	-0.07	-1.515, 1.381	1.00	28,034
β_drainageQuare:locationR	1.30	0.125, 2.431	1.00	29,228
β_drainageQuare:locationSP	-0.56	-1.676, 0.471	1.00	31,492
β_originKO:locationR	-0.66	-1.863, 0.435	1.00	30,230
β_originKO:locationSP	-0.95	-1.934, 0.110	1.00	30,936
β_guppiesPresent:locationR	-0.43	-1.759, 0.787	1.00	30,845
β_guppiesPresent:locationSP	0.75	-0.322, 1.715	1.00	30,048
β_drainageQuare:originKO:guppiesPresent	-0.42	-2.134, 1.305	1.00	31,469
β_drainageQuare:originKO:locationR	-0.19	-1.574, 1.288	1.00	33,052
β_drainageQuare:originKO:locationSP	0.39	-0.959, 1.875	1.00	36,146
β_drainageQuare:guppiesPresent:locationR	0.04	-1.409, 1.570	1.00	34,277
β_drainageQuare:guppiesPresent:locationSP	0.08	-1.335, 1.413	1.00	34,165
β_originKO:guppiesPresent:locationR	0.10	-1.355, 1.628	1.00	34,058
β_originKO:guppiesPresent:locationSP	-1.03	-2.466, 0.348	1.00	35,404
β_drainageQuare:originKO:guppiesPresent:locationR	0.87	-0.790, 2.761	1.00	39,378
β_drainageQuare:originKO:guppiesPresent:locationSP	0.32	-1.385, 2.188	1.00	43,395
σ_channel__Intercept	0.47	0.123, 1.055	1.00	12,728

Table 3.4. Parameter estimates and diagnostics for model of egg abundance in artificial stream experiments during June-July 2017. Estimates presented as mode and 99% highest density interval (HDI). $\hat{R}$ and N_{eff} give the Gelman-Rubin convergence diagnostic and the effective posterior sample size, respectively. β terms refer to population-level effects and the shape parameter represents the negative binomial dispersion. Reference categories taken as pool habitat, Aripo drainage KG killifish origin and guppies absent.

Parameter	Mode	99% HDI	$\hat{R}$	N_{eff}
β_Intercept	1.16	0.315, 1.996	1.00	28,122
β_drainageQuare	0.71	-0.245, 1.701	1.00	25,697
β_originKO	-0.11	-1.120, 0.945	1.00	24,972
β_guppiesPresent	-0.52	-1.600, 0.551	1.00	26,112
β_habR	0.51	-0.518, 1.540	1.00	26,352
β_habSP	-0.19	-1.249, 0.947	1.00	28,085
β_drainageQuare:originKO	-0.12	-1.305, 1.133	1.00	26,411
β_drainageQuare:guppiesPresent	0.06	-1.258, 1.305	1.00	26,093
β_originKO:guppiesPresent	-0.41	-1.824, 0.881	1.00	28,984
β_drainageQuare:habR	-0.39	-1.668, 0.854	1.00	27,420
β_drainageQuare:habSP	0.00	-1.256, 1.324	1.00	27,556
β_originKO:habR	0.82	-0.460, 2.072	1.00	24,631
β_originKO:habSP	0.11	-1.215, 1.552	1.00	30,426
β_guppiesPresent:habR	0.49	-0.822, 1.802	1.00	26,216
β_guppiesPresent:habSP	-0.12	-1.667, 1.240	1.00	32,836
β_drainageQuare:originKO:guppiesPresent	-0.23	-1.863, 1.302	1.00	32,134
β_drainageQuare:originKO:habR	-0.70	-2.218, 0.844	1.00	29,233
β_drainageQuare:originKO:habSP	-0.38	-1.906, 1.306	1.00	31,837
β_drainageQuare:guppiesPresent:habR	0.44	-1.184, 1.918	1.00	30,655
β_drainageQuare:guppiesPresent:habSP	0.13	-1.568, 1.758	1.00	35,034
β_originKO:guppiesPresent:habR	-0.09	-1.663, 1.509	1.00	30,246
β_originKO:guppiesPresent:habSP	1.19	-0.510, 2.906	1.00	33,952
β_drainageQuare:originKO:guppiesPresent:habR	0.11	-1.682, 1.992	1.00	37,104
β_drainageQuare:originKO:guppiesPresent:habSP	-0.06	-1.943, 1.862	1.00	38,675
shape	4.70	0.747, 92.648	1.00	15,173

Table 3.5. Parameter estimates and diagnostics for model of egg productivity in streams during February-April 2017 and 2018. Estimates presented as mode and 99% highest density interval (HDI). $\hat{R}$ and N_{eff} give the Gelman-Rubin convergence diagnostic and the effective posterior sample size, respectively. β terms refer to population-level effects, σ terms represent the standard deviations of inter-stream variation effects and ρ terms refer to correlations between the stream variation effects. Reference categories taken as pool habitat, contemporary introductions and KG reach. The 'zi' prefix indicates parameters from the zero-inflation component of the model.

Parameter	Mode	99% HDI	$\hat{R}$	N_{eff}
β_Intercept	-0.81	-2.015, 0.440	1.00	18,702
β_zi_Intercept	-0.97	-1.952, -0.100	1.00	34,299
β_typeHist	1.07	-1.399, 3.223	1.00	20,851
β_typeNat	-0.11	-2.228, 1.820	1.00	19,923
β_reachKO	0.64	-0.669, 1.804	1.00	17,073
β_habM	0.44	-1.430, 1.410	1.00	12,303
β_typeHist:reachKO	-1.51	-3.723, 1.251	1.00	20,744
β_typeNat:reachKO	0.22	-1.781, 2.396	1.00	21,089
β_typeHist:habM	-1.08	-3.187, 2.033	1.00	17,670
β_typeNat:habM	-0.72	-2.790, 1.902	1.00	20,137
β_reachKO:habM	-1.36	-3.056, 0.794	1.00	17,459
β_typeHist:reachKO:habM	1.70	-2.230, 4.848	1.00	23,020
β_typeNat:reachKO:habM	0.20	-2.828, 3.299	1.00	25,236
σ_stream__Intercept	0.55	0.001, 1.702	1.00	18,535
σ_stream__reachKO	0.60	0.000, 1.757	1.00	16,444
σ_stream__habM	0.29	0.000, 1.942	1.00	10,903
σ_stream__reachKO:habM	1.14	0.049, 2.513	1.00	19,652
σ_stream__zi_Intercept	0.09	0.000, 1.449	1.00	20,986
ρ _stream__Intercept__reachKO	-0.17	-0.867, 0.862	1.00	20,700
ρ_stream__Intercept__habM	0.31	-0.844, 0.964	1.00	27,448
ρ_stream__reachKO__habM	0.19	-0.788, 0.958	1.00	28,337
ρ_stream__Intercept__reachKO:habM	-0.31	-0.948, 0.660	1.00	25,446
ρ_stream__reachKO__reachKO:habM	-0.30	-0.910, 0.730	1.00	25,638
ρ _stream__habM__reachKO:habM	-0.33	-0.953, 0.813	1.00	19,203

Table 3.6. Parameter estimates and diagnostics for model of guppy diel activity in streams during April-July 2015-2018. Estimates presented as mode and 99% highest density interval (HDI). $\hat{R}$ and N_{eff} give the Gelman-Rubin convergence diagnostic and the effective posterior sample size, respectively. β terms refer to population-level effects, σ terms represent the standard deviations of pool and stream variation effects, ρ terms refer to correlations between the stream variation effects and the shape parameter represents the negative binomial dispersion. Reference categories taken as contemporary introductions and daytime.

Parameter	Mode	99% HDI	$\hat{R}$	N_{eff}
β_Intercept	0.61	-0.529, 1.608	1.00	14,873
β_typeHist	-0.56	-2.299, 1.297	1.00	16,118
β_typeNat	-1.25	-3.038, 0.598	1.00	15,501
β_DayNightNight	-0.75	-2.058, 0.614	1.00	15,414
β_typeHist:DayNightNight	-0.95	-3.217, 1.238	1.00	19,217
β_typeNat:DayNightNight	0.11	-2.129, 2.285	1.00	18,717
σ_Pool__Intercept	1.20	0.940, 1.587	1.00	8,875
σ_Stream__Intercept	0.41	0.000, 1.491	1.00	5,351
σ_Stream__DayNightNight	0.77	0.367, 1.925	1.00	16,774
ρ_Stream__Intercept__DayNightNight	0.32	-0.849, 1.000	1.00	6,929
shape	4.37	3.137, 6.850	1.00	34,510

Table 3.7. Parameter estimates and diagnostics for model of juvenile killifish diel activity in streams during April-July 2015-2018. Estimates presented as mode and 99% highest density interval (HDI). $\hat{R}$ and N_{eff} give the Gelman-Rubin convergence diagnostic and the effective posterior sample size, respectively. β terms refer to population-level effects, σ terms represent the standard deviations of pool and stream variation effects and ρ terms refer to correlations between the stream variation effects. Reference categories taken as contemporary introductions, KG reach, and daytime.

Parameter	Mode	99% HDI	$\hat{R}$	N_{eff}
β_Intercept[1]	2.73	0.917, 4.208	1.00	14,588
β_Intercept[2]	5.10	3.333, 6.658	1.00	14,947
β_Intercept[3]	7.03	5.253, 8.669	1.00	15,786
β_Intercept[4]	8.51	6.625, 10.259	1.00	17,565
β_Intercept[5]	9.53	7.510, 11.512	1.00	21,321
β_Intercept[6]	10.88	8.624, 14.094	1.00	30,186
β_typeHist	0.16	-2.430, 2.650	1.00	17,510
β_typeNat	2.30	-0.379, 4.853	1.00	17,262
β_ReachKO	0.87	-1.267, 2.869	1.00	15,832
β_DayNightNight	0.90	-0.948, 2.522	1.00	15,794
β_typeHist:ReachKO	0.21	-3.122, 3.676	1.00	21,286
β_typeNat:ReachKO	-1.38	-4.600, 2.134	1.00	21,221
β_typeHist:DayNightNight	-0.49	-3.292, 2.303	1.00	19,405
β_typeNat:DayNightNight	-0.42	-3.105, 2.494	1.00	19,655
β_ReachKO:DayNightNight	-0.58	-2.722, 1.651	1.00	18,909
β_typeHist:ReachKO:DayNightNight	-0.64	-4.011, 2.984	1.00	26,168
β_typeNat:ReachKO:DayNightNight	-0.69	-3.966, 2.911	1.00	24,295
σ_Pool__Intercept	1.10	0.875, 1.412	1.00	12,516
σ_Stream__Intercept	1.21	0.691, 2.186	1.00	18,676
σ_Stream__ReachKO	1.58	0.844, 2.876	1.00	25,106
σ_Stream__DayNightNight	1.32	0.806, 2.400	1.00	25,014
σ_Stream__ReachKO:DayNightNight	1.71	1.034, 3.027	1.00	31,357
ρ_Stream__Intercept__ReachKO	-0.61	-0.921, 0.148	1.00	19,340
ρ_Stream__Intercept__DayNightNight	-0.87	-0.995, -0.073	1.00	18,935
ρ_Stream__ReachKO__DayNightNight	0.24	-0.433, 0.796	1.00	33,536
ρ_Stream__Intercept__ReachKO:DayNightNight	0.56	-0.215, 0.923	1.00	20,718
ρ_Stream__ReachKO__ReachKO:DayNightNight	-0.36	-0.817, 0.379	1.00	30,552
ρ_Stream__DayNightNight__ ReachKO:DayNightNight	-0.58	-0.906, 0.165	1.00	32,095

Table 3.8. Parameter estimates and diagnostics for model of adult killifish diel activity in streams during April-July 2015-2018. Estimates presented as mode and 99% highest density interval (HDI). $\hat{R}$ and N_{eff} give the Gelman-Rubin convergence diagnostic and the effective posterior sample size, respectively. β terms refer to population-level effects, σ terms represent the standard deviations of pool and stream variation effects and ρ terms refer to correlations between the stream variation effects. Reference categories taken as contemporary introductions, KG reach, and daytime.

