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Author(s): Reznick, David N.; De Bona, Sebastiano; López-Sepulcre, Andrés; Torres, Mauricio; Bassar, Ronald D.; Benzen, Paul; Travis, Joseph

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MR. SEBASTIANO DE BONA (Orcid ID : 0000-0001-6193-7073)

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Experimental study of species invasion: early population dynamics and role of disturbance in invasion success

David N. Reznick[1*], Sebastiano De Bona[2,3], Andrés López-Sepulcre[4,5], Mauricio Torres[6.7], Ronald D. Bassar[8], Paul Benzen[9], and Joseph Travis[10]

*Corresponding Author. E-mail: david.reznick@ucr.edu

[1]Department of Evolution, Ecology and Organismal Biology, University of California, Riverside, CA 92521, USA

[2]Department of Biological and Environmental Science, University of Jyväskylä, Survontie 9C Jyvaskyla, Finland

[3]Current Address: Integrative Ecology lab, Center for Biodiversity, Department of Biology, Temple University, 1925 N 12th St., Philadelphia, PA USA

[4]CNRS UMR 7618, Institute of Ecology and Environmental Sciences of Paris (iEES), Sorbonne Université, France

[5]Department of Biology, Campus Box 1137, Washington University, St. Louis, MO 63130 USA

[6]Senate of the Republic of Colombia, Cra. 7 8-62 Bogata, Colombia

[7]Fundación Iguaque, Calle 52 35a-23, Bucaramanga, Santander, Colombia

[8]Department of Biology, Williams College, 59 Lab Campus Drive, Williamstown, MA 01267 USA

[9]Department of Biology, Dalhousie University LSC 6052, 1355 Oxford St., PO Box 15000 Halifax, NS B3H 4R2, Canada

[10]Department of Biological Science, Florida State University, Tallahassee, FL 32306-4340 USA

ABSTRACT: Much of our understanding of natural invasions is retrospective, based on data acquired after invaders become established. As a consequence, we know little about the characteristics of the early population growth and habitat use of the invaders during establishment. Here we report on experimental introductions of guppies into natural streams in which we conducted monthly censuses of each population. Two of the four introductions were in streams with thinned canopies, which mimics a common form of habitat disturbance. We conducted similar censuses of natural populations to characterize natural population densities and generate a null distribution against which we could test *a priori* hypotheses about the establishment of the experimental invaders. We constructed a pedigree for one population, which enabled us to quantify lifetime reproductive success. Population simulations predict that the nature of the introduced population's life history, in combination with reduced risk of predation in the introduction sites, will result in explosive population growth; however, populations of introduced invaders instead grew to match densities observed in natural streams with intact canopies. Experimental populations in streams with thinned canopies grew to densities that often exceeded those of natural streams with intact canopies. High population densities were associated with the increased use of marginal habitat. Adult females and males that moved into marginal habitat suffered no apparent fitness loss, suggesting lower population densities found there compensated for lower habitat quality. Our results suggest that the ecological setting in which invasions occur plays a role at least comparable in importance to that of the invader's inherent characteristics in shaping early population growth and habitat use.

Key Words: *Poecilia reticulata*, invasive species, habitat disturbance, enemy release, experimental introduction, habitat selection

Introduction

The growing prevalence of invasive species begs the question of why some succeed, in spite of the majority failing (Williamson 2006). Invasions are usually recognized after the invasive species becomes established, so the answers to this question are usually based on retrospective analyses of a reconstructed history of an invasion (Mack et al. 2000, Marsico et al. 2010, Simberloff 2010, Van Wilgen and Richardson 2012, Blackburn et al. 2015). Here we offer a prospective analysis of an invasion in the form of a replicated experimental introduction to natural communities that enables us to detail the population dynamics and habitat occupancy patterns associated with the initial

establishment of an invasive species. We focus on the role of a common form of habitat disturbance in shaping those dynamics.

The role of habitat disturbance in facilitating invasions was recognized first by Elton (1958). Hobbs and Hueneke (1992) note that certain disturbances, such as fire or herbivory, can be normal occurrences, so they refined Elton's hypothesis to suggest that the best opportunities for invaders will be associated with novel disturbances or patterns of typical disturbance that exceed the normal regime in magnitude or frequency. Davis et al. (2000) proposed instead that the input of resources following a disturbance, such as tree cutting and the subsequent increase of light availability, creates opportunities for invaders. A common theme to such disturbances is the rapid, substantial increase in the availability of a limiting resource like space, nutrients, or light.

Empirical studies of well-established invasive species yield clues about the role of disturbance, relative to other factors, in facilitating species invasions. Insights gained from these studies are that disturbance can indeed facilitate invasions, but for diverse reasons that involve interactions among the properties of the invader, native species and the native ecosystem. One theme has been to address whether invaders succeed because they are competitively superior to natives or if they are instead better at exploiting disturbances. Seabloom et al. (2003) showed that native grasses are competitively superior to the invasive grasses in the Central Valley of California. The invasive species succeed despite their poor competitive ability because their seeds disperse more widely and they are better able to exploit disturbed habitats. Likewise, Prevey et al. (2010) showed that the dominant shrub (*Artemesia tridentata*) on the sagebrush steppe inhibits some invasive grasses. Removal of the shrub enables invasion by grasses because it increases the availability of soil moisture. Marvier et al. (2004) model such a balance between invasion and competitive ability and suggest that invasive species will tend to be habitat generalists that are better able to take advantage of the opportunities offered by habitat disturbance, despite being competitively inferior to specialists.

Other studies reflect a different balance between competitive ability and disturbance. Sebert-Cuvillier et al. (2007) developed an empirical, demographic model of the population biology of the American black cherry (*Prunus serotina*) as it invaded European forests and showed that disturbance is a facilitator of seedling establishment. Once established, the tree is competitively superior and capable of converting a diverse woodland into a monoculture. MacDougal and Turkington (2005)

found invasive species of grasses in the understory of an oak woodland were competitively superior to the native grasses. Their invasion was facilitated by fire suppression. Native species were better adapted to the periodic disturbance caused by fires but were outcompeted by the invaders when this form of disturbance was removed.

More generally, Mack and D'Antonio (1998) argue that there can be a cascading relationship between invasion and disturbance. The establishment of invasive species can disrupt normal disturbance regime, either by increasing, decreasing or changing the nature of the disturbance and, in that way, make communities more susceptible to further invasion and permanently change the structure of the ecosystem.

A second feature of invasions is that the population growth that follows the establishment of an invader is often accompanied by a diversification of the habitats occupied (Simberloff 2010). The way habitat use diversifies can be a direct function of population density, especially if habitats differ in quality (Arim et al. 2006). At low population densities, organisms occupy the best available habitat. As population densities increase and absolute fitness declines with density, some individuals will emigrate to progressively less desirable habitat with lower densities, where their fitness may be comparable to those in more desirable habitats with higher densities (the ideal free distribution; (Fretwell and Lucas 1969).

The importance of density-dependent habitat expansion is supported by analyses of time series censuses of invading species as they spread over the landscape. Arim et al. (2006) report that 28 of 30 well-characterized invasions bear a clear signature of population regulation, as inferred from the rate of invasion of new sites as the invaders range expanded. They suggest that, when a new locality is colonized, the invader's population takes some time to grow to carrying capacity before it once again generates propagules that will colonize new localities. Starrfelt and Kokko (2008) show that Arim et al's result may also be attributable to other processes, but other investigators report temporal patterns of invasion that are suggestive of density-dependent population expansion. For example, Pietrek and Gonzalez-Roglich (2015) used satellite imagery to track the invasion of the Patagonian steppe by beavers and found that they first occupied small watercourses in canyons and only later, after most canyons were occupied, colonized streams in plains or u-shaped valleys. Van Beest et al. (2014)

report that the invasive population of horses on Sable Island increased their use of less desirable habitat as the population expanded.

While such results support the idea of density-dependent habitat expansion, they are inferences from patterns of range expansion made in the absence of a direct assessment of population dynamics or the fitness consequence of the habitat occupied. The limitations of such retrospective analyses leave some key ecological questions about the early phase of invasions unresolved. These are: 1) What role does habitat disturbance play in enabling invaders to establish then expand their range? 2) What are the population dynamics during the early phases of the invasion? Do populations approach the carrying capacity of the local environment or does rapid population growth produce an overshoot of carrying capacity? 3) If invaders do exceed carrying capacity, does this lead to the invasion of less preferred environments or are such habitats invaded as part of the process of population growth even before attaining carrying capacity?

