Oikos 000: 001–011, 2015
doi: 10.1111/oik.01769

Subject Editor: Jessica Abbott. Editor-in-Chief: Dries Bonte. Accepted 14 November 2014

Intraspecific phenotypic differences in fish affect ecosystem processes as much as bottom–up factors

Rana W. El-Sabaawi, Ronald D. Bassar, Chase Rakowski, Michael C. Marshall, Brynne L. Bryan, Steven N. Thomas, Catherine Pringle, David N. Reznick and Alexander S. Flecker

R. W. El-Sabaawi (rana@uvic.ca), C. Rakowski and A. S. Flecker, Dept of Ecology and Evolutionary Biology, Cornell Univ., Ithaca, NY 14853, USA. Present address for RWES: Dept of Biology, Univ. of Victoria, PO Box 1700, Station CSC, Victoria, BC V8W 2Y2, Canada. Present addressfor CR: School of Natural Resources and Environment, Univ.y of Michigan, Ann Arbor, MI 48109, USA. – R. D. Bassar and D. N. Reznick, Dept of Biology, Univ. of California, Riverside, CA 92521, USA. Present address for RDB: Dept of Environmental Conservation, Univ. of Massachusetts, Amherst, MA 01003, USA. – M. C. Marshall and C. Pringle, Odum School of Ecology, Univ. of Georgia, Athens, GA 306024, USA. – B. L. Bryan, Biology Dept, California State Univ. Dominguez Hills, Carson, CA 90747, USA. – S. N. Thomas, School of Natural Resources, Univ. of Nebraska, Lincoln, NE 68583, USA.

Evolution of life history traits can occur rapidly and has the potential to influence ecological processes, which can also be shaped by abiotic and biotic factors. Few studies have shown that life history phenotype can affect ecological processes as much as commonly studied biotic ecological variables, but currently we do not know how the ecological effects of life history phenotype compare in size to the effects of abiotic factors, or whether the ecological effects of phenotypes are sensitive to variability in abiotic conditions. Using a factorial mesocosm experiment we compared the ecosystem effects of guppy *Poecilia reticulata* life history phenotypes in two light treatments representing a four-fold difference in light levels, which was comparable to upstream–downstream differences in light availability in Trinidadian streams. Light and phenotype had significant effects on similar aspects of ecosystem function. Whereas light had a stronger effect on ecosystem structure (algal and invertebrate stocks) than phenotype, phenotype and light had nearly equal effects on many ecosystem processes (nutrient recycling, nutrient fluxes, ecosystem metabolism and leaf litter decomposition). Light had a stronger effect on most guppy life history traits and guppy fitness than differences between phenotypes. The effect of light on these traits was consistent with higher availability of food resources in the high light treatments. Interactions between light and phenotype were weak for the majority of response variables suggesting that abiotic variability did not alter the mechanisms by which phenotypes affect ecosystem function. We conclude that subtle phenotypic differences in consumers can affect ecosystem processes as much as meaningful variability in abiotic factors which until recently were thought to be the primary drivers of ecosystem function in nature. However, despite its effects on traits and the ecosystem, light did not alter the effect of guppy phenotype on ecosystem function.

Characterizing interactions between ecological and evolutionary processes is of interest to ecologists because rapidly evolving or locally adapted populations can influence temporal or spatial variation in population, community and ecosystem processes or states (Post and Palkovacs 2009, Reznick 2013). An important question is whether the effects of evolutionary processes on ecological variables are meaningful, especially when compared to the biotic and abiotic drivers of ecological processes. To this end, a few studies have compared the effect sizes of phenotypic variation within species to the effect sizes of biotic variables (e.g. density and presence/absence of species) and demonstrated that evolutionary processes can have ecological effects that are equal to or larger than the effects of doubling population density or adding a species to the community (Palkovacs et al. 2009, Bassar et al. 2010).

Most studies examining the effects of evolution on ecological studies have focused on population and community states or processes (Bailey et al. 2009, Reznick 2013). Studies examining the effects of evolution on local ecosystems are less common, but have revealed that evolution can significantly alter ecosystem standing stocks (e.g. algal biomass), and ecosystem processes (e.g. primary production)(Harmon et al. 2009, Bassar et al. 2010). However, ecosystem function is also affected by abiotic factors such as light and nutrient availability that can vary temporally and spatially. Currently we do not know how evolutionary effects on ecosystem function compare to the effects of manipulated abiotic variables, and whether these evolutionary effects are consistent across abiotic gradients.

In this study we assess the effect of guppy life history phenotype on ecosystem function under two light treatments. We chose light because it is an important limiting factor in

aquatic ecosystems, and because it varies dramatically and consistently among sites containing different guppy life history phenotypes. Guppies on the island of Trinidad live along a gradient of fish community types. At the one extreme in downstream locations, guppies live with a variety of predatory species (including *Hoplias malabaricus* and *Crenicichla* spp.) that consume guppies (hereafter: high predation or HP communities). At the other extreme, in upstream locations, they live only with the killifish *Rivulus hartii*, which are thought to be only mild predators of juvenile guppies (hereafter: low predation or LP communities) (Reznick et al. 1996a, b, Torres Dowdall et al. 2012). High predation guppies typically grow faster, mature earlier, reproduce more frequently and produce smaller offspring than LP guppies (Magurran 2005). Decades of research in this system have shown that life history trait differences between HP and LP phenotypes are heritable (i.e. they are evolved differences), and that they can evolve rapidly (within four years) after HP guppies are transplanted from HP sites to upstream sites containing only killifish (Reznick and Endler 1982, Reznick et al. 1990, Reznick and Bryga 1996).