Parameter	Mode	99% HDI	$\hat{R}$	N_{eff}
β_Intercept[1]	3.18	1.060, 5.089	1.00	8,588
β_Intercept[2]	5.19	3.057, 7.090	1.00	8,672
β_Intercept[3]	6.99	4.755, 8.834	1.00	8,864
β_Intercept[4]	8.24	6.054, 10.215	1.00	9,397
β_Intercept[5]	9.16	6.913, 11.189	1.00	9,958
β_Intercept[6]	9.82	7.387, 11.804	1.00	10,893
β_Intercept[7]	10.18	7.810, 12.455	1.00	11,804
β_Intercept[8]	10.86	8.341, 13.455	1.00	14,131
β_Intercept[9]	11.49	8.894, 14.820	1.00	16,536
β_Intercept[10]	12.77	9.585, 17.539	1.00	23,222
β_typeHist	-0.31	-3.529, 2.679	1.00	11,637
β_typeNat	1.00	-2.064, 3.898	1.00	10,389
β_ReachKO	1.51	-0.341, 3.189	1.00	9,019
β_DayNightNight	1.82	0.290, 3.326	1.00	11,466
β_typeHist:ReachKO	-0.56	-3.548, 2.389	1.00	10,710
β_typeNat:ReachKO	0.21	-2.433, 3.189	1.00	10,579
β_typeHist:DayNightNight	1.14	-1.403, 3.733	1.00	13,514
β_typeNat:DayNightNight	0.19	-2.220, 2.693	1.00	13,153
β_ReachKO:DayNightNight	-0.67	-2.390, 1.033	1.00	12,118
β_typeHist:ReachKO:DayNightNight	-0.02	-2.677, 3.121	1.00	14,286
β_typeNat:ReachKO:DayNightNight	-0.25	-2.960, 2.534	1.00	13,975
σ_Pool__Intercept	1.53	1.235, 1.906	1.00	7,814
σ_Stream__Intercept	1.21	0.507, 2.563	1.00	12,313
σ_Stream__ReachKO	1.06	0.018, 2.307	1.00	6,180
σ_Stream__DayNightNight	0.96	0.304, 2.132	1.00	14,873
σ_Stream__ReachKO:DayNightNight	1.07	0.392, 2.345	1.00	16,328
ρ_Stream__Intercept__ReachKO	-0.21	-0.831, 0.753	1.00	11,265
ρ_Stream__Intercept__DayNightNight	-0.75	-0.985, 0.279	1.00	14,175
ρ_Stream__ReachKO__DayNightNight	-0.03	-0.822, 0.764	1.00	13,062
ρ_Stream__Intercept__ReachKO:DayNightNight	-0.25	-0.878, 0.556	1.00	14,693
ρ_Stream__ReachKO__ReachKO:DayNightNight	-0.59	-0.982, 0.445	1.00	12,778
ρ_Stream__DayNightNight__ ReachKO:DayNightNight	0.22	-0.600, 0.885	1.00	19,375

Table 3.9. Parameter estimates and diagnostics for model of juvenile killifish diel activity in streams with manipulated guppy densities during June-July 2015. Estimates presented as mode and 99% highest density interval (HDI). $\hat{R}$ and N_{eff} give the Gelman-Rubin convergence diagnostic and the effective posterior sample size, respectively. β terms refer to population-level effects, σ terms represent the standard deviations of pool and stream variation effects and ρ terms refer to correlations between the stream variation effects. Reference categories taken as guppies present, KG reach, and daytime.

Parameter	Mode	99% HDI	$\hat{R}$	N_{eff}
β_Intercept[1]	2.85	1.407, 4.247	1.00	14,092
β_Intercept[2]	5.22	3.837, 6.721	1.00	14,597
β_Intercept[3]	7.83	6.148, 9.470	1.00	19,357
β_GuppiesPresent	-0.13	-1.699, 1.449	1.00	13,118
β_ReachKO	0.99	-0.475, 2.358	1.00	9,849
β_DayNightNight	0.90	-0.706, 2.550	1.00	12,666
β_GuppiesPresent:ReachKO	0.22	-1.420, 1.741	1.00	17,555
β_GuppiesPresent:DayNightNight	0.15	-1.041, 1.511	1.00	18,811
β_ReachKO:DayNightNight	-0.75	-2.724, 1.428	1.00	16,537
b_GuppiesPresent:ReachKO:DayNightNight	0.03	-2.238, 2.158	1.00	17,872
σ_Pool__Intercept	1.06	0.804, 1.452	1.00	10,037
σ_Stream__Intercept	0.53	0.000, 1.875	1.00	11,499
σ_Stream__GuppiesPresent	0.78	0.170, 2.192	1.00	18,871
σ_Stream__ReachKO	0.34	0.000, 1.861	1.00	11,111
σ_Stream__DayNightNight	0.81	0.192, 2.296	1.00	19,646
σ_Stream__GuppiesPresent:ReachKO	0.62	0.000, 2.106	1.00	15,904
σ_Stream__GuppiesPresent:DayNightNight	0.14	0.000, 1.671	1.00	17,987
σ_Stream__ReachKO:DayNightNight	1.18	0.474, 2.724	1.00	23,049
σ_Stream__GuppiesPresent:ReachKO:DayNightNight	1.26	0.425, 2.853	1.00	23,496
ρ_Stream__Intercept__GuppiesPresent	-0.24	-0.870, 0.556	1.00	20,094
ρ_Stream__Intercept__ReachKO	-0.03	-0.726, 0.777	1.00	29,697
ρ_Stream__GuppiesPresent__ReachKO	-0.13	-0.813, 0.678	1.00	27,819
ρ_Stream__Intercept__DayNightNight	-0.12	-0.745, 0.684	1.00	20,927
ρ_Stream__GuppiesPresent__DayNightNight	0.00	-0.704, 0.683	1.00	26,973
ρ_Stream__ReachKO__DayNightNight	-0.01	-0.722, 0.780	1.00	18,202
ρ_Stream__Intercept__GuppiesPresent:ReachKO	0.11	-0.693, 0.783	1.00	25,641
ρ_Stream__GuppiesPresent__GuppiesPresent:ReachKO	-0.22	-0.812, 0.626	1.00	27,367
ρ_Stream__ReachKO__GuppiesPresent:ReachKO	0.14	-0.694, 0.797	1.00	21,044
ρ_Stream__DayNightNight__GuppiesPresent:ReachKO	0.13	-0.617, 0.809	1.00	28,967
ρ_Stream__Intercept__GuppiesPresent:DayNightNight	0.04	-0.766, 0.757	1.00	36,825
ρ_Stream__GuppiesPresent__GuppiesPresent:DayNightNight	0.04	-0.715, 0.788	1.00	35,031

ρ_Stream__ReachKO__ GuppiesPresent:DayNightNight	-0.09	-0.802, 0.735	1.00	26,450
ρ_Stream__DayNightNight__ GuppiesPresent:DayNightNight	-0.18	-0.832, 0.685	1.00	27,318
ρ_Stream__GuppiesPresent:ReachKO__ GuppiesPresent:DayNightNight	-0.13	-0.787, 0.723	1.00	27,603
ρ_Stream__Intercept__ ReachKO:DayNightNight	0.03	-0.687, 0.723	1.00	21,608
ρ_Stream__GuppiesPresent__ ReachKO:DayNightNight	0.09	-0.620, 0.719	1.00	26,871
ρ_Stream__ReachKO__ReachKO:DayNightNight	-0.18	-0.836, 0.627	1.00	16,455
ρ_Stream__DayNightNight__ ReachKO:DayNightNight	-0.19	-0.782, 0.549	1.00	26,266
ρ_Stream__GuppiesPresent:ReachKO__ ReachKO:DayNightNight	-0.29	-0.872, 0.512	1.00	21,826
ρ_Stream__GuppiesPresent:DayNightNight__ ReachKO:DayNightNight	0.17	-0.669, 0.809	1.00	20,591
ρ_Stream__Intercept__ GuppiesPresent:ReachKO:DayNightNight	0.30	-0.527, 0.880	1.00	21,038
ρ_Stream__GuppiesPresent__ GuppiesPresent:ReachKO:DayNightNight	-0.35	-0.899, 0.414	1.00	32,597
ρ_Stream__ReachKO__ GuppiesPresent:ReachKO:DayNightNight	0.18	-0.668, 0.803	1.00	21,090
ρ_Stream__DayNightNight__ GuppiesPresent:ReachKO:DayNightNight	0.09	-0.634, 0.714	1.00	28,668
ρ_Stream__GuppiesPresent:ReachKO__ GuppiesPresent:ReachKO:DayNightNight	0.05	-0.639, 0.763	1.00	26,304
ρ_Stream__GuppiesPresent:DayNightNight__ GuppiesPresent:ReachKO:DayNightNight	-0.19	-0.822, 0.671	1.00	23,240
ρ_Stream__ReachKO:DayNightNight__ GuppiesPresent:ReachKO:DayNightNight	-0.09	-0.698, 0.629	1.00	25,823

Table 3.10. Parameter estimates and diagnostics for model of adult killifish diel activity in streams with manipulated guppy densities during June-July 2015. Estimates presented as mode and 99% highest density interval (HDI). $\hat{R}$ and N_{eff} give the Gelman-Rubin convergence diagnostic and the effective posterior sample size, respectively. β terms refer to population-level effects, σ terms represent the standard deviations of pool and stream variation effects and ρ terms refer to correlations between the stream variation effects. Reference categories taken as guppies present, KG reach, and daytime.