Here we address these questions with an experimental study of the establishment of new populations of guppies, *Poecilia reticulata,* set in a natural environment. Our project is distinctive for three reasons. First, it represents a replicated range extension followed by a detailed quantification of population establishment. Second, the experiment includes a treatment that mimics a common form of habitat disturbance that has the potential to influence the demography of the invader and hence affect invasion success. Third, we contrast the results of our introductions with patterns of density and habitat use in comparable natural populations. The censuses of natural populations provide estimates of population density and distribution in natural environments and enable us to generate confidence limits for the expected distribution in similar habitats. Doing so makes it possible to statistically evaluate whether or not our experimental introductions exceed the population densities typical of natural, undisturbed streams. Our experiment thus provides unprecedented detail about this earliest critical phase of invasion.

Background: Guppies naturally occur in the Northern Range Mountains of Trinidad. They are frequent, successful invaders, often as a byproduct of their use for mosquito control (El-Sabaawi et al. 2016). Guppies have successfully invaded all continents except Antarctica (Lever 1996, Deacon et al. 2011). They are competitors and predators of native species of invertebrates, fish, and amphibians and

have altered native ecosystems in other ways (Holitzki 2010, Deacon et al. 2011, MacKenzie and Bruland 2012, El-Sabaawi et al. 2016).

The colonization of new environments is an inherent feature of the natural history of guppies. In their native habitat, guppies range from the mouths of rivers up to small, headwater tributaries, where they are one of two fish species present. Patterns of genetic variation suggest that guppies originated in the main river, then colonized the upstream tributaries (Willing et al. 2010). We have witnessed such natural colonization events in our study sites.

In earlier experiments, we extended the range of guppies from downstream localities, where they co-occur with a diversity of predators, into guppy-free tributaries upstream, isolated by barrier waterfalls. These sites are occupied only by the killifish *Rivulus hartii* (Reznick et al. 1990, Reznick et al. 1997). These artificial transplants mimic natural colonization events. Introduced guppies readily multiply in their new setting. They reduce the abundance of the killifish by up to 70% and cause the evolution of killifish life histories (Walsh and Reznick 2011). They alter the abundance of aquatic insects, algae, and change nutrient cycling and other ecosystems processes (Bassar et al. 2010, Travis et al. 2014, Bassar et al. 2017a, Bassar et al. 2017b, Simon et al. 2017).

We performed a thought experiment in which we modeled the fate of guppy populations from high predation environments that invade previously guppy-free headwater streams (Reznick et al. 2001b). Guppies from downstream, high predation localities suffer higher mortality rates (Reznick et al. 1996b, Reznick and Bryant 2007), but their life histories evolve in response to mortality risk. They are genetically predisposed to mature at an earlier age and produce more offspring than guppies adapted to the low predation environments represented by our experimental streams (Reznick 1982, Reznick and Bryga 1996). The introductions are thus a manifestation of the conditions envisioned by the "enemy release" hypothesis for invasion success (Colautti et al. 2004) because the introduced guppies experience release from predation risk.

In our simulations, we assumed that when guppies from high predation localities downstream invade predator and guppy-free headwater streams, their mortality rates decline, but they initially retain their genetic predisposition to mature at an early age and produce many offspring. We parameterized the simulations with real estimates of guppy mortality rates in low predation streams (Reznick et al. 1996a) and life history traits characteristic of guppies from high predation streams

(Reznick and Bryga 1996, Reznick et al. 1996c). The predicted consequence of this mismatch between the invaders' life history and the mortality rate experienced in their new environment is that the introduced population will rapidly multiply and overshoot the population densities typical of the invaded locality. On this basis, we defined the three following questions.

(1) Do populations of invasive guppies grow to the population density typical of low predation habitats or overshoot it? Our model predicts the potential to exceed typical population densities because the invaders have high reproductive capacity but face reduced mortality risk.

(2) Do anthropogenic modifications of the habitat influence the time course and ultimate fate of an invasive population? Human activities often change the environment in ways that give invaders a competitive advantage over residents (e.g. (Winsome et al. 2006) and hence facilitate the invasion process (Didham et al. 2007). Tree cutting in the vicinity of streams is a common form of disturbance that increases primary productivity and the standing biomass of primary producers and invertebrates (Noel et al. 1986, Stone and Wallace 1998). Such increases in productivity can, in turn, facilitate increase the population density of guppies. This effect occurs in guppy streams (Kohler et al. 2012) and is sometimes enhanced by increased nutrient runoff from the surrounding terrain (Reznick et al. 2001a, Collins et al. 2016).

(3) Does the increase of guppy population density in preferred habitats cause guppies to increase occupancy of less preferred habitats, as predicted by Rosenzweig (1981)? This prediction was upheld in experiments (Abramsky et al. 1990, Abramsky et al. 1991) and long-term observational studies (McLoughlin et al. 2006, Bradbury et al. 2015, Castagneyrol et al. 2016). The mountain streams occupied by guppies are naturally sub-divided into alternating pools and riffles. Guppy population densities are much higher in pools than riffles, suggesting that pools are the preferred habitat. We ask whether the increasing population density of guppies causes them to increase occupancies of riffles.

We mimicked natural invasions by introducing guppies derived from a high predation locality into four natural guppy-free streams, then followed their progress with monthly mark-recapture censuses. We mimicked habitat disturbance in two of the four streams by thinning the tree canopy while leaving the canopy intact in the other two streams. In addition, we censused native guppy populations in six natural streams with intact canopies, similar to the two introduction streams with

intact canopies. We used these censuses to characterize the natural densities of guppies in pools and riffles and to simulate 95% predicted intervals for these natural population densities. We addressed our questions by comparing the population densities attained in our introduced populations with those of natural populations. These data enabled us to follow population growth, monitor habitat choice and changes in habitat occupancy over time. We considered the population density observed in the introduced populations to exceed natural levels only when it was significantly greater than the range of densities observed in natural streams. We collected scale samples for all founders and new recruits to provide DNA, then genotyped and developed a pedigree for one of the four introduced populations. We then combined the pedigree with the census data and estimated the fitness, in terms of lifetime reproductive success, of all individuals as a function of their habitat use.

Methods

Censuses of Natural Streams: We quantified the population densities and distributions of guppies in 50-meter portions of six natural streams in March, May (dry season), July and September (wet season) of 2013 to create a null distribution for comparison with the experimental streams (Fig. 1). Sampling in the wet and dry seasons enabled us to incorporate seasonal variation in abundance in our assessment of natural population densities. These reference sites define density and habitat use in natural populations and thus provide a frame of reference for addressing whether the four experimental streams overshoot the densities seen in natural streams with intact canopies or change their habitat occupation relative to what we see in natural streams with intact canopies.

We sampled each stream on three consecutive days and applied a depletion sampling design to estimate population size. Our capture rates proved so high that the cumulative probability of capture exceeded 99% so we simply used the total number caught as the population size (See Appendix S1: Section S1).

Experiment: We introduced guppies into small sections of four headwater streams of the Guanapo River, two in March 2008 (Upper La Laja, UL, and Lower La Laja, LL) and two in March 2009 (Taylor, TY, and Caigual, CA). We introduced thirty-eight pairs of fish to each of the first pair of streams in 2008. We introduced fifty-one pairs to each of the second pair of streams. We added 12 additional pairs to the Caigual River to equalize the initial density with the Taylor; the Caigual has a larger benthic area. The introduced guppies were collected from high predation localities in the lower

portions of the Guanapo River for which the life history was representative of a typical high predation locality (Torres-Dowdall et al. 2012). The introduction sites have a waterfall on the downstream side that previously excluded all species of fish save *Rivulus hartii*. All replicates have a waterfall upstream that is a barrier to the upstream dispersal of guppies and hence defined the upstream boundary of the experimental populations. The length of the introduction sites varies from 68 to 156 meters. We thinned the canopy of one randomly selected stream in each pair (UL and TY), which increased light levels and enhanced primary productivity (Kohler et al. 2012). The thinning initially increased photosynthetically active radiation by 30% in the UL and 800% in the TY. The canopies were regularly re-thinned to maintain the differences in light level, but light levels were also affected by periodic treefalls. By 2013 light levels were 388% higher in the UL than LL and 285% higher in the TY than CA.

All founders were individually marked with subcutaneous injections of colorized elastomer (Northwest Marine Technologies). All new recruits over 14 mm standard length also receive a unique mark. Guppies are 6 to 7 mm at birth and take 1-2 months to attain 14 mm. We cannot mark smaller guppies without increasing the risk of mortality so we must forego knowledge of their early life history.