Parameter	Mode	99% HDI	$\hat{R}$	N_{eff}
β_Intercept[1]	3.17	2.155, 4.204	1.00	14,348
β_Intercept[2]	5.15	4.124, 6.210	1.00	15,019
β_Intercept[3]	6.76	5.634, 7.819	1.00	16,216
β_Intercept[4]	7.95	6.853, 9.248	1.00	19,279
β_Intercept[5]	8.75	7.471, 10.080	1.00	22,169
β_Intercept[6]	9.54	8.229, 11.273	1.00	26,715
β_Intercept[7]	10.38	8.832, 12.678	1.00	34,839
β_Intercept[8]	11.83	9.553, 16.341	1.00	49,275
β_GuppiesPresent	0.26	-1.070, 1.707	1.00	16,067
β_ReachKO	1.35	0.124, 2.569	1.00	12,177
β_DayNightNight	2.79	1.306, 4.233	1.00	16,186
β_GuppiesPresent:ReachKO	0.07	-1.142, 1.181	1.00	23,227
β_GuppiesPresent:DayNightNight	-1.19	-2.946, 0.992	1.00	18,770
β_ReachKO:DayNightNight	-1.28	-2.929, 0.677	1.00	18,453
β_GuppiesPresent:ReachKO:DayNightNight	0.68	-0.592, 1.959	1.00	25,042
σ_Pool__Intercept	1.27	0.968, 1.623	1.00	10,032
σ_Stream__Intercept	0.06	0.000, 1.332	1.00	21,094
σ_Stream__GuppiesPresent	0.56	0.004, 1.905	1.00	20,304
σ_Stream__ReachKO	0.08	0.000, 1.527	1.00	18,354
σ_Stream__DayNightNight	0.70	0.037, 2.024	1.00	19,563
σ_Stream__GuppiesPresent:ReachKO	0.08	0.000, 1.527	1.00	20,860
σ_Stream__GuppiesPresent:DayNightNight	1.03	0.407, 2.581	1.00	26,340
σ_Stream__ReachKO:DayNightNight	0.90	0.259, 2.41	1.00	23,159
σ_Stream__GuppiesPresent:ReachKO:DayNightNight	0.08	0.000, 1.542	1.00	28,385
ρ_Stream__Intercept__GuppiesPresent	-0.02	-0.778, 0.752	1.00	25,371
ρ_Stream__Intercept__ReachKO	0.02	-0.816, 0.721	1.00	45,441
ρ_Stream__GuppiesPresent__ReachKO	-0.10	-0.788, 0.748	1.00	37,473
ρ_Stream__Intercept__DayNightNight	0.00	-0.789, 0.744	1.00	23,687
ρ_Stream__GuppiesPresent__DayNightNight	0.15	-0.620, 0.804	1.00	30,868
ρ_Stream__ReachKO__DayNightNight	-0.10	-0.798, 0.729	1.00	23,033
ρ_Stream__Intercept__GuppiesPresent:ReachKO	-0.01	-0.777, 0.760	1.00	45,560
ρ_Stream__GuppiesPresent__GuppiesPresent:ReachKO	0.01	-0.725, 0.788	1.00	40,419
ρ_Stream__ReachKO__GuppiesPresent:ReachKO	-0.07	-0.783, 0.753	1.00	32,012
ρ_Stream__DayNightNight__GuppiesPresent:ReachKO	0.14	-0.701, 0.802	1.00	31,051
ρ_Stream__Intercept__ GuppiesPresent:DayNightNight	0.05	-0.756, 0.761	1.00	22,089

ρ_Stream__GuppiesPresent__ GuppiesPresent:DayNightNight	-0.32	-0.871, 0.505	1.00	30,504
ρ_Stream__ReachKO__ GuppiesPresent:DayNightNight	0.07	-0.717, 0.785	1.00	24,617
ρ_Stream__DayNightNight__ GuppiesPresent:DayNightNight	-0.20	-0.801, 0.553	1.00	27,947
ρ_Stream__GuppiesPresent:ReachKO__ GuppiesPresent:DayNightNight	-0.12	-0.807, 0.689	1.00	23,416
ρ_Stream__Intercept__ReachKO:DayNightNight	-0.04	-0.778, 0.755	1.00	23,714
ρ_Stream__GuppiesPresent__ ReachKO:DayNightNight	-0.19	-0.791, 0.614	1.00	33,897
ρ_Stream__ReachKO__ReachKO:DayNightNight	0.09	-0.728, 0.785	1.00	23,030
ρ_Stream__DayNightNight__ ReachKO:DayNightNight	-0.35	-0.912, 0.455	1.00	28,866
ρ_Stream__GuppiesPresent:ReachKO__ ReachKO:DayNightNight	-0.11	-0.816, 0.683	1.00	25,373
ρ_Stream__GuppiesPresent:DayNightNight__ ReachKO:DayNightNight	0.14	-0.559, 0.778	1.00	28,527
ρ_Stream__Intercept__ GuppiesPresent:ReachKO:DayNightNight	-0.07	-0.766, 0.771	1.00	50,695
ρ_Stream__GuppiesPresent__ GuppiesPresent:ReachKO:DayNightNight	0.05	-0.753, 0.754	1.00	46,225
ρ_Stream__ReachKO__ GuppiesPresent:ReachKO:DayNightNight	0.01	-0.758, 0.771	1.00	38,120
ρ_Stream__DayNightNight__ GuppiesPresent:ReachKO:DayNightNight	0.02	-0.776, 0.751	1.00	34,498
ρ_Stream__GuppiesPresent:ReachKO__ GuppiesPresent:ReachKO:DayNightNight	-0.13	-0.784, 0.748	1.00	27,326
ρ_Stream__GuppiesPresent:DayNightNight__ GuppiesPresent:ReachKO:DayNightNight	0.05	-0.757, 0.752	1.00	29,438
ρ_Stream__ReachKO:DayNightNight__ GuppiesPresent:ReachKO:DayNightNight	-0.01	-0.766, 0.754	1.00	26,736

Figures

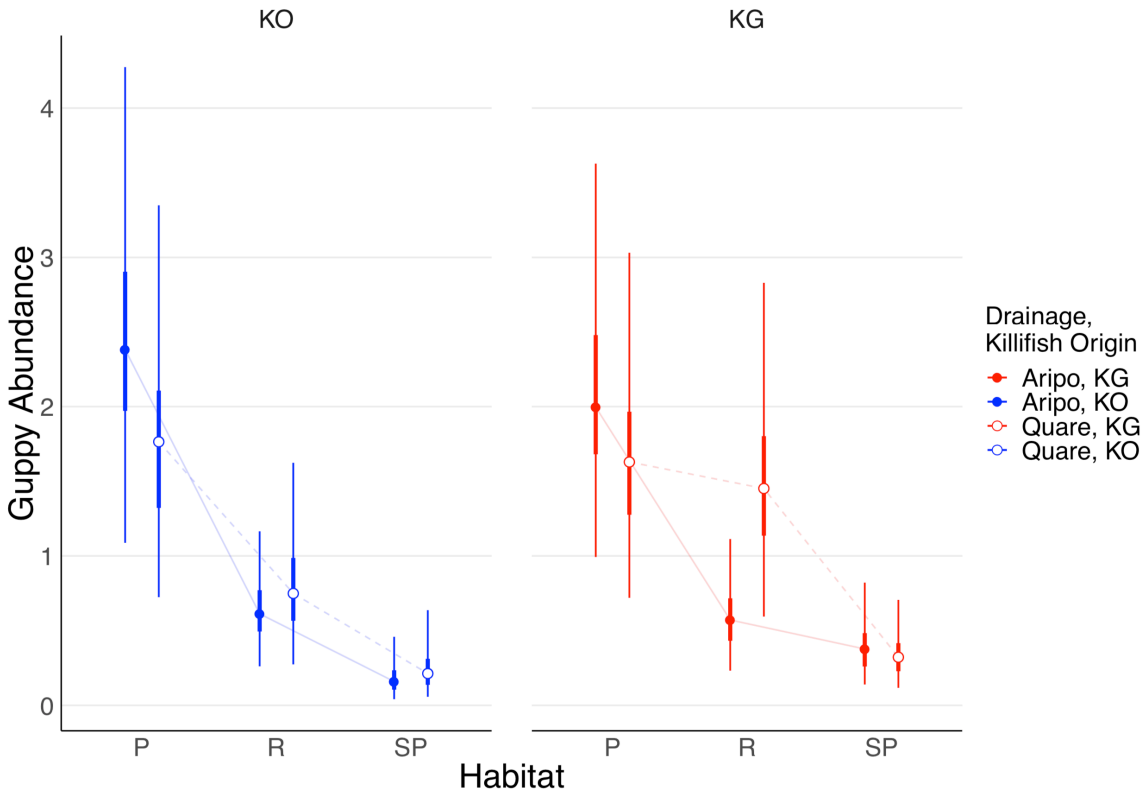

Figure 3.1. Guppy abundance in pool (P), riffle (R) and side pool (SP) compartments of the artificial stream experiments during June-July 2017. Abundance of guppies placed in channels with killifish-only (KO) killifish shown in blue (left panel) and that of those placed in channels with killifish-guppy (KG) killifish shown in red (right panel). Solid circles represent the Aripo tributary replicate and open circles represent the Quare tributary replicate. Points represent posterior population modes, thick bars represent the 66% highest posterior density interval (HDI) and thin bars capture the 99% HDI.

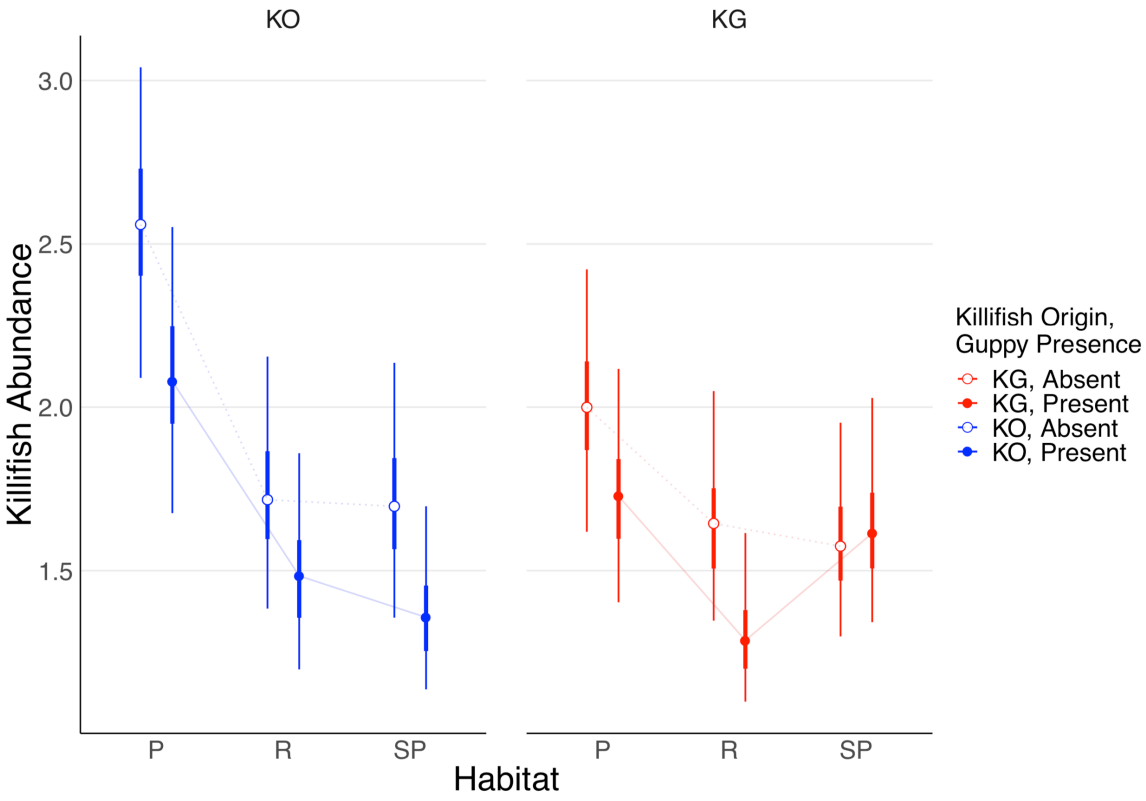

Figure 3.2. Killifish abundance in pool (P), riffle (R) and side pool (SP) compartments of the artificial stream experiments during June-July 2017. Response of killifish-only (KO) killifish shown in blue (left panel) and that of killifish-guppy (KG) killifish shown in red (right panel). Solid circles represent the guppy present treatment and open circles represent the guppy absent treatment. Points represent posterior population modes, thick bars represent the 66% highest posterior density interval (HDI) and thin bars capture the 99% HDI. Displayed estimates have been marginalized over the two drainage replicates.