We kept three scales from each founder and collected three scales from each new recruit. These scales are a source of DNA, from which we genotyped all individuals from one replicate (LL). We constructed a pedigree for this population that enabled us to quantify individual reproductive success. We quantified lifetime reproductive success (number of recruited offspring) for the founding females and all females born through December 2011. We quantified lifetime mating success (the number of females who sired young by that male) for all founding and recruited males through December 2011. The end dates were chosen to include cohorts for which we had complete reproduction and mating histories. All included individuals had died long enough before the end of 2013 (which represents the latest time point for which pedigree reconstruction is currently available) for all offspring who could have been sired by stored sperm to grow large enough to be included in the mark-recapture study. Further details on the experimental design, genotyping, pedigree construction and estimation of lifetime reproductive success appear in Appendix S1: Section S2.

Censuses of Experimental Populations: All populations were censused once per month. We kept the fish from each pool and riffle separate from each other plus separated males and females as they were collected. In the laboratory, we identified each fish by its individual mark, weighed it, and photographed it for later quantification of standard length. Successive length and weight measurements enabled us to quantify growth rate. We returned fish to the site of capture either one or two days after being caught. Formal analyses reveal that we have, on average, a greater than 90% probability of seeing every fish >14 mm each time we census the population. See Appendix S1: Section S2 for additional details.

Stream Morphology: Streams are naturally subdivided into discrete pools and riffles. A riffle has a steeper gradient than pools and a linear water flow. Pools are bracketed by riffles and lack linear flow. Water instead flows into the pool from a riffle upstream and out of the pool through a riffle downstream. Within the pool, there are regions of turbulent flow or no flow. Streams also have sidepools, disconnected from the main channel, and backwaters, or peripheral embayments, with null or circular flow and a single, restricted connection with the main channel. The physical characteristics of riffles cause them to be more different from any other habitat type. All others share similar features of still or partially still water with higher detritus deposits. Therefore, we merged the habitat types different from riffles into a single category hence referred to as *pool.* Guppies tend to be more abundant in pools.

We quantified benthic area by representing each stream surface as a polygon, then dividing the polygon into triangles. Each triangle had two sides crossing the stream and one side on the shore. We measured the length of the three sides of the triangle. For the two sides that cross the stream, we measured three depths at 0.25, 0.5, and 0.75 of side length. With these measurements, we were then able to quantify the surface area and volume of each section of stream. Using geometry, we estimate the top (surface) and bottom (benthic) areas and the volume of the stream by dividing it into slices and then added slice values to get the stream section totals by type of habitat. Area and volume of boulders or logs interrupting any triangular section of the stream were accounted for by subtracting their volume and benthic surface and adding submerged lateral surfaces to benthic area. Further details on these methods are presented in Appendix S1: Section S3. Habitat size was calculated using custom code in R (R Development Core Team, 2016), available in Data S1.

Tests of Hypotheses About the Invaders in Experimental Streams: We estimated population size by dividing the number of captured individuals by the estimated probability of being captured if alive. Capture probabilities were estimated separately per each of the eight stream-by-habitat type combination, and for males and females separately. To do so, we implemented a multistate Cormac-Jolly-Seber (CJS) capture-recapture model, where the state variable denoted the habitat in which a given individual was captured (pool or riffle). Capture probability, transition probability, and survival probability were set as state (habitat), time and sex-dependent. Models were fit using the *crm* function in the R package *marked* ((Laake et al. 2013)version 3.2.4). Capture probability, and therefore population size, were estimated in four different months (March, May, July, and September) in order to capture seasonal fluctuations and to match the sampling scheme of the natural streams. Each target month was bracketed by data from 3 months before and 3 months after to allow for robust capture probability estimates. The estimated number of males and females in a specific habitat (pools or riffles) within a stream in a given month were summed to obtain the estimated population size in that habitat at that time point. We then estimated population density as individuals/m^2 for each stream, habitat type, and time point by dividing the estimates of population size by the estimated total benthic area of that habitat (see Appendix S1: Section S3 for details on this estimation). These calculations give us the mean and variance of population density for pools and riffles separately, for each stream and each month.

Hypothesis 1 –To construct predicted confidence intervals for expected population densities in natural streams we performed Monte Carlo simulations on the natural stream GLMMs by drawing 100,000 month- (March, May, July, September) and habitat-specific (pools, riffles) predictions at the level of the stream (see Appendix S1: Section S4). We then asked if the density estimate for the experimental streams was significantly higher than the null expectation. Doing this involves making multiple comparisons (one-tailed tests), one for each year, month, habitat and stream combination, for a total of 240 tests. We used Holm's step-down procedure to correct for multiple testing (Holm 1979, Rice 1989). See Table S2 for the results of statistical tests for individual stream-month combinations.

Hypothesis 2 –We tested whether the predicted increase in population density under thinned canopies was attained by fitting a GLMM with a negative binomial error distribution. We used the estimated number of guppies from our Cormac-Jolly-Seber model as our response variable, canopy

treatment (thinned vs. natural), habitat (pool vs. riffle), and month (March, May, July, or September) as fixed effects and year and stream as random effects. We included benthic area as an offset to express the results in terms of density, which is the same procedure used for the analyses of natural streams (see Appendix S1: Section S4).

Hypothesis 3 – To test for increased use of riffle habitats after the invasion, we compared the estimates of habitat density with the habitat-specific reference levels produced by our simulation (Appendix S1: Section S4). We again calculated the p-value, corrected for multiple comparisons, by counting the proportion of times the null model described above exceeded the focal stream estimate (one-tailed test). We tested for changes in riffle use with time with a one-way analysis of variance on the average proportion of an individual's lifetime spent in riffles as a function of cohort and using an a priori contrast for a linear trend.

Assessment of performance in experimental streams with intact versus thinned canopies: Because canopy thinning had a strong impact on our results for population density under Hypothesis 2, we assessed the demographic consequences of canopy thinning. We analyzed adult lifespan and recruitment rates under thinned and intact canopy streams. Thinning increases primary productivity, which likely increased resource availability at all trophic levels (Kohler et al. 2012), so we also examined two measures of individual performance, growth rate of immature females and size at maturity in males, that reflect the consequences of increased productivity under open canopies. We know from diverse prior laboratory experiments and manipulations of population density in the field that growth rate and male size at maturity both increase in response to increased food availability (e.g. (Reznick 1982, Reznick 1983, Reznick 1990, Reznick and Bryga 1996)). Our linear mixed model for female growth had growth increment (mass t_2 – mass t_1) as a response variable, standard length (initial size) as a covariate, habitat and canopy treatment as discrete explanatory factors, and stream identity as a random effect. Our measure for male size at maturity was the mass when an individual was first recorded as being sexually mature. We inferred maturity from the development of the gonopodium, which is the metamorphosed anal fin used as an intromittent reproductive organ. We analyzed male size in pools and riffles separately because size at maturity was density-dependent in pools but not riffles. For pools, we used an analysis of covariance, with biomass density as covariate and stream as a fixed effect. We tested the effect of canopy type with an *a priori* single-degree-of-

freedom contrast between the adjusted means of the two streams with intact canopies and the two with thinned canopies. For riffles, we used an analysis of variance and the same *a priori* contrast.

Assessment of population structure and fitness in pools and riffles: The lower population densities in riffles may be a simple consequence of this habitat type being more accessible to some fish; e.g. larger fish are better able to navigate in higher currents. To assess the effects of habitat on population structure, we examined sex ratios (proportion of fish that were male) and, for each gender, average body sizes of fish found on each sampling date in each habitat. We applied a general linear model to the factorial combination of stream and habitat, treating sampling date as a stratum so that the analyses contrast habitats accounting for stream differences and temporal variation. (See Appendix S1: Section S5).

The higher densities typically found in pools (Reznick et al. 1996a) suggest that guppies prefer pools to riffles. Preferred habitats are often those where individuals have higher fitness because of improved reproductive success and or/survival (McLoughlin et al. 2006). To assess the effects of habitat type on fitness, we quantified and compared the consequences of pool versus riffle occupancy on lifetime reproductive success for females and lifetime mating success for males. The latter analyses were done for the one replicate (LL) for which we have a pedigree and hence a capacity to quantify individual reproductive success. We employed generalized linear models with fixed, continuous predictors and a quasi-Poisson error structure (See Appendix S1: Section S5 for additional detail).

Ethical Considerations: Given the expected ecological implications of introducing guppy populations in guppy-free environments, we considered the ethical issues surrounding this experiment carefully. We extended the range of guppies in streams in which they already occurred, simulating the natural colonization of upstream locations by guppies, which has defined the natural history of guppies in the Northern Range of Trinidad and still occurs naturally. Over the course of our research careers, we have witnessed guppy populations disappear from upstream locations and successfully re-colonize from sites downstream. Therefore this experiment follows the natural pattern of colonization of tributaries and does not alter the natural range of guppies.

We presented our methodological proposal to representatives of the Fisheries Division, Ministry of Agriculture, Land, and Fisheries of Trinidad and Tobago, which oversees all work on fish,

and to scientific colleagues at the University of the West Indies at St. Augustine. The Fisheries Division informed us that no permits were required to transplant guppies. Our colleagues at the University of West Indies did not object to our proposed experimental manipulation once they understood the nature of the experiment.

Results

Analysis of six natural streams: We first assessed guppy population densities in six natural populations to provide a frame of reference for evaluating the densities of guppies in the experimental introductions. Our sampling dates included two dry-season (March, May) and two wet-season (July, September) censuses to provide estimates of seasonal variation in population size.

We initially fit a model that included the natural streams as a random effect with two habitat types (pool vs. riffle) and the four sampling times (March, May, July and September) as fixed effects, together with the interaction between habitat and time. We fit two additional models that included two rather than four time-periods. Our prior research revealed that the rate of reproduction tends to be higher during the dry than the wet season because food is more abundant (Reznick 1989) so it was reasonable to expect that population density could be higher during the dry season as well. We combined March and May (dry season) as one-time period and July and September (wet season) as the second to model the effects of the dry versus wet season, respectively (the Season model). The nature of the data (Fig. 2) inspired us to fit a second wet-dry season model (the Lag model) with a built-in time lag. There is a lag in the increase in census population size after the onset of the dry season because guppies are 6 to 7mm at birth but we only sampled and marked fish >14 mm long because of risk of mortality associated with handling smaller fish. Newborn fish grow to 14 mm in one to two months (Reznick et al. 1996a). Since the dry-season extends from approximately February until May, the lag between when the dry-season increase in resources begins and when we see an increase in population density via the recruitment of unmarked fish 14 mm or larger would cause the increase in census population size to appear in May, rather than March. Likewise, a lag between when the dry-season ends and recruitment slows down would cause the population decline to become apparent in September rather than July. Our second model thus contrasted May and July (expected

peak season) versus March and September (expected low season) to accommodate this time lag (Table 1).

The best model included the effects of habitat (pool vs. riffle) and the Lag Model for the effects of time (Table 2). The next three models fall within or close to ΔAICc values of 4 and hence merit some consideration. The next best-fit model (the Month Model, Table 2) treats each month separately, followed by a Lag Model that includes an interaction between lag and habitat then a month model that includes an interaction between month and habitat. These analyses reveal that population densities were significantly higher in pools than riffles. Densities in pools were typically 3-5 times higher than those in riffles, although in some streams at some censuses they were as much as an order of magnitude higher (e.g. Quare in July and September) and as little as 50% higher (e.g. Tumbason River in September; Fig. 2).

Patterns in Experimental Streams: Our GLMM analyses of the experimental streams revealed effects of habitat and time on density that closely mirror those of the natural streams (Table 3). Guppy population densities are considerably higher in pools than riffles in three of the four streams, typically three- to four-fold higher in LL and UL and an order of magnitude higher in CA (Fig. 3). The exception was TY, in which pool densities were typically about two-thirds higher than riffle densities, but sometimes very similar. Population density increased significantly from March to May, remained high in July, and then declined significantly in August. This close match with the Lag Model in natural streams supports the legitimacy of using the censuses of natural streams as a basis for comparison with the experimental streams. We also found that population densities tended to be higher in the two streams with thinned canopies, and hence higher light availability.

Comparison of Natural vs. Experimental Streams: Pools and riffles in the two experimental streams with thinned canopies (UL and TY) had population densities that often significantly exceeded those of natural streams. By contrast, on only two occasions did the experimental streams with intact canopies (LL and CA) display significantly higher population densities than the natural streams (Fig. 3, Appendix S1: Table S2).

All experimental streams had lower population densities than the natural streams during the first two years of the introduction. Thereafter, all experimental streams exhibited seasonal cycles of

abundance similar to those of natural streams, with the highest population densities appearing in the dry seasons and in 2009-2010 and 2014-2015.

Why do population densities exceed expectations in streams with thinned canopies? Higher light levels in the two streams with thinned canopies are associated with increased primary productivity and invertebrate abundance (Kohler et al. 2012, Travis et al. 2014, Simon et al. 2017), suggesting that these higher densities reflect higher carrying capacities in these streams.

Demographic analyses reveal that the higher population densities under thinned canopies are attributable to increased recruitment rather than lower mortality rates. Adult male monthly survival averaged 0.74 + 0.009 (1 se) and was independent of biomass density ($F_{1,386} = 0.06$, NS) and canopy treatment ($F_{1,386} = 0.59$, NS). We use biomass density when analyzing growth, survival, and recruitment because biomass density is a more accurate measure of the pressure of population numbers on resources than the number of individuals. Adult female survival was independent of biomass density ($F_{1,386} = 2.02$, NS) but was slightly higher in streams with intact canopies ($F_{1,386} = 3.97$, P = 0.047; LS MEANS - Open: 0.838 + 0.007; Closed: 0.858 + 0.007). Per capita recruitment decreased as total biomass density increased; however, the rate of decrease in recruitment with increasing density was much steeper under intact than thinned canopies (Fig. 4: $F_{1,337} = 5.73$, P < 0.02). The intercepts were statistically indistinguishable ($F_{1,337} = 0.36$, NS). These relationships have two consequences. First, while recruitment rates converged at the lowest densities, thinned canopy sites had much higher recruitment rates through nearly the full range of observed densities. Second, the biomass density at which monthly recruitment is predicted to be zero is nearly four-fold higher in the thinned canopy streams (2.68 g/m^2) than in the closed canopy streams (0.73 g/m^2). These densities are at or slightly beyond the maximum densities observed in thinned and intact canopies (2.80 and 0.70 g/m^2 respectively) so the extrapolation in this deduction is minimal.

Did canopy thinning cause higher productivity and leave a signature of higher per capita resource availability on individual performance? Canopy thinning is indeed associated with increased primary productivity (Kohler et al. 2012, Collins et al. 2016), higher per capita resource availability, more rapid growth of individual guppies, higher rates of recruitment and higher population densities.

We focused first on the growth rate of juvenile females because they, unlike males, have indeterminate growth and have not yet initiated investment in reproduction, so all available energy is

invested in growth. The rate of growth is indeed significantly higher in streams with thinned vs. intact canopies by about 9% (Table 4).

Second, we asked if the size of males at maturity was larger under the thinned canopy because, in the laboratory, male size at maturity increases with food availability (Reznick 1982, 1990, Reznick and Bryga 1996). We had to analyze male size separately for pools and riffles because size at maturity was density-dependent in pools but not in riffles.

In pools, higher biomass densities two months prior to maturation led to smaller male size at maturity ($F_{1,79} = 12.02$, $P < 0.001$). There was no interaction among streams between biomass density and male size ($F_{3,76} = 1.10$). The lagged density reflects the density experienced by a male during the initial period of juvenile growth. After adjusting for biomass density, there was a significant difference among the four streams in male size at maturity ($F_{3,79} = 13.83$, $P < 0.001$). We examined the effect of canopy by the *a priori* contrast between the two thinned-canopy streams (UL and TY) and the two intact canopy streams (CA and LL). After adjusting for biomass density, male size in pools was larger in the thinned canopy streams ($F_{1,79} = 25.72$, $P < 0.0001$) by about 17% (intact canopy: 0.079 + 0.002 g, thinned canopy: 0.093 + 0.003 g).

In riffles, where the biomass densities were much lower than in pools, there was no relationship between size at maturity and biomass density two months earlier ($F_{1,61} = 0.27$) so we made no adjustment for biomass density. Male size at maturity in riffles differed among the four streams ($F_{3,62} = 5.49$, $P < 0.003$). The same *a priori* contrast between thinned and intact canopy streams showed that, as in pools, males in riffles were larger in the thinned-canopy streams ($F_{1,62} = 15.75$, $P < 0.0005$) by about 21% (intact canopy: 0.075 + 0.003 g, thinned canopy: 0.091 + 0.003 g). These values for male size in riffles in intact and thinned canopies are similar to those found in pools.

Are riffles marginal habitats? Do guppies that occupy riffles suffer a loss of fitness? The persistently low population densities of guppies in riffles, compared to the very high densities often seen in pools, suggests that riffles are a less desirable habitat. Nevertheless, as population densities increased in pools, more guppies appeared in riffles (Fig. 3). This pattern of movement from pools into riffles suggests that elevated densities in pools caused migration into riffles and inspired us to evaluate the consequences of occupying pools versus riffles. We found that the substantially lower

population densities in riffles compensate for what appears to be lower quality habitat, such that the fitness of guppies occupying riffles is similar to the fitness of guppies occupying pools.