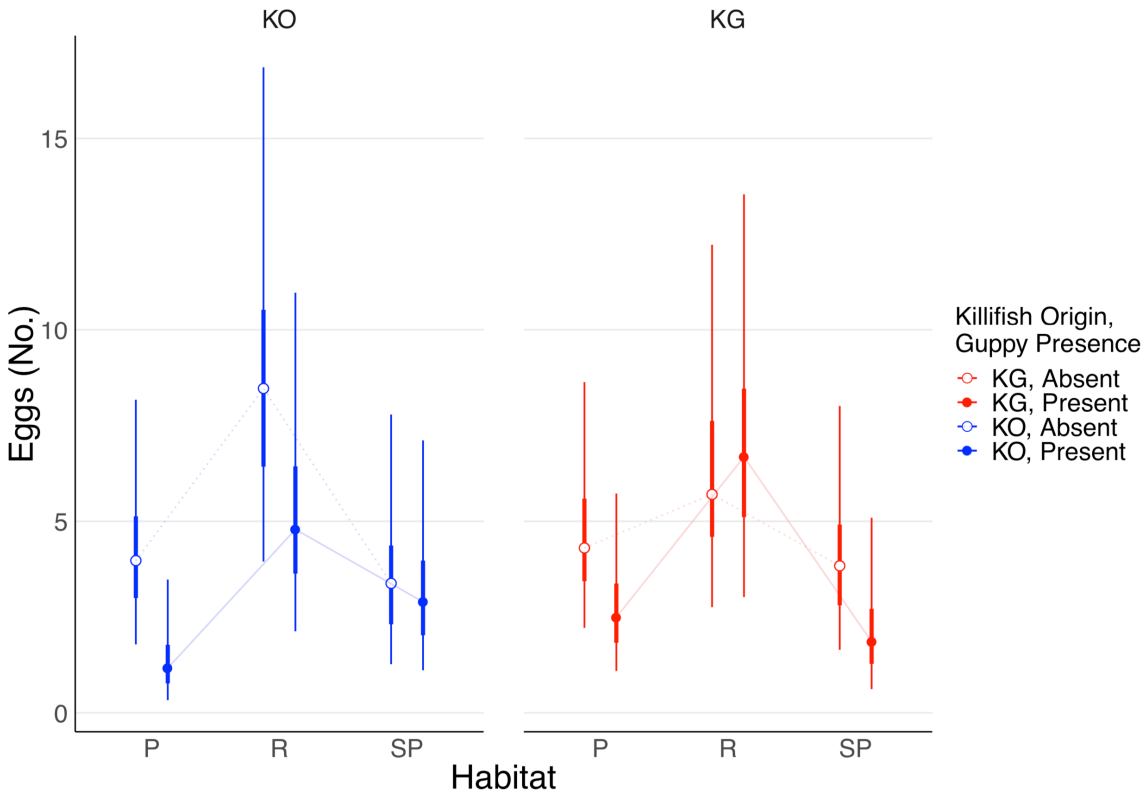

Figure 3.3. Egg abundance in pool (P), riffle (R) and side pool (SP) compartments of the artificial stream experiments during June-July 2017. Response of killifish-only (KO) killifish shown in blue (left panel) and that of killifish-guppy (KG) killifish shown in red (right panel). Solid circles represent the guppy present treatment and open circles represent the guppy absent treatment. Points represent posterior population modes, thick bars represent the 66% highest posterior density interval (HDI) and thin bars capture the 99% HDI. Displayed estimates have been marginalized over the two drainage replicates.

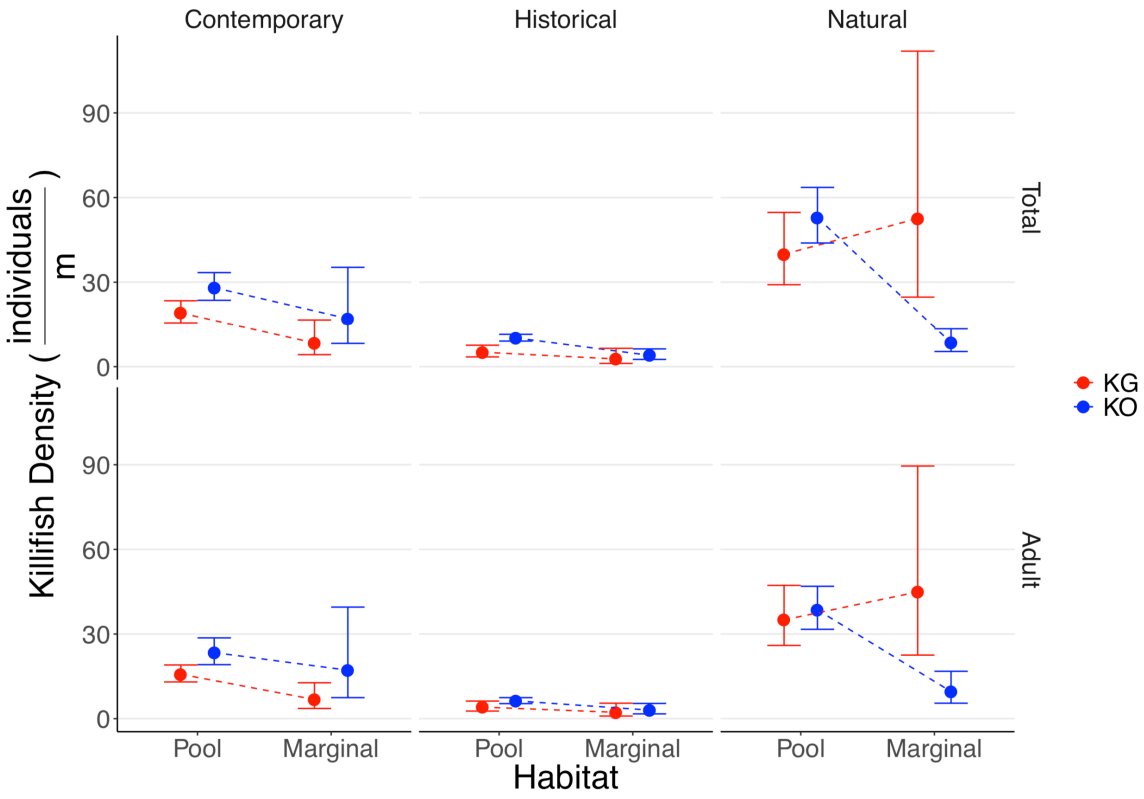

Figure 3.4. Killifish density (individuals/m) in pool and marginal habitats in streams with contemporary guppy introductions (left panels), historical guppy introductions (center panels) and naturally colonized guppy populations (right panels) for all killifish (top panels) and adult (≥ 30 mm) individuals only (bottom panels) from model averaged closed population mark-recapture estimates from April-July 2017 and 2018. Density in killifish-only (KO) reaches shown in blue and that of killifish-guppy (KG) reaches shown in red. Points represent mean density estimates and error bars capture the 95% confidence intervals. Displayed estimates from the contemporary guppy introduction streams have been marginalized over the four streams of this type.

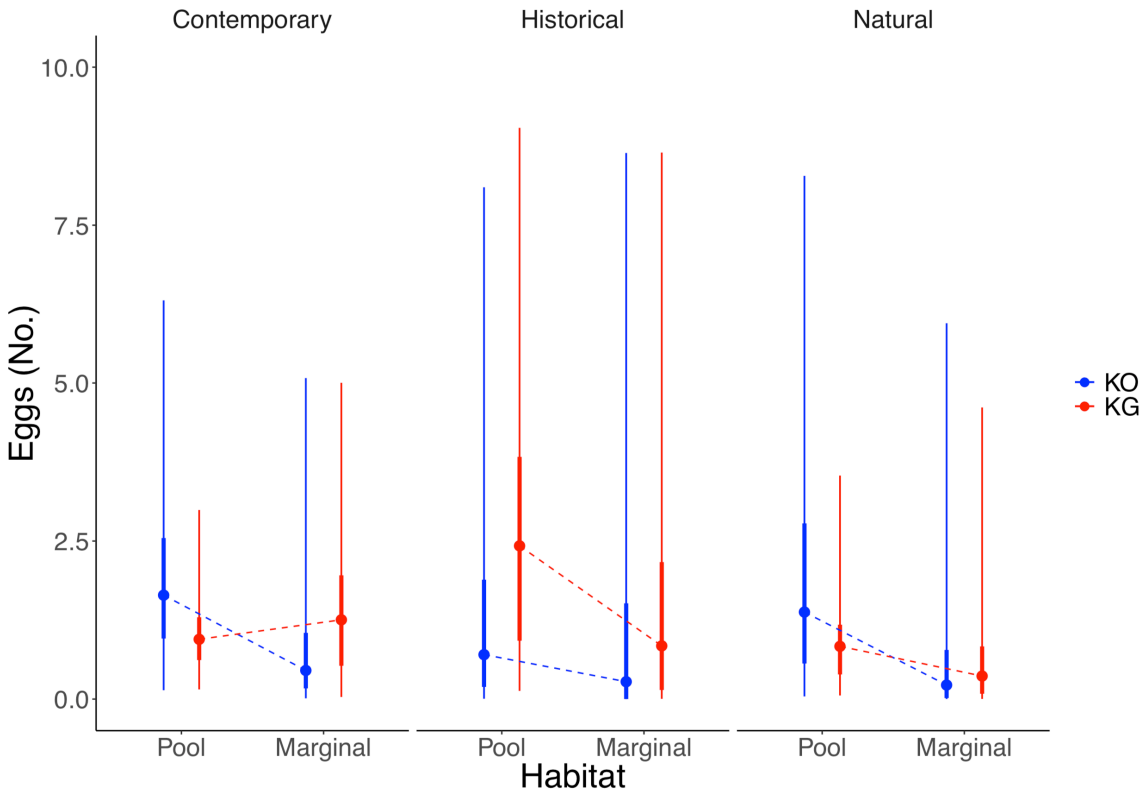

Figure 3.5. Eggs spawned in artificial substrates in pool and marginal habitats in streams with contemporary guppy introductions (left panel), historical guppy introductions (center panel) and naturally colonized guppy populations (right panel) during February-April 2017 and 2018. Egg productivity in killifish-only (KO) reaches shown in blue and that of killifish-guppy (KG) reaches shown in red. Points represent posterior population modes, thick bars represent the 66% highest posterior density interval (HDI) and thin bars capture the 99% HDI.