First, we examine patterns in the use of pools and riffles over time, along with the differences observed between fish found in pools and those in riffles. Second, we examine the fitness consequences of pool vs. riffle occupancy for fish in the LL (intact canopy), for which we have a pedigree and hence can estimate reproductive success. We only have a pedigree for this locality because of funding limitations. Here we present a summary of our results; we present the details in Appendix S1: Section S5.

In any given month, riffles are decidedly more male-biased than pools. The least squares mean proportion of males in pools was 0.31 and for riffles was 0.40 (se = 0.008). Streams differ in the magnitude of this effect so there was a strong stream by habitat interaction. In the LL, individual males spent a greater proportion of their lives in riffles than females but, over time, as overall densities increased, females increased the proportion of their lives spent in riffles (Fig. 5). The average proportion of a female's life spent in riffles exceeded 0.10 only three times in the course of the study and was usually much lower; about half the males in our study spent more than 10% of their time in riffles.

For both genders, the increase in riffle use with time was statistically significant. We tested the pattern of riffle use by performing a one-way analysis of variance on the proportion of time in riffles as a function of cohort and then doing an a priori contrast for a linear trend. "Cohort" refers to those individuals marked for the first time in any given month. For females, there was a significant effect of cohort ($F_{29,727} = 1.65$, $P < 0.02$), which was driven by the strong, positive linear trend with time ($F_{1,727} = 14.14$, $P < 0.002$). For males, the difference among cohorts in pool vs. riffle use was close to significant ($F_{(28,221)} = 1.48$, $P = 0.06$) but there was a significant linear trend towards increasing riffle use over time (slope = 0.004 + 0.001, t = 3.62, $P < 0.001$); this proportion increased slowly over time (Fig. 5).

While the mass of males at maturity was not different between pools and riffles, once we adjusted for the higher densities in pools (see above), mean female mass was slightly lower in riffles. Females have indeterminate growth so here we are examining the average body mass of adult females in each month. The overall difference is small (0.235 g in pools vs. 0.212 g in riffles, se = 0.002) but

significant because of the large sample sizes. The magnitude of difference varies among streams so there is an interaction of stream and habitat. The analysis accounted for 43 % of the total variation.

We analyzed data on whether riffle use affected lifetime reproductive success for females and lifetime mating success for males. For each female, her lifetime reproductive success is the number of surviving offspring; for each male, lifetime mating success is the number of females with which he produced at least one surviving offspring. We analyzed lifetime reproductive success and lifetime mating success separately for the earliest period (June 2008-May 2009) and the last period for which we had complete pedigree data (January 2010-December 2010). We divided the data in this fashion for two reasons. First, population density and riffle use co-vary with each other and with time, which compromises our statistical power to distinguish the effect of each factor in the data taken as a whole. Population densities during the early phase of the study ranged from 0.184 to 1.052 grams of fish (wet weight) per m^2. Densities in the late phase ranged from 2.523-3.760 g/m^2. Riffle use in females ranged from about 6% in the early period to 11% in the later period (Fig. 5). Second, the relationships among the putative predictors of reproductive success, lifespan, riffle use, and density, changed during the course of the experiment (see Appendix S1: Section S5). Were we to combine the periods into a single analysis, these differences could lead to inaccurate results and a reduction in statistical power to separate the contributions of density and riffle use.

We estimated each individual's lifespan as the number of months between its first and last capture. We also estimated each individual's "experienced density", which is the density regime experienced by an individual during its lifetime. An individual's experienced density is calculated as density of the habitat (pool or riffle) in which it was captured each month, averaged across all months of its lifespan. For example, if an individual's capture history across months 7-11 were "(7) pool, (8) pool, (9) riffle, (10) riffle, and (11) pool, then its experienced density would be the average of the densities in pools at months 7, 8, and 11 and in riffles at months 9 and 10.

We analyzed lifetime reproductive success and lifetime mating success with generalized linear models, using a quasi-Poisson error structure, with riffle use, lifespan, experienced density, and their squared values, as continuous predictors. We included quadratic terms in the initial model in order to allow for the possibility of Allee effects (for experienced density), an optimal level of riffle use, or a plateau of lifetime reproductive success or lifetime mating success with lifespan. We began with a

model including all six predictors and used backward elimination to find the best model, which we defined as the model from which further deletion did not significantly change the deviance. We eliminated one outlier for males in the late period (see Appendix S1: Section S5).

For females, once lifespan and experienced density were taken into account in our best model, there was no significant effect of habitat use on lifetime reproductive success either in the early or late period (Fig. 6; $t_{(early)}$=-0.66, p = 0.51; $t_{(late)}$ = 1.85, p = 0.07). In both periods, lifetime reproductive success increased as lifespan increased and decreased as experienced density increased, with the final models for the two periods being very similar to each other.

The results for males were mostly the same as for females but differed from females in a few details. For males, as for females, there was no effect of habitat use on lifetime mating success in either period once lifespan and experienced density were taken into account (Fig. 6; $t_{(early)}$ = -0.27, p = 0.79; $t_{(late)}$ = -0.77, p = 0.44). The effects of lifespan and experienced density on lifetime mating success differed between periods. In the early period, just as was the case for lifetime reproductive success in females, lifetime mating success increased as lifespan increased but, unlike females, reached a plateau at and beyond about 13 months lifespan (Appendix S1: Section S5). In general, just as for females, as experienced density increased, lifetime mating success decreased, although there is a hint of an Allee effect at very low values of experienced density (Appendix S1: Section S5). In the later period, lifetime mating success decreased as experienced density increased, but the effect was not statistically significant (t = -1.66, p = 0.10)). As in the early period, lifetime mating success increased as lifespan increased, with evidence for a plateau in lifetime mating success occurring at and beyond a lifespan of 13 months (Appendix S1: Section S5).

In summary, habitat use had little effect on females either early or late in the study. The persistently lower rate of riffle use suggests that they represent lower quality habitat; however, for females, any potential loss of fitness associated with migrating into riffles was compensated for by lower population densities. Riffle use did not affect male mating success, which largely decreased as population density increased. For both genders, fitness increased as lifespan increased but male fitness appeared to reach a plateau at and beyond 13 months lifespan.

Discussion

Do invaders exceed expected population densities? We predicted, based on simulations (Reznick et al. 2001b) and expectations of the "enemy release" hypothesis, that all introduced populations would explode because of the mismatch between the guppy phenotype and the environment. Guppies from high predation environments in general (Reznick and Bryga 1996) and from the locality used as a source for the introduction (Torres-Dowdall et al. 2012) have adapted to predation by evolving earlier ages at maturity and a higher rate of offspring production. When this life history is paired with the low predation and low mortality rates in the introduction sites, the prediction is rapid population growth and possibly an overshoot of the population densities typical of this habitat type. Prior studies suggest that this mismatch between local adaptation and risk of predation plays an important role in population establishment. All attempted introductions of guppies derived from high predation localities to guppy-free, low predation environments have been successful, while two attempts to introduce guppies from low predation environments into a guppy-free high predation environment failed (Reznick et al. 2004). However, the populations of introduced guppies in streams with intact forest canopies did not exceed the population sizes predicted by our assessments of natural streams. Instead, we found that "enemy release" failed and ecology prevailed in the sense that the populations grew to the same densities as those observed in natural streams.

This study presents only the short-term population dynamics of the invader, which includes the run up to population densities typical of this habitat type in the first few years after the invasion. We know from past and ongoing research that the story of the invasion does not end here. More generally, Strayer et al. (2006) offer compelling arguments for why a longer-term perspective is required to understand the impact of invasive species because the nature of an invader's full impact can take so long to develop. Elsewhere, we and others have shown that the attainment of population sizes typical of low predation habitats imposes significant selection on the introduced guppies, causing their life histories (Reznick et al. 1990, Reznick et al. 1997) and other aspects of their phenotypes (Endler 1980, O'Steen et al. 2002) to evolve, but also causing changes in habitat use in ways that impact the structure of the ecosystem (Bassar et al. 2010, Simon et al. 2017). We have also found that introduced guppies change the population dynamics, growth rate, and cause the evolution

of the life history of the other fish found in this community (Walsh et al. 2011, Walsh and Reznick 2011). More generally, invasions are known to be associated with the evolution of the invasive species (Reznick and Ghalambor 2001) and native species in response to invaders (Strauss et al. 2006). There is good cause to think that the ultimate consequences of invasions will often include such complex interactions between ecology and evolution that will take years to decades to mature (Strauss 2014, Faillace and Morin 2017).

Does habitat disturbance influence the density attained by the invader? Elton (1958), Hobbs and Huenneke (1992), Lonsdale (1999), Davis et al. (2000) and many others argue that anthropogenic disturbance can facilitate invasion. It can do so by creating ecological vacancies in the form of patches of habitat with reduced species abundance, disrupting trophic networks or creating opportunities by increasing the availability of some resources. Canopy thinning is a disturbance, albeit a mild one, that can have important ecological consequences. Casatti et al (2009) found that streams surrounded by grassy vegetation had less diverse fish communities, dominated by invasive guppies, in comparison to streams surrounded by riparian forest.

We found that canopy thinning produced an increase in primary productivity with cascading effects through the ecosystem (Kohler et al. 2012), causing populations to exceed the expected population density of streams with intact canopies. The high population growth rates were primarily attributable to increased recruitment, which is in turn a function of a higher rate of reproduction and/or increased juvenile survival, both of which could be attributable to higher resource availability. Juvenile females grew faster and males were larger at maturity, which are again typical responses to our experimental reductions of population density in natural populations (Reznick et al. 2012, Bassar et al. 2013) or augmentation of food availability in laboratory experiments (Reznick 1982, 1990, Reznick and Bryga 1996). Population outbreaks in our system were thus a product of habitat modification, which in turn increased primary productivity, rather than the biological properties of the invader or the fact that the invasion was associated with "enemy release" in the form of reduced risk of predation. In the context of our experiment, canopy thinning only caused a local increase in primary productivity (Kohler et al. 2012) which in turn facilitated an increase in population density. In a less restrictive setting, it could also cause an increase in the rate of spread of the invasive species across the landscape.

Does the population expansion of the invader cause it to occupy marginal habitat? As guppy populations increased over time, the rate of increase was higher in pools than riffles, causing the differences in population density between the two types of habitat to magnify and become statistically significant. At the same time, at higher overall densities, females were spending a greater proportion of their lives in riffles. The persistently lower population densities of guppies in riffles and slower rate of increase in density suggests that this habitat type is less preferred. Nevertheless, the number of guppies in riffles increased and the individuals that chose to move into riffles fared as well as those that remained in pools. They sustained fitness because of the much lower population densities in riffles. Our results thus conform well to the ideal free distribution hypothesis (Fretwell and Lucas 1969) in the sense that there is little evidence of a loss of fitness in those that move to the less-well occupied and presumably less preferred habitat.

It is of interest to speculate on what the consequences of such behavior might be if played out on a larger geographical scale and for a longer interval of time. In our setting, the spatial pattern of habitats is fine grained. Individuals can readily move among habitat patches (pools and riffles) and each patch is too small to sustain a viable population, so there is little chance of local adaptation or differentiation among populations. If this same pattern of dispersal occurred on a larger geographical scale, with habitat patches being larger and better separated from one another, then it is possible to imagine the density-dependent dispersal of an invader resulting in the filling of vacant ecological niches. Such a scenario is what we see fulfilled in observations of natural invasions (e.g.(Pietrek and Gonzalez-Roglich 2015). It is also among those proposed by Schluter (2000) as a cause of the adaptive radiations that have followed the invasion of new habitats.

Conclusion

When invaders succeed, how much of it is attributable to the invader vs. the ecosystem? Some analyses suggest that ecosystems differ in their susceptibility to invasion (Lonsdale 1999, Davis et al. 2000). Disturbance is one factor thought to increase susceptibility to invasion because it creates novel niches and increases resource availability (Hobbs and Huenneke 1992, Davis et al. 2000) while at the same time disrupting the balance of native communities (Hobbs and Huenneke 1992, Jauni et al. 2015). An alternative perspective is that invasion success is an attribute of the species (Williamson and Fitter 1996, Ehrenfeld 2010, van Kleunen et al. 2015, Iles et al. 2016, Lee 2016). One outcome of

all of the efforts to determine if we can predict which species will be successful invaders is that one of the best predictors is whether or not a species has been a successful invader elsewhere (Ewel et al. 1999, Caley and Kuhnert 2006). This result suggests that successful invasion is indeed an attribute of the species, but does not reveal what that attribute might be. Successful invasion may instead be a product of some interaction between the properties of the organism and invaded community (Didham et al. 2007, Pearson et al. 2012, Godoy and Levine 2014). For example, Godoy and Levine (2014) and Pearson et al. (2012) found that successful invaders differed from the native flora in phenology and/or morphology in ways that either gave them a competitive edge or enabled them to occupy different ecological niches.

The success of guppies as invaders may be attributable to features of their life history, with invasion being part of their natural history, but our results also suggest that the interaction between their attributes and the invaded community are important. Their distribution in Trinidad suggests they are better at penetrating natural barriers than other species found further downstream. Our mark-recapture studies reveal that adult females are best able to penetrate upstream barriers. They store sperm, are often mated to multiple males and give birth to well-developed offspring, so a single female can initiate a new population with a modicum of genetic diversity (e.g. (Hughes et al. 2013). This study reveals that these attributes alone will enable them to establish a new population, but habitat disturbance enhanced establishment because it caused an increase in population density The added effects of canopy thinning were required to sustain explosive population growth, which is a likely precursor to the range expansion and invasion of new ecological niches characteristic of the most damaging invasions. (9,126 words)

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Data Availability

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.70rxwdbtn

Table 1: The AIC values, delta AIC and weight for the different models fit to the analyses of population distributions in natural streams. The models include three different treatments of time – Month, in which each of the four censuses are treated separately, Season, in which we contract the dry (March, May) versus wet season, and Lag, in which we accommodate the anticipated time lag between the beginning and end of the dry season and the increase and decrease in population size (March and September vs. May and July).

formula	df	AICc	ΔAICc	weight
~ lag+habitat	5	2286.99	0.000	0.49
~ month+habitat	7	2288.57	1.58	0.23
~ lag*habitat	6	2289.04	2.05	0.17
~ month*habitat	10	2291.22	4.23	0.06
~ habitat	4	2293.08	6.09	0.02
~ season*habitat	6	2293.80	6.81	0.02
~ season+habitat	5	2294.58	7.59	0.01
~1	3	2397.43	110.44	0.00
~ lag	4	2399.34	112.35	0.00
~ season	4	2399.41	112.42	0.00
~ month	6	2405.97	118.98	0.00

Table 2. Parameter estimates derived from the two models that best fit the data. We fit models with either a negative binomial or Poisson distribution. The negative binomial models provide a far better fit to the data than a Poisson distribution (all $\Delta AICc > 100$) so we only report results for the Negative Binomial models.

Lag Model	Estimate	Std. Error	ZValue	P-Vale
(Intercept)	0.782	0.131	5.984	<0.001**
Habitat(riffle)	-1.471	0.135	-10.854	<0.001***
Month(lag)	0.376	0.131	2.872	0.004**
Month Model				
(Intercept)	0.720	0.169	4.270	<0.01**
Habitat(riffle)	-1.503	0.136	-11.009	<0.001***
Month (05)	0.594	0.195	3.040	0.002**
Month (07)	0.322	0.184	1.752	0.079
Month (09)	0.188	0.183	0.646	0.517

Table 3: Parameter estimates from the GLMM analysis of the four experimental streams

	Estimate	Std. Error	Z value	P-value
(Intercept)	0.491	0.310	1.582	0.114
Canopy(Open)	0.847	0.181	4.692	<0.001 ***
Habitat(riffle)	-1.371	0.091	-15.069	<0.001 ***
month(05)	0.603	0.125	4.822	0.001 **
month(07)	0.414	0.126	3.281	<0.001 ***
month(09)	0.068	0.124	0.549	0.583

Table 4. Analysis of growth between first and second capture for juvenile females. The complete results show that growth rate (SL= standard length) decelerates with increasing body size, is higher under thinned canopies (Canopy(Open)) and there is no difference in growth rate in fish from pools vs. riffles (Habitat(Riffle)).

	Value	Std. Error	DF	t-value	p-value
(Intercept)	7.458	0.175	7674	42.456	0.0001
SL	-0.308	0.006	7674	-46.452	0.0001
Canopy(Open)	0.687646	0.140111	7674	4.907	0.0001
Habitat(Riffle)	0.040235	0.033752	7674	1.19208	0.2333

Figure Legends

Figure 1. (a) Trinidad, with box outlining the portion of the island represented in Fig. 1b. (b) The Northern Range Mountains, illustrating the locations of the six natural streams used to provide estimates of guppy population densities and the four experimental streams. (c) Magnification of the location of the four experimental streams, all of which are tributaries of the Guanapo River. CA = Caigual River (intact canopy), LL = Lower La Laja River (intact canopy), TY = Taylor River (thinned canopy), UL = Upper La Laja River (thinned canopy).