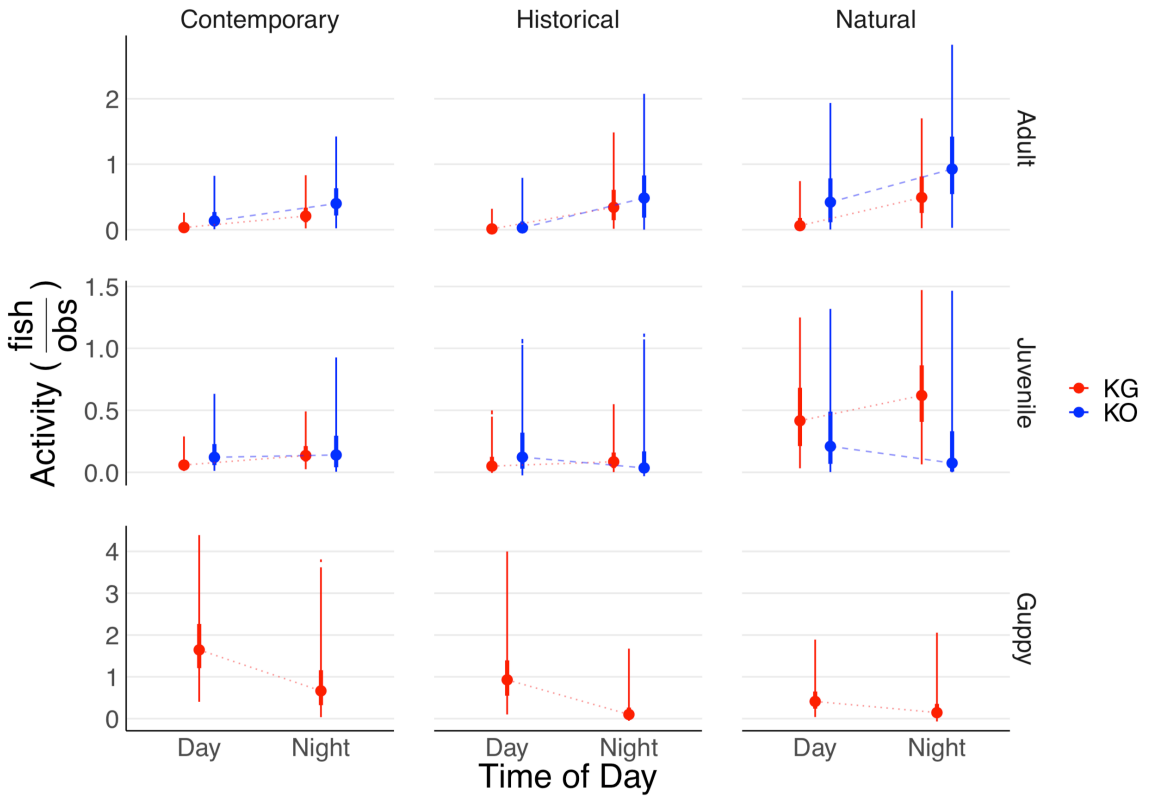

Figure 3.6. Killifish and guppy activity rates during the day and night in streams with contemporary guppy introductions (left panels), historical guppy introductions (center panels) and naturally colonized guppy populations (right panels) for guppies (bottom panels), and juvenile (middle panels) and adult (top panels) individuals in observations taken in April-July 2015-2018. Activity rates in killifish-only (KO) reaches shown in blue and that of killifish-guppy (KG) reaches shown in red. Points represent posterior population modes, thick bars represent the 66% highest posterior density interval (HDI) and thin bars capture the 99% HDI.

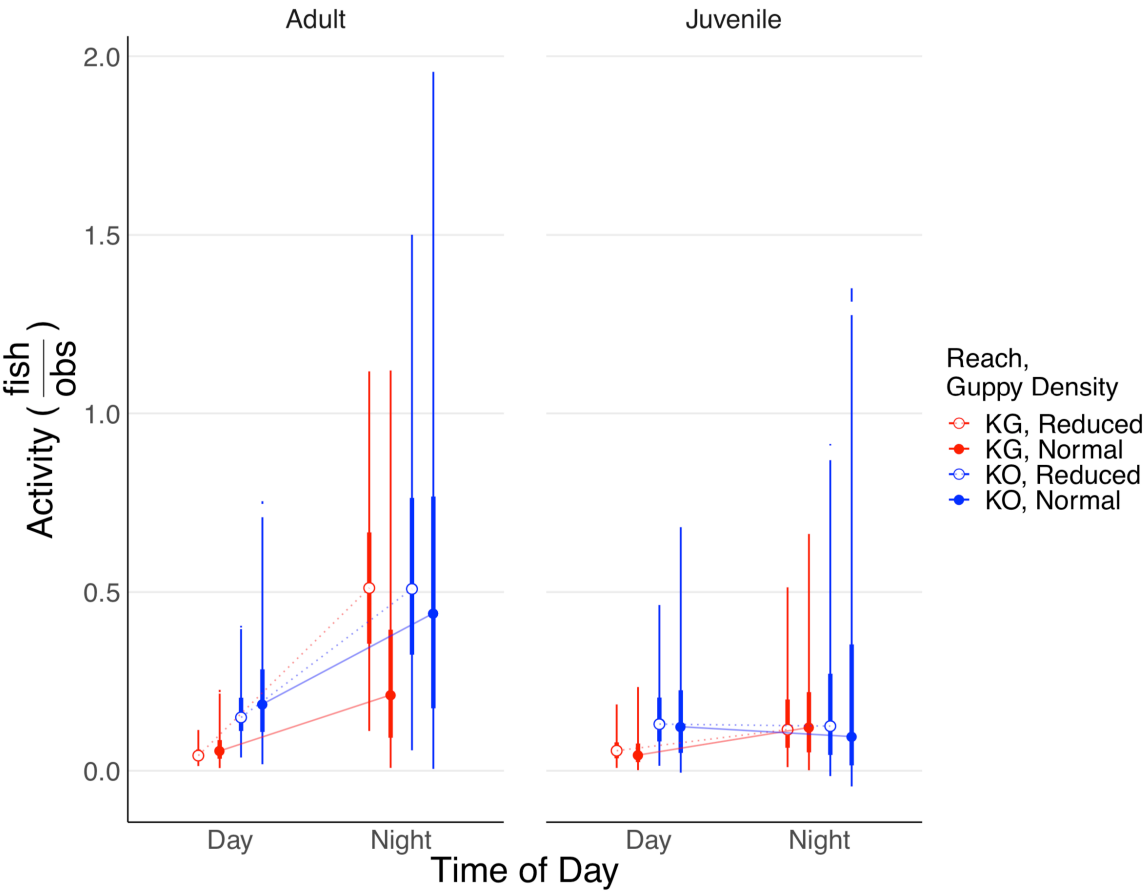

Figure 3.7. Killifish activity rates during the day and night in streams with manipulated guppy densities in contemporary guppy introductions for juvenile (right panel) and adult (left panel) individuals in observations taken in June-July 2015. Activity rates in killifish-only (KO) reaches shown in blue and that of killifish-guppy (KG) reaches shown in red. Solid circles represent the observations taken at normal guppy density and open circles represent those taken at reduced guppy density. Points represent posterior population modes, thick bars represent the 66% highest posterior density interval (HDI) and thin bars capture the 99% HDI.

Epilogue

The persistence of ecologically similar species in biological communities has long puzzled ecologists. Coexistence theory predicts that persistent community members should be more sensitive to intraspecific interactions than interspecific interactions with other species. In this dissertation, I assess the evidence for this prediction in a freshwater stream fish community on the island of Trinidad. I describe the demographic effects on killifish of size-structured intra- and interspecific interactions upon the initiation of killifish-guppy communities. I then examine the factors underlying killifish persistence in a broader ecological and evolutionary context in which the strength of interactions may vary spatially and temporally as the community develops.

Chapter one demonstrated that killifish can persist across a range of killifish and guppy population densities and size structures when these two species first meet. Upon contact, size-selective guppy predation of neonate killifish complemented the negative impacts of killifish-guppy competition on killifish and led to a decline in population growth rates. The significant decrease in killifish population growth rates with reduced density indicated that killifish should recover when rare to persist in the community. However, the roughly equivalent effects of size structure variation in either species showed that the distribution of body sizes and, therefore, competitive abilities alter long-term killifish population dynamics in these communities. Thus, killifish population

dynamics and persistence depended upon intraspecific density-dependence, intra- and interspecific size-structure dependence, and guppy predation on hatchling killifish.

Chapter two extended our view of killifish-guppy interactions and their demographic impacts on killifish to a natural stream environment with alternative habitats over a time course of three to four years. In this setting, killifish population densities declined as predicted. Underlying this trend, killifish and guppies showed distinct habitat use. This pattern of habitat use correlated with predicted habitat-specific increases in killifish mean size and decreases in killifish recruitment. These patterns in body size and recruitment could not be explained by observed differences in killifish growth rates. Taken together, these results indicated that differential habitat use between these two species may structure antagonistic competitive and predatory interactions with guppies so as to facilitate killifish recruitment and, ultimately, persistence.

Chapter three further explored the contribution of killifish and guppy habitat use, as well as diel activity patterns, to killifish persistence over an evolutionary gradient of killifish-guppy communities. This chapter found that killifish habitat use depended upon life stage and experience with guppies. In contrast, killifish and guppy diel activity patterns remained consistent with evolutionary experience, although they also reflected probable ecological divergence between adult, but not juvenile, killifish and guppies. These

responses of killifish habitat use and diel activity to evolutionary experience with guppies indicated that multiple mechanisms may promote persistence. Moreover, the mechanisms favoring persistence differed as the community developed both ecologically and evolutionarily.

A growing empirical consensus has coalesced around the central predictions of coexistence theory. Species often exhibit greater sensitivity to intraspecific interactions than interspecific interactions, implying that species have sufficiently different resource use or requirements to persist in the community. This underlying differentiation among species may rely upon multiple factors and the contribution of each of these mechanisms may change dynamically as interactions unfold in the community. Thus, coexistence can entail an intricate interplay between ecological and evolutionary processes, however, the frequency and strength with which these ecological-evolutionary interactions influence community outcomes remains largely unknown. Future work may reveal how ecology, evolution and their interactions play a part in the persistence of individual species, coexistence within communities and the maintenance of global biodiversity.

References

Abrams, P. A. 2011. Simple life-history omnivory: responses to enrichment and harvesting in systems with intraguild predation. The American Naturalist **178**:305-319.

Abrams, P. A., and L. Rowe. 1996. The effects of predation on the age and size of maturity of prey. Evolution **50**:1052-1061.

Adler, P. B., S. P. Ellner, and J. M. Levine. 2010. Coexistence of perennial plants: an embarrassment of niches. Ecology Letters **13**:1019-1029.

Adler, P. B., J. HilleRisLambers, and J. M. Levine. 2007. A niche for neutrality. Ecology Letters **10**:95-104.

Adler, P. B., D. Smull, K. H. Beard, R. T. Choi, T. Furniss, A. Kulmatiski, J. M. Meiners, A. T. Tredennick, and K. E. Veblen. 2018. Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. Ecology Letters **21**:1319-1329.

Alexander, H. J., J. S. Taylor, S. S. T. Wu, and F. Breden. 2006. Parallel evolution and vicariance in the guppy (Poecilia reticulata) over multiple spatial and temporal scales. Evolution **60**:2352-2369.

Amarasekare, P. 2000. Coexistence of competing parasitoids on a patchily distributed host: local vs. spatial mechanisms. Ecology **81**:1286-1296.

Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. Ecology Letters **6**:1109-1122.

Amarasekare, P. 2006. Productivity, dispersal and the coexistence of intraguild predators and prey. Journal of Theoretical Biology **243**:121-133.

Amarasekare, P. 2007a. Spatial dynamics of communities with intraguild predation: the role of dispersal strategies. The American Naturalist **170**:819-831.

Amarasekare, P. 2007b. Trade-offs, temporal variation, and species coexistence in communities with intraguild predation. Ecology **88**:2720-2728.

Amarasekare, P. 2008. Coexistence of intraguild predators and prey in resource-rich environments. Ecology **89**:2786-2797.

Anderson, R. B., and S. P. Lawler. 2016. Behavioral changes in tadpoles after multigenerational exposure to an invasive intraguild predator. Behavioral Ecology **27**:1790-1796.

Anderson, S. R., and J. J. Wiens. 2017. Out of the dark: 350 million years of conservatism and evolution in diel activity patterns in vertebrates. Evolution **71**:1944-1959.

Araújo, M. S., D. I. Bolnick, and C. A. Layman. 2011. The ecological causes of individual specialisation. Ecology Letters **14**:948-958.

Arim, M., and P. A. Marquet. 2004. Intraguild predation: a widespread interaction related to species biology. Ecology Letters **7**:557-564.

Bassar, R. D., D. Z. Childs, M. Rees, S. Tuljapurkar, D. N. Reznick, and T. Coulson. 2016. The effects of asymmetric competition on the life history of Trinidadian guppies. Ecology Letters:1-11.

Bassar, R. D., R. Ferriere, A. Lopez-Sepulcre, M. C. Marshall, J. Travis, C. M. Pringle, and D. N. Reznick. 2012. Direct and Indirect Ecosystem Effects of Evolutionary Adaptation in the Trinidadian Guppy (Poecilia reticulata). American Naturalist **180**:167-185.

Bassar, R. D., A. Lopez-Sepulcre, D. N. Reznick, and J. Travis. 2013. Experimental evidence for density-dependent regulation and selection on Trinidadian guppy life histories. American Naturalist **181**:25-38.

Bassar, R. D., M. C. Marshall, A. Lopez-Sepulcre, E. Zandona , S. K. Auer, J. Travis, C. M. Pringle, A. S. Flecker, S. A. Thomas, D. F. Fraser, and D. N. Reznick. 2010. Local adaptation in Trinidadian guppies alters ecosystem

processes. Proceedings of the National Academy of Sciences **107**:3616-3621.

Bassar, R. D., T. Simon, W. Roberts, J. Travis, and D. N. Reznick. 2017a. The evolution of coexistence: Reciprocal adaptation promotes the assembly of a simple community. Evolution **71**:373-385.

Bassar, R. D., J. Travis, and T. Coulson. 2017b. Predicting coexistence in species with continuous ontogenetic niche shifts and competitive asymmetry. Ecology **98**:2823-2836.

Bates, D., M. Maechler, B. M. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software **67**:1-48.

Blaustein, L., M. Kiflawi, A. Eitam, M. Mangel, and J. E. Cohen. 2004. Oviposition habitat selection in response to risk of predation in temporary pools: mode of detection and consistency across experimental venue. Oecologia **138**:300-305.

Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur. 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology & Evolution **26**:183-192.

Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L. Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. The American Naturalist **161**:1-28.

Borer, E. T. 2006. Does adding biological detail increase coexistence in an intraguild predation model? Ecological Modelling **196**:447-461.

Borer, E. T., C. J. Briggs, W. W. Murdoch, and S. L. Swarbrick. 2003. Testing intraguild predation theory in a field system: does numerical dominance shift along a gradient of productivity? Ecology Letters **6**:929-935.

Borer, E. T., W. W. Murdoch, and S. L. Swarbrick. 2004. Parasitoid coexistence: linking spatial field patterns with mechanism. Ecology **85**:667-678.

Briggs, C. J., and E. T. Borer. 2005. Why short-term experiments may not allow long-term predictions about intraguild predation. Ecological Applications **15**:1111-1117.

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Machler, and B. M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R journal **9**:378-400.

Bürkner, P.-C. 2017. brms: An R package for Bayesian multilevel models using Stan. Journal of Statistical Software **80**:1-28.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Springer, New York.

Byström, P., L. Persson, E. Wahlström, and E. Westman. 2003. Size-and density-dependent habitat use in predators: consequences for habitat shifts in young fish. Journal of Animal Ecology **72**:156-168.

Camacho-Cervantes, M., A. F. Ojanguren, O. Domínguez-Domínguez, and A. E. Magurran. 2018. Sociability between invasive guppies and native topminnows. PloS one **13**:e0192539.

Carpenter, B., A. Gelman, M. D. Hoffman, D. Lee, B. Goodrich, M. Betancourt, M. Brubaker, J. Guo, P. Li, and A. Riddell. 2017. Stan: A probabilistic programming language. Journal of Statistical Software **76**:1-32.

Caswell, H. 1989. Analysis of life table response experiments I. Decomposition of effects on population growth rate. Ecological Modelling **46**:221-237.

Caswell, H. 2001. Matrix population models: construction, analysis and interpretation. 2nd edition. Sinauer Associates, Sunderland, MA.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics **31**:343-366.

Chu, C., and P. B. Adler. 2015. Large niche differences emerge at the recruitment stage to stabilize grassland coexistence. Ecological Monographs **85**:373-392.

Clark, G. F. 2013. Biodiversity–invasibility mechanisms are mediated by niche dimensionality. Functional Ecology **27**:5-6.

Clark, J. S., D. Bell, C. Chu, B. Courbaud, M. Dietze, M. Hersh, J. HilleRisLambers, I. Ibášez, S. LaDeau, and S. McMahon. 2010. High-dimensional coexistence based on individual variation: a synthesis of evidence. Ecological Monographs **80**:569-608.

Cooch, E. G., and G. C. White. 2018. Program MARK: a gentle introduction. Colorado State University, Fort Collins.

Corbet, P. S. 1980. Biology of odonata. Annual review of entomology **25**:189-217.

Costa-Pereira, R., V. H. Rudolf, F. L. Souza, and M. S. Araújo. 2018. Drivers of individual niche variation in coexisting species. Journal of Animal Ecology **87**:1452-1464.

Daugherty, M. P., J. P. Harmon, and C. J. Briggs. 2007. Trophic supplements to intraguild predation. Oikos **116**:662-677.

De Bona, S., M. Bruneaux, A. E. Lee, D. N. Reznick, P. Bentzen, and A. López-Sepulcre. 2019. Spatio-temporal dynamics of density-dependent dispersal during a population colonisation. Ecology Letters **22**.

De Meester, L., P. Dawidowicz, E. Van Gool, and C. J. Loose. 1999. Ecology and evolution of predator-induced behavior of zooplankton: depth selection behavior and diel vertical migration. The ecology and evolution of inducible defenses:160-176.

De Roos, A. M., and L. Persson. 2013. Population and community ecology of ontogenetic development. Princeton University Press, Princeton NJ.

Dick, C., D. N. Reznick, and C. Y. Hayashi. 2018. Sex-biased expression between guppies varying in the presence of ornamental coloration. PeerJ **6**:e5782.

Diehl, S., and M. Feissel. 2000. Effects of enrichment on three-level food chains with omnivory. American Naturalist **155**:200-218.

Easterling, M. R., S. P. Ellner, and P. M. Dixon. 2000. Size-specific sensitivity: applying a new structured population model. Ecology **81**:694-708.

Eklöv, P., and L. Persson. 1995. Species-specific antipredator capacities and prey refuges: interactions between piscivorous perch (Perca fluviatilis) and juvenile perch and roach (Rutilus rutilus). Behavioral Ecology and Sociobiology **37**:169-178.

Ellner, S. P., and L. Becks. 2011. Rapid prey evolution and the dynamics of two-predator food webs. Theoretical Ecology **4**:133-152.

Endler, J. A. 1978. A predator's view of animal color patterns. Pages 319-364 Evolutionary biology. Springer.

Endler, J. A. 1980. Natural selection on color patterns in Poecilia reticulata. Evolution **34**:76-91.

Evans, M. E., K. E. Holsinger, and E. S. Menges. 2010. Fire, vital rates, and population viability: a hierarchical Bayesian analysis of the endangered Florida scrub mint. Ecological Monographs **80**:627-649.

Finke, D. L., and R. F. Denno. 2006. Spatial refuge from intraguild predation: implications for prey suppression and trophic cascades. Oecologia **149**:265-275.

Fontaine, J. J., and T. E. Martin. 2006. Habitat selection responses of parents to offspring predation risk: an experimental test. The American Naturalist **168**:811-818.

Fraser, D. F., and J. F. Gilliam. 1992. Nonlethal impacts of predator invasion: facultative suppression of growth and reproduction. Ecology **73**:959-970.

Fraser, D. F., J. F. Gilliam, J. T. Akkara, B. W. Albanese, and S. B. Snider. 2004. Night feeding by guppies under predator release: effects on growth and daytime courtship. Ecology **85**:312-319.

Fraser, D. F., J. F. Gilliam, M. P. MacGowan, C. M. Arcaro, and P. H. Guillozet. 1999. Habitat quality in a hostile river corridor. Ecology **80**:597-607.

Fraser, D. F., and B. A. Lamphere. 2013. Experimental evaluation of predation as a facilitator of invasion success in a stream fish. Ecology **94**:640-649.

Furness, A. I., and D. N. Reznick. 2015. The comparative ecology of a killifish (Rivulus hartii) across aquatic communities different in fish predator intensity. Evolutionary Ecology Research **16**:249-265.

Furness, A. I., M. R. Walsh, and D. N. Reznick. 2012. Convergence of life-history phenotypes in a Trinidadian killifish (Rivulus hartii). Evolution **66**:1240-1254.

Gascon, C., and J. Travis. 1992. Does the spatial scale of experimentation matter? A test with tadpoles and dragonflies. Ecology **73**:2237-2243.

Gasparini, M. 1995. Exact multivariate Bayesian bootstrap distributions of moments. The annals of statistics **23**:762-768.

Gelman, A., J. B. Carlin, H. S. Stern, D. B. Dunson, A. Vehtari, and D. B. Rubin. 2013. Bayesian data analysis. Chapman and Hall/CRC.

Gelman, A., J. Hill, and M. Yajima. 2012. Why we (usually) don't have to worry about multiple comparisons. Journal of Research on Educational Effectiveness **5**:189-211.

Gelman, A., D. Simpson, and M. Betancourt. 2017. The prior can often only be understood in the context of the likelihood. Entropy **19**:555-567.

Gilliam, J. F., and D. F. Fraser. 2001. Movement in corridors: enhancement by predation threat, disturbance, and habitat structure. Ecology **82**:258-273.

Gilliam, J. F., D. F. Fraser, and M. Alkins-Koo. 1993. Structure of a tropical fish community: a role for biotic interactions. Ecology **74**:1856-1870.

Granados, M., S. Duffy, C. W. McKindsey, and G. F. Fussmann. 2017. Stabilizing mechanisms in a food web with an introduced omnivore. Ecology and Evolution **7**:5016-5025.

Hall, R. J. 2011. Intraguild predation in the presence of a shared natural enemy. Ecology **92**:352-361.

Hart, S. P., S. J. Schreiber, and J. M. Levine. 2016. How variation between individuals affects species coexistence. Ecology Letters **19**:825-838.

Haskins, C., E. Haskins, J. McLaughlin, and R. Hewitt. 1961. Polymorphism and population structure in Lebistes reticulatus, an ecological study. Vertebrate Speciation. Pages 320-395 *in* W. F. Blair, editor. Vertebrate Speciation. University of Texas Press, Austin.

Hastings, A., K. C. Abbott, K. Cuddington, T. Francis, G. Gellner, Y.-C. Lai, A. Morozov, S. Petrovskii, K. Scranton, and M. L. Zeeman. 2018. Transient phenomena in ecology. Science **361**:eaat6412.

Hausch, S., S. M. Vamosi, and J. W. Fox. 2018. Effects of intraspecific phenotypic variation on species coexistence. Ecology **99**:1453-1462.

Hayward, M. W., and R. Slotow. 2009. Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. African Journal of Wildlife Research **39**:109-126.

Heithaus, M. R. 2001. Habitat selection by predators and prey in communities with asymmetrical intraguild predation. Oikos **92**:542-554.