Figure 2; Population densities of the six natural streams, all with intact canopies, across the four sampling periods. The habitat types are pools (P, solid line) versus riffles (R, stippled line)

Figure 3: Observed time series of population sizes in pools and riffles in the four experimental streams (solid lines) in comparison with the mean and 95% confidence intervals for the seasonal changes in population size in the six natural streams (broken lines). Points marked with an asterisk represent individual monthly censuses in which the experimental populations significantly exceeded the range of population sizes observed in natural streams. Table S2 reports the statistical results for each stream-month comparison.
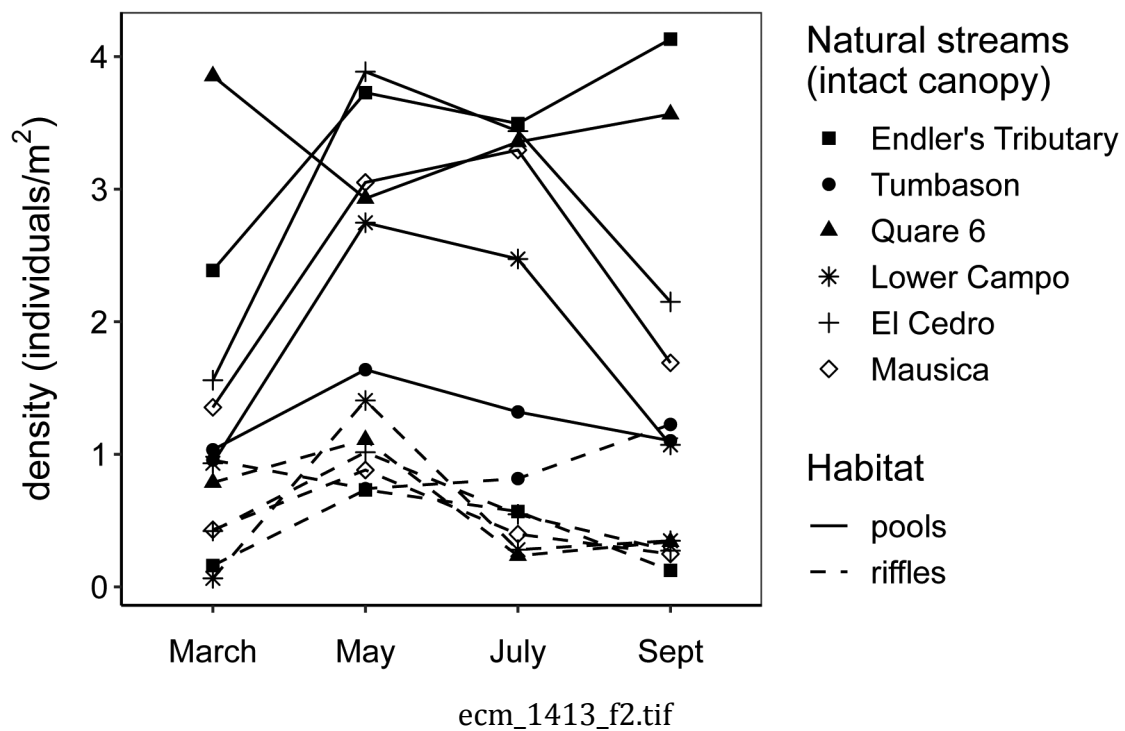
Figure 4. Regression lines for recruitment rate as a function of biomass density under the thinned canopy treatment (blue line: slope = -0.380 ± 0.121, t = -3.313, p = 0.002) and the intact canopy treatment (red line: slope = -1.977 ± 0.282, t = -7.02, p < 0.0001).
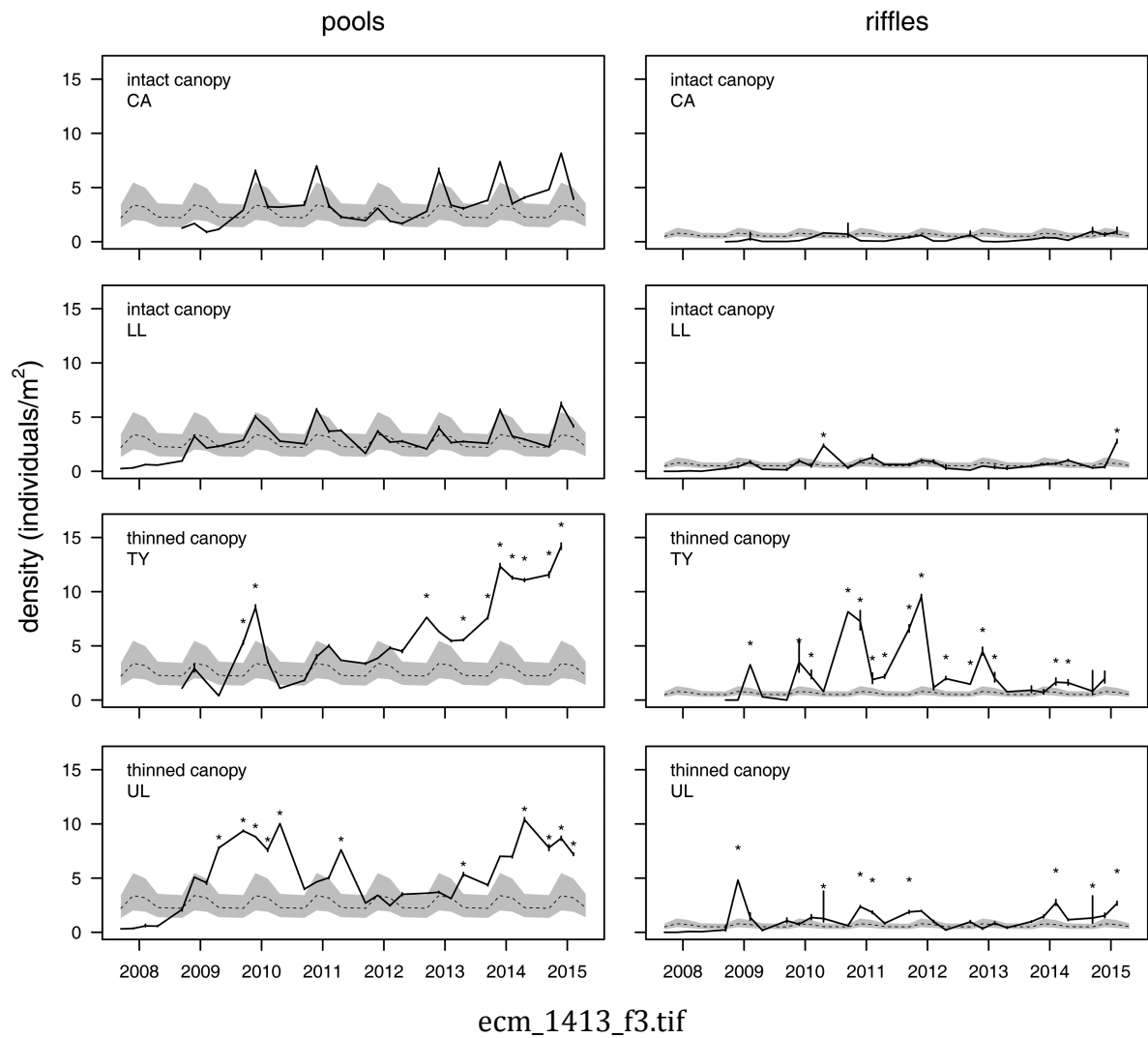
Figure 5: Average use of riffles by males and females in all four experimental streams. Males spend more time in riffles, on average, than females.

Figure 6: Lifetime Reproductive Success for females (top two panels) and Lifetime Mating Success for Males (bottom two panels) as a function of riffle use in the early period (left-hand panels) and the late period (right-hand panels).
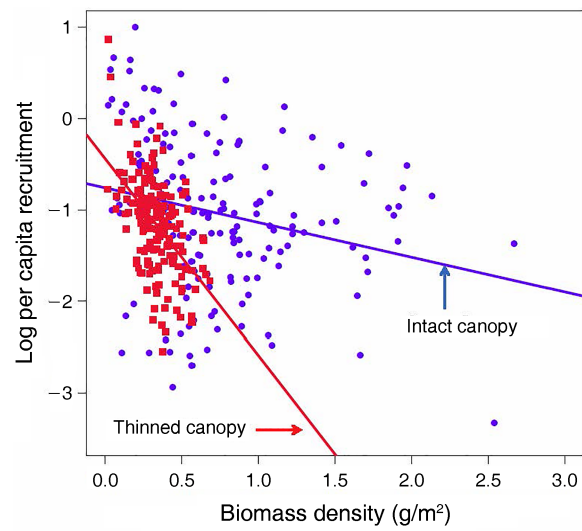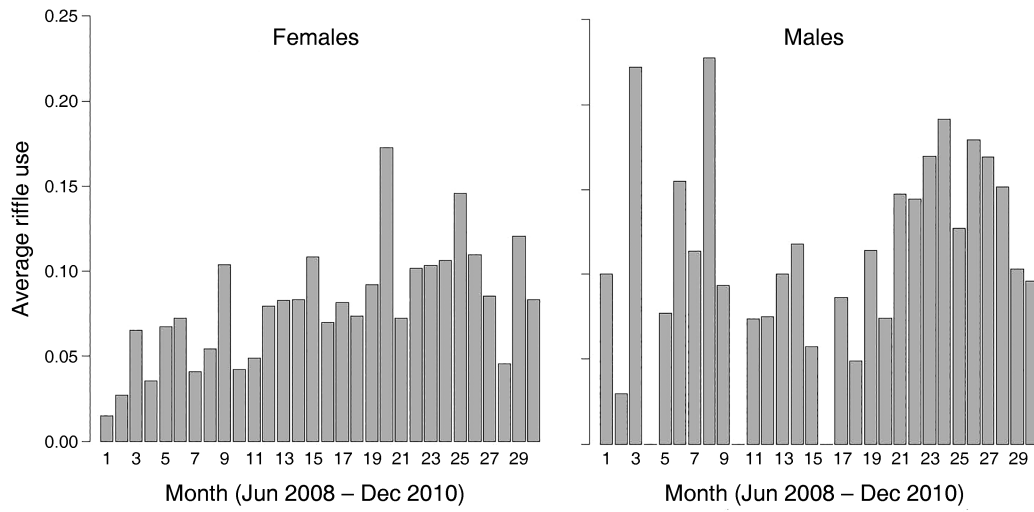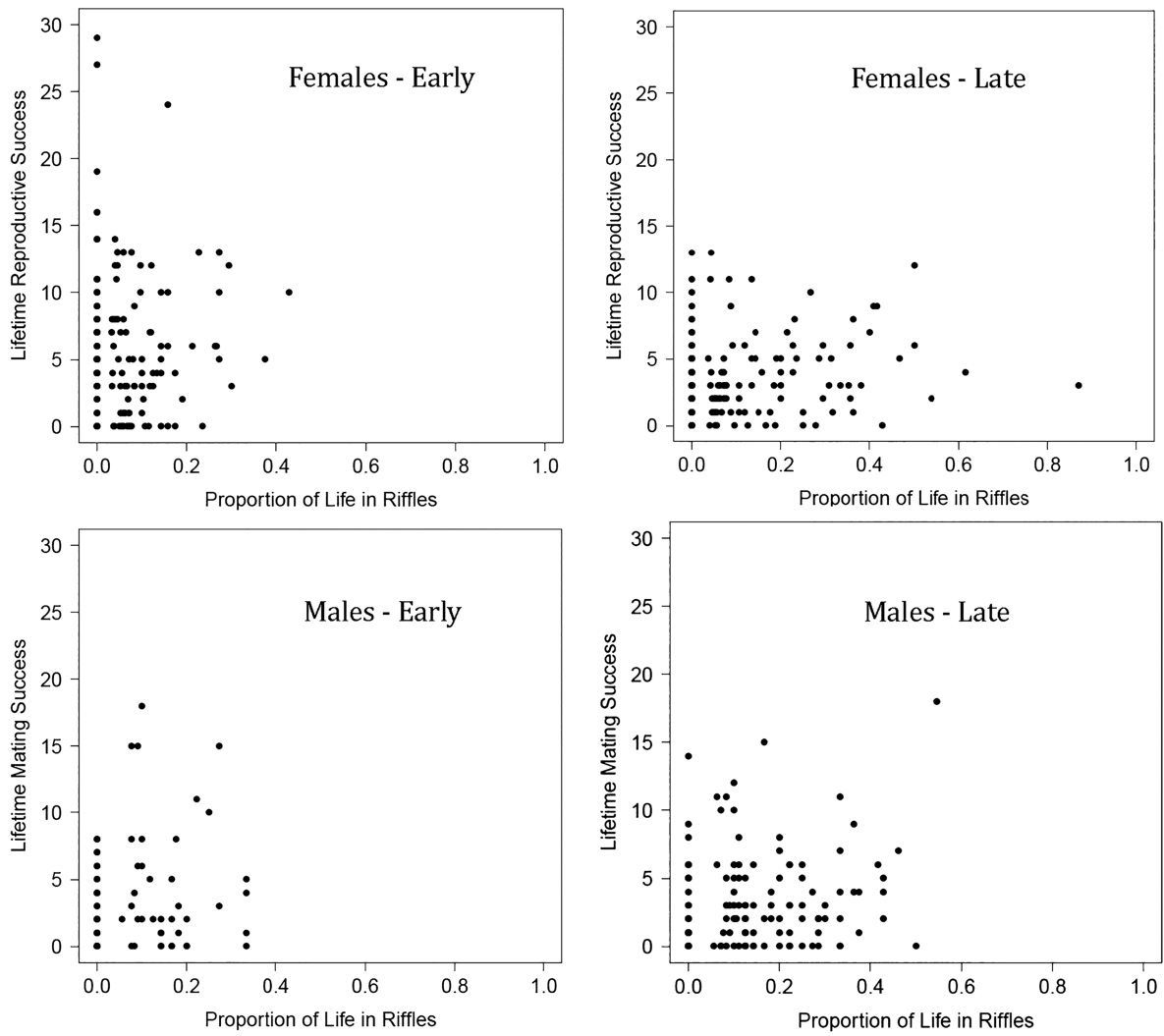
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pools   riffles

density (individuals/m²)

intact canopy CA

intact canopy LL

thinned canopy TY

thinned canopy UL

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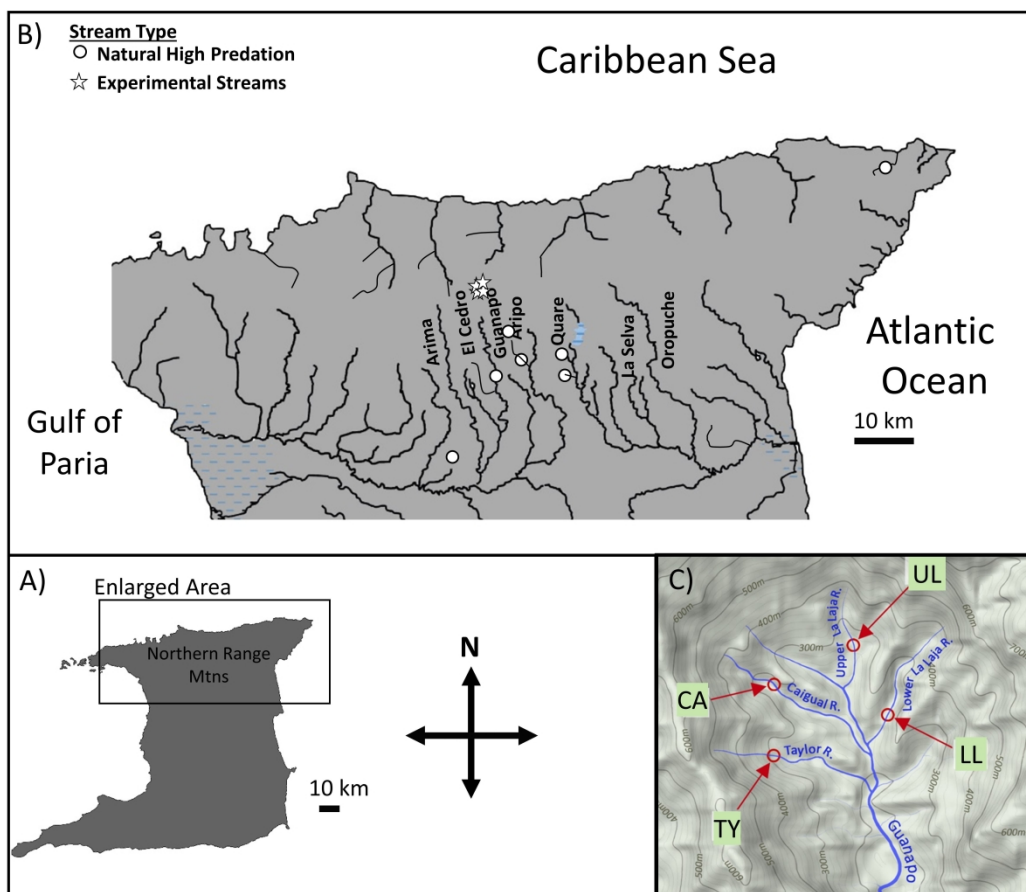
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