Henkanaththegedara, S. M., and C. A. Stockwell. 2014. Intraguild predation may facilitate coexistence of native and non-native fish. Journal of Applied Ecology **51**:1057-1065.

HilleRisLambers, R., and U. Dieckmann. 2003. Competition and predation in simple food webs: intermediately strong trade-offs maximize coexistence. Proceedings of the Royal Society of London B: Biological Sciences **270**:2591-2598.

HilleRisLambers, R., J. Van De Koppel, and P. M. Herman. 2006. Persistence despite omnivory: benthic communities and the discrepancy between theory and observation. Oikos **113**:23-32.

Hiltunen, T., S. P. Ellner, G. Hooker, L. E. Jones, and N. G. Hairston. 2014a. Eco-evolutionary dynamics in a three-species food web with intraguild predation: intriguingly complex. Advances in Ecological Research **50**:41-72.

Hiltunen, T., N. G. Hairston, G. Hooker, L. E. Jones, and S. P. Ellner. 2014b. A newly discovered role of evolution in previously published consumer-resource dynamics. Ecology Letters **17**:915-923.

Hin, V., T. Schellekens, L. Persson, and A. M. de Roos. 2011. Coexistence of predator and prey in intraguild predation systems with ontogenetic niche shifts. The American Naturalist **178**:701-714.

Holt, R. D., and G. R. Huxel. 2007. Alternative prey and the dynamics of intraguild predation: theoretical perspectives. Ecology **88**:2706-2712.

Holt, R. D., and G. A. Polis. 1997. A theoretical framework for intraguild predation. American Naturalist **149**:745-764.

Holway, D. A., and A. V. Suarez. 1999. Animal behavior: an essential component of invasion biology. Trends in Ecology & Evolution **14**:328-330.

Hostetler, J. A., D. P. Onorato, B. M. Bolker, W. E. Johnson, S. J. O'Brien, D. Jansen, and M. K. Oli. 2012. Does genetic introgression improve female reproductive performance? A test on the endangered Florida panther. Oecologia **168**:289-300.

Hut, R. A., N. Kronfeld-Schor, V. van der Vinne, and H. De la Iglesia. 2012. In search of a temporal niche: environmental factors. Pages 281-304 Progress in brain research. Elsevier.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals. American Naturalist **93**:145-159.

Ingram, T. I., R. Svanbäck, N. J. B. Kraft, P. Kratina, L. Southcott, and D. S. Schluter. 2012. Intraguild predation drives evolutionary niche shift in threespine stickleback. Evolution **66**:1819-1832.

Jaenike, J., and R. D. Holt. 1991. Genetic variation for habitat preference: evidence and explanations. The American Naturalist **137**:S67-S90.

Janssen, A., M. W. Sabelis, S. Magalhães, M. Montserrat, and T. Van der Hammen. 2007. Habitat structure affects intraguild predation. Ecology **88**:2713-2719.

Kemp, D. J., F. K. Batistic, and D. N. Reznick. 2018. Predictable adaptive trajectories of sexual coloration in the wild: evidence from replicate experimental guppy populations. Evolution **72**:2462-2477.

Kimbrell, T., R. D. Holt, and P. Lundberg. 2007. The influence of vigilance on intraguild predation. Journal of Theoretical Biology **249**:218-234.

Kneitel, J. M., and J. M. Chase. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. Ecology Letters **7**:69-80.

Kohler, T. J., T. N. Heatherly, R. W. El-Sabaawi, E. Zandonà, M. C. Marshall, A. S. Flecker, C. M. Pringle, D. N. Reznick, and S. A. Thomas. 2012. Flow, nutrients, and light availability influence Neotropical epilithon biomass and stoichiometry. Freshwater Science **31**:1019-1034.

Kokkoris, G., A. Troumbis, and J. Lawton. 1999. Patterns of species interaction strength in assembled theoretical competition communities. Ecology Letters **2**:70-74.

Kratina, P., E. Hammill, and B. R. Anholt. 2010. Stronger inducible defences enhance persistence of intraguild prey. Journal of Animal Ecology **79**:993-999.

Krivan, V. 2000. Optimal intraguild foraging and population stability. Theoretical Population Biology **58**:79-94.

Krivan, V., and S. Diehl. 2005. Adaptive omnivory and species coexistence in tri-trophic food webs. Theoretical Population Biology **67**:85-99.

Kronfeld-Schor, N., and T. Dayan. 2003. Partitioning of Time as an Ecological Resource. Annual Review of Ecology, Evolution, and Systematics **34**:153-181.

Laake, J. 2013. RMark: an R interface for analysis of capture-recapture data with MARK. AFSC Processed Rep 2013-01, 25 p. Alaska. Fisheries Science Center, NOAA, National Marine Fisheries Service, Seattle, WA.

Langellotto, G. A., and R. F. Denno. 2004. Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. Oecologia **139**:1-10.

Lankau, R. A. 2011. Rapid evolutionary change and the coexistence of species. Annual Review of Ecology, Evolution, and Systematics **42**:335-354.

Levine, J. M., and J. HilleRisLambers. 2009. The importance of niches for the maintenance of species diversity. Nature **461**:254-257.

López-Sepulcre, A., S. P. Gordon, I. G. Paterson, P. Bentzen, and D. N. Reznick. 2013. Beyond lifetime reproductive success: the posthumous reproductive dynamics of male Trinidadian guppies. Proceedings of the Royal Society B: Biological Sciences **280**:20131116.

Loreau, M., and W. Ebenhoh. 1994. Competitive exclusion and coexistence of species with complex life cycles. Theoretical Population Biology **46**:58-77.

MacArthur, R. H. 1972. Geographical Ecology: Patterns in the Distribution of Species. Harper and Row, New York.

MacArthur, R. H., and R. Levins. 1967. The limiting similarity, convergence and divergence of coexisting species. American Naturalist **101**:377-285.

Maciel, G. A., and R. A. Kraenkel. 2017. Theory does not meet experiment: transient dynamics changes patterns of exclusion in an intraguild predation system. Population Ecology **59**:371-378.

Marshall, M. C., A. J. Binderup, E. Zandonà, S. Goutte, R. D. Bassar, R. W. El-Sabaawi, S. A. Thomas, A. S. Flecker, S. S. Kilham, and D. N. Reznick. 2012. Effects of consumer interactions on benthic resources and ecosystem processes in a Neotropical stream. PloS one **7**:e45230.

Martin, T. E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? Ecology **79**:656-670.

Mattingly, H. T., and M. J. Butler IV. 1994. Laboratory predation on the Trinidadian guppy: implications for the size-selective predation hypothesis and guppy life history evolution. Oikos:54-64.

Michod, R. E. 1979. Evolution of life histories in response to age-specific mortality factors. American Naturalist **113**:531-550.

Miller, S. E., D. Metcalf, and D. Schluter. 2015. Intraguild predation leads to genetically based character shifts in the threespine stickleback. Evolution **69**:3194-3203.

Miller, T. E., and V. H. Rudolf. 2011a. Thinking inside the box: community-level consequences of stage-structured populations. Trends in Ecology & Evolution **26**:457-466.

Miller, T. E. X., and V. H. W. Rudolf. 2011b. Thinking inside the box: community-level consequences of stage-structured populations. Trends in Ecology & Evolution **26**:457-466.

Min, Y., and A. Agresti. 2005. Random effect models for repeated measures of zero-inflated count data. Statistical modelling **5**:1-19.

Moll, J. D., and J. S. Brown. 2008. Competition and coexistence with multiple life-history stages. The American Naturalist **171**:839-843.

Monterroso, P., P. C. Alves, and P. Ferreras. 2014. Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe: implications for species coexistence. Behavioral Ecology and Sociobiology **68**:1403-1417.

Montserrat, M., S. Magalhaes, M. Sabelis, A. De Roos, and A. Janssen. 2012. Invasion success in communities with reciprocal intraguild predation depends on the stage structure of the resident population. Oikos **121**:67-76.

Montserrat, M., S. Magalhães, M. W. Sabelis, A. M. De Roos, and A. Janssen. 2008. Patterns of exclusion in an intraguild predator–prey system depend on initial conditions. Journal of Animal Ecology **77**:624-630.

Morin, P. 1999. Productivity, intraguild predation, and population dynamics in experimental food webs. Ecology **80**:752-760.

Morosinotto, C., A. Villers, R. L. Thomson, R. Varjonen, and E. Korpimäki. 2017. Competitors and predators alter settlement patterns and reproductive success of an intraguild prey. Ecological Monographs **87**:4-20.

Morris, D. W. 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia **136**:1-13.

Murdoch, W., B. Kendall, R. Nisbet, C. Briggs, E. McCauley, and R. Bolser. 2002. Single-species models for many-species food webs. Nature **417**:541-543.

Mylius, S. D., K. Klumpers, A. M. de Roos, and L. Persson. 2001. Impact of intraguild predation and stage structure on simple communities along a productivity gradient. The American Naturalist **158**:259-276.

Nakazawa, T. 2015. Ontogenetic niche shifts matter in community ecology: a review and future perspectives. Population Ecology **57**:347-354.

Novak, M. 2013. Trophic omnivory across a productivity gradient: intraguild predation theory and the structure and strength of species interactions. Proceedings of the Royal Society of London B: Biological Sciences **280**:1-9.

Ogle, K., D. Peltier, M. Fell, J. Guo, H. Kropp, and J. Barber. 2019. Should we be concerned about multiple comparisons in hierarchical Bayesian models? Methods in Ecology and Evolution **10**:553-564.

Okuyama, T. 2008. Intraguild predation with spatially structured interactions. Basic and Applied Ecology **9**:135-144.

Owens, D. C. 2010. Seasonal variation in terrestrial insect subsidies to tropical streams and implications for the diet of Rivulus hartii. University of Nebraska, Lincoln.

Patel, S., and S. J. Schreiber. 2015. Evolutionarily Driven Shifts in Communities with Intraguild Predation. The American Naturalist **186**:E98-E110.

Persson, L., S. Diehl, L. Johansson, G. Andersson, and S. F. Hamrin. 1991. Shifts in fish communities along the productivity gradient of temperate lakes - patterns and the importance of size-structured interactions. Journal of Fish Biology **38**:281-293.

Persson, L., and P. Eklov. 1995. Prey Refuges Affecting Interactions Between Piscivorous Perch and Juvenile Perch and Roach. Ecology **76**:70-81.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, S. Heisterkamp, B. Van Willigen, and R. Maintainer. 2017. Package 'nlme'. Linear and Nonlinear Mixed Effects Models, version:3.1-137.

Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation - potential competitors that eat each other. Annual Review of Ecology and Systematics **20**:297-330.

Potter, T., L. King, J. Travis, and R. D. Bassar. 2019. Competitive asymmetry and local adaptation in Trinidadian guppies. Journal of Animal Ecology **88**:330-342.

Pruitt, J. N., and M. C. Ferrari. 2011. Intraspecific trait variants determine the nature of interspecific interactions in a habitat-forming species. Ecology **92**:1902-1908.

Quince, C., P. A. Abrams, B. J. Shuter, and N. P. Lester. 2008a. Biphasic growth in fish I: theoretical foundations. Journal of Theoretical Biology **254**:197-206.

Quince, C., B. J. Shuter, P. A. Abrams, and N. P. Lester. 2008b. Biphasic growth in fish II: empirical assessment. Journal of Theoretical Biology **254**:207-214.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for statistical computing, Vienna, Austria.

Rael, R., T. Vincent, and J. M. Cushing. 2011. Competitive outcomes changed by evolution. Journal of Biological Dynamics **5**:227-252.

Reebs, S. G. 2002. Plasticity of diel and circadian activity rhythms in fishes. Reviews in Fish Biology and Fisheries **12**:349-371.

Reichstein, B., A. Schröder, L. Persson, and A. M. Roos. 2013. Habitat complexity does not promote coexistence in a size-structured intraguild predation system. Journal of Animal Ecology **82**:55-63.

Relyea, R. A. 2002. The many faces of predation: how induction, selection, and thinning combine to alter prey phenotypes. Ecology **83**:1953-1964.

Reznick, D., and J. A. Endler. 1982. The impact of predation on life history evolution in Trinidadian guppies (Poecilia reticulata). Evolution **36**:160-177.

Reznick, D. N. 1982. The impact of predation on life history evolution in Trinidadian guppies: the genetic components of observed life history differences. Evolution **36**:1236-1250.

Reznick, D. N., R. D. Bassar, C. A. Handelsman, C. K. Ghalambor, J. Arendt, T. Coulson, T. Potter, E. W. Ruell, J. Torres-Dowdall, P. Bentzen, and J. Travis. *in press*. Eco-evolutionary feedbacks predict the time course of rapid life history evolution. The American Naturalist.

Reznick, D. N., R. D. Bassar, J. Travis, and F. H. Rodd. 2012. Life-history evolution in guppies VIII: the demographics of density regulation in guppies (Poecilia reticulata). Evolution **66**:2903-2915.

Reznick, D. N., and H. Bryga. 1987. Life-history evolution in guppies. I. Phenotypic and genotypic changes in an introduction experiment. Evolution **41**:1370-1385.

Reznick, D. N., and H. Bryga. 1996. Life-history evolution in guppies (Poecilia reticulata: Poeciliidae). V. Genetic basis of parallelism in life histories. American Naturalist **147**:339-359.

Reznick, D. N., H. Bryga, and J. A. Endler. 1990. Experimentally induced life-history evolution in a natural population. Nature **346**:357-359.

Reznick, D. N., M. J. I. Butler, and F. H. Rodd. 2001. Life history evolution in guppies. VII. The comparative ecology of high and low predation environments. American Naturalist **157**:126-140.

Reznick, D. N., S. De Bona, A. López-Sepulcre, M. Torres, R. D. Bassar, P. Benzen, and J. Travis. *in review*. Experimental study of species invasion - early population dynamics and role of disturbance in invasion success. Ecological Monographs.

Reznick, D. N., F. H. Rodd, and M. Cardenas. 1996. Life-history evolution in guppies (Poecilia reticulata: Poeciliidae). IV. Parallelism in life-history phenotypes. American Naturalist **147**:319-338.

Reznick, D. N., F. H. Shaw, F. H. Rodd, and R. G. Shaw. 1997. Evaluation of the rate of evolution in natural populations of guppies (Poecilia reticulata). Science **275**:1934-1937.

Rieger, J. F., C. A. Binckley, and W. J. Resetarits. 2004. Larval performance and oviposition site preference along a predation gradient. Ecology **85**:2094-2099.

Rodd, F. H., and D. N. Reznick. 1997. Variation in the demography of guppy populations: the importance of predation and life histories. Ecology **78**:405-418.

Rubin, D. B. 1981. The bayesian bootstrap. The annals of statistics:130-134.

Rudolf, V. H., and J. Armstrong. 2008. Emergent impacts of cannibalism and size refuges in prey on intraguild predation systems. Oecologia **157**:675-686.

Rudolf, V. H. W. 2007. The interaction of cannibalism and omnivory: consequences for community dynamics. Ecology **88**:2697-2705.

Savino, J. F., and R. A. Stein. 1982. Predator-Prey Interaction between Largemouth Bass and Bluegills as Influenced by Simulated, Submersed Vegetation. Transactions of the American Fisheries Society **111**:255-266.

Schellekens, T., and T. van Kooten. 2012. Coexistence of two stage-structured intraguild predators. Journal of Theoretical Biology **308**:36-44.

Schmitz, O. J., J. R. B. Miller, A. M. Trainor, and B. Abrahms. 2017. Toward a community ecology of landscapes: predicting multiple predator–prey interactions across geographic space. Ecology **98**:2281-2292.

Schoener, T. W. 1983. Field experiments on interspecific competition. The American Naturalist **122**:240-285.

Schröder, A., K. A. Nilsson, L. Persson, T. Van Kooten, and B. Reichstein. 2009a. Invasion success depends on invader body size in a size-structured mixed predation–competition community. Journal of Animal Ecology **78**:1152-1162.

Schröder, A., L. Persson, and A. De Roos. 2009b. Culling experiments demonstrate size-class specific biomass increases with mortality. Proceedings of the National Academy of Sciences **106**:2671-2676.

Seghers, B. H. 1973. An analysis of geographic variation in the antipredator adaptations of the guppy, Poecilia reticulata. University of British Colombia, Vancouver, British Colombia.

Seghers, B. H. 1974. Schooling Behavior in the guppy (Poecilia reticulata): an evolutionary response to predation. Evolution **28**:486-489.

Siepielski, A. M., and M. A. McPeek. 2010. On the evidence for species coexistence: a critique of the coexistence program. Ecology **91**:3153-3164.

Sih, A., G. Englund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. Trends in Ecology & Evolution **13**:350-355.

Silvertown, J. 2004. Plant coexistence and the niche. Trends in Ecology & Evolution **19**:605-611.

Simon, T. N., R. D. Bassar, A. J. Binderup, A. S. Flecker, M. C. Freeman, J. F. Gilliam, M. C. Marshall, S. A. Thomas, J. Travis, and D. N. Reznick. 2017. Local adaptation in Trinidadian guppies alters stream ecosystem structure at landscape scales despite high environmental variability. Copeia **105**:504-513.

Snyder, R. E., E. T. Borer, and P. Chesson. 2005. Examining the relative importance of spatial and nonspatial coexistence mechanisms. The American Naturalist **166**:E75-E94.

Sullam, K. E., C. M. Dalton, J. A. Russell, S. S. Kilham, R. El-Sabaawi, D. P. German, and A. S. Flecker. 2015. Changes in digestive traits and body nutritional composition accommodate a trophic niche shift in Trinidadian guppies. Oecologia **177**:245-257.

Teh, Y. W., M. I. Jordan, M. J. Beal, and D. M. Blei. 2006. Hierarchical Dirichlet Processes. Journal of the american statistical association **101**:1566-1581.

Thompson, K. A., J. E. Hill, and L. G. Nico. 2012. Eastern mosquitofish resists invasion by nonindigenous poeciliids through agonistic behaviors. Biological Invasions **14**:1515-1529.

Tilman, D. 1982. Resource competition and community structure. Princeton university press, Princeton, NJ.

Toscano, B. J., B. R. Rombado, and V. H. Rudolf. 2016. Deadly competition and life-saving predation: the potential for alternative stable states in a stage-structured predator–prey system. Proceedings of the Royal Society of London B: Biological Sciences **283**:1-7.

Travis, J., D. Reznick, R. D. Bassar, A. López-Sepulcre, R. Ferriere, and T. Coulson. 2014. Do Eco-Evo Feedbacks Help Us Understand Nature? Answers From Studies of the Trinidadian Guppy. Pages 1-40 *in* J. Moya-Larano, J. Rowntree, and G. Woodward, editors. Advances in Ecological Research: Eco-Evolutionary Dynamics. Academic Press, Amsterdam.

Urban, M. C. 2013. Evolution mediates the effects of apex predation on aquatic food webs. Proceedings of the Royal Society of London B: Biological Sciences **280**:1-9.

Urban, M. C., J. J. Tewksbury, and K. S. Sheldon. 2012. On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. Proceedings of the Royal Society B: Biological Sciences **279**:2072-2080.

Urbani, P., and R. Ramos-Jiliberto. 2010. Adaptive prey behavior and the dynamics of intraguild predation systems. Ecological Modelling **221**:2628-2633.

van de Wolfshaar, K. E., A. M. de Roos, and L. Persson. 2006. Size-dependent interactions inhibit coexistence in intraguild predation systems with life-history omnivory. American Naturalist **168**:62-75.

Vehtari, A., A. Gelman, and J. Gabry. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Statistics and Computing **27**:1413-1432.

Walsh, M. R., D. F. Fraser, R. D. Bassar, and D. N. Reznick. 2011. The direct and indirect effects of guppies: implications for life-history evolution in Rivulus hartii. Functional Ecology **25**:227-237.

Walsh, M. R., and D. N. Reznick. 2008. Interactions between the direct and indirect effects of predators determine life history evolution in a killifish. Proceedings of the National Academy of Sciences **105**:594-599.

Walsh, M. R., and D. N. Reznick. 2009. Phenotypic diversification across an environmental gradient: a role for predators and resource availability on the evolution of life histories. Evolution **63**:3201-3213.

Walsh, M. R., and D. N. Reznick. 2010. Influence of the indirect effects of guppies on life-history evolution in Rivulus hartii. Evolution **64**:1583-1593.

Walsh, M. R., and D. N. Reznick. 2011. Experimentally induced life-history evolution in a killifish in response to introduced guppies. Evolution **65**:1021-1036.

Wang, X., M. Fan, and L. Hao. 2016. Adaptive evolution of foraging-related trait in intraguild predation system. Mathematical Biosciences **274**:1-11.

Werner, E. 1988. Size, scaling and the evolution of complex life cycles. Pages 60-81 *in* B. Ebenman and L. Persson, editors. Size-Structured Populations: Ecology and Evolution. Springer, Berlin.

Werner, E. E., and B. R. Anholt. 1996. Predator-induced behavioral indirect effects: consequences to competitive interactions in anuran larvae. Ecology **77**:157-169.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics **15**:393-425.

Werner, E. E., and D. J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology **69**:1352-1366.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird study **46**:S120-S139.

Wikelski, M., and C. Thom. 2000. Marine iguanas shrink to survive El Niño. Nature **403**:37-38.

Williams, J. L., T. E. Miller, and S. P. Ellner. 2012. Avoiding unintentional eviction from integral projection models. Ecology **93**:2008-2014.

Wilson, K. L., A. E. Honsey, B. Moe, and P. Venturelli. 2018. Growing the biphasic framework: Techniques and recommendations for fitting emerging growth models. Methods in Ecology and Evolution **9**:822-833.

Yamaguchi, M., Y. Takeuchi, and W. Ma. 2007. Dynamical properties of a stage structured three-species model with intra-guild predation. Journal of computational and applied mathematics **201**:327-338.

Yao, Y., A. Vehtari, D. Simpson, and A. Gelman. 2018. Using stacking to average Bayesian predictive distributions (with discussion). Bayesian Analysis **13**:917-1003.

Zandonà, E., S. K. Auer, S. S. Kilham, J. L. Howard, A. López-Sepulcre, M. P. O'Connor, R. D. Bassar, A. Osorio, C. M. Pringle, and D. N. Reznick. 2011. Diet quality and prey selectivity correlate with life histories and predation regime in Trinidadian guppies. Functional Ecology **25**:964-973.

Zandonà, E., S. K. Auer, S. S. Kilham, and D. N. Reznick. 2015. Contrasting population and diet influences on gut length of an omnivorous tropical fish, the Trinidadian guppy (Poecilia reticulata). PloS one **10**:e0136079.