Guppy HP and LP phenotypes have distinct effects on ecosystem function that are mediated by phenotypic differences in diet selectivity and nutrient recycling (i.e. excretion rate)(Palkovacs et al. 2009, Bassar et al. 2010, Zandona et al. 2011). High predation guppies consume more invertebrates and excrete more nitrogen (N) per capita than LP guppies, which consume more algae and detritus and excrete less N per capita (Palkovacs et al. 2009, Bassar et al. 2010). However, in Trinidadian rivers light limits some of the ecosystem processes that are affected by guppy phenotype (e.g. primary production and nutrient fluxes) (Grether et al. 2001, Kohler et al. 2012, Moslemi et al. 2012). Although light is a limiting variable in a large number of aquatic ecosystems (Gosselin et al. 1990, Hill et al. 1995, Karlsson et al. 2009), it is particularly interesting in Trinidadian rivers because it is confounded with the presence or absence of predators. As in other river systems, canopy openness and light availability increase downstream in Trinidadian rivers, which means that HP sites are typically more productive and have more abundant standing stocks than LP sites (Vannote et al. 1980, Reznick et al. 2001, Kohler et al. 2012). Light availability can also vary dramatically within sites of the same predator regime (Grether et al. 2001, Moslemi et al. 2012). Light limits algal and invertebrate standing stocks, which are important food resources for guppies (Grether et al. 2001). Laboratory experiments have shown that changes in resource availability can affect some guppy life history traits (age at maturity, offspring size) and growth rates (Grether et al. 2001, Arendt and Reznick 2005). Light can therefore affect ecosystem function either directly by enhancing primary production, standing stocks, and nutrient fluxes, or indirectly by altering guppy life history phenotype or by acting as a selective agent on guppy fitness.

Our goals were to: 1) test the effects of light and guppy predation phenotype on guppy life history traits, population growth rates and ecosystem function, 2) test whether the effect of guppy phenotype on ecosystem function varied between light treatments, and 3) compare the relative effect sizes of light and guppy phenotype for all response variables. Using a factorial mesocosm experiment we crossed HP and LP phenotype treatments with two light levels that approximated natural difference in light between HP and LP sites. We assessed the relative effects of light, guppy phenotype, and their interactions on guppy life history traits, population growth rates and ecosystem function metrics using general linear models. A significant interaction between phenotype and light would suggest that the ecosystem effects of guppy life history phenotype were not consistent under variable light conditions. Likewise, significant interactions between light and phenotype in guppy traits or population growth rates would suggest that light could modulate the ecosystem effects of guppies by altering the phenotype or fitness of guppies. Finally we measured and compared the relative effect sizes of light and guppy phenotype on all response variables in order to assess whether phenotypic differences in life history traits had meaningful effects on ecosystem function, which can also be influenced by abiotic variability in natural ecosystems.

Methods

Experimental design

Eight flow-through cinder block channels were built adjacent to Ramdeen Stream, a tributary of the Arima River (Trinidad), and were laterally divided into 16 experimental units (mesocosms, 3.0×0.5 m) (Palkovacs et al. 2009, Bassar et al. 2010, 2013). Water was fed to the mesocosms from a nearby fishless spring, with discharge maintained at 75 l h^{-1}, and channel depth at ~15 cm. The flow rates were lower than average flow rates of many 2nd and 3rd order streams in Trinidad, but they were comparable to flow rates obtained in other guppy experiments (Palkovacs et al. 2009). Because the mesocosm channels were fed from a natural spring similar to those that feed Trinidadian streams, the flow rates we observed in the mesocosms reflected natural variability in the water supply in Trinidad at the time of our experiment (May – late dry season). The bottom of each mesocosm was prepared using a commercial gravel and sand mix that was rinsed to remove silt. The mesocosms were seeded with insects from a nearby stream (St. Patrick's Creek in the Arima River, GPS: 10°68′46.1″N 61°29′11.9″W), which were allowed to acclimate in the mesocosm for ~ 1 week prior to the experiment (see Supplementary material Appendix 1 for more details).

The experimental design consisted of crossing a light treatment (low versus high) with guppy phenotypes (LP versus HP) in a full factorial, complete random block design divided across four blocks (Supplementary material Appendix 1). The light treatment was created by fitting each channel with a box-shaped shade tent (2 m tall, 1.5 m wide and 3 m long). Twenty percent grade black agricultural shade cloth was used for the high light treatment, and 80% black agricultural shade cloth was used for the low light treatment. Light levels were measured using light meters set to record every 15 min immediately above the water surface.

Guppies were collected from High predation (HP) and Low predation (LP) locations in the Aripo River ~ 5 days before the experiment began (HP location GPS: 10°66′56.8″N, 61°22′78.9″W, LP location GPS: 10°69′04.8″N 61°23′68.9″W). These same source popula-

tions were used in previous eco-evolutionary studies (Bassar et al. 2010), and their diets and life history traits had been previously described (Reznick and Endler 1982, Zandona et al. 2011). In each location light was measured over a period of three days using light meters set to record every 30 min to provide a point of comparison with the mesocosm light treatment. Each guppy was measured for standard length, weighed to the nearest 0.001 gram and marked with colored elastomer to identify individuals for growth rate measurements. Twelve guppies (six males and six females) were added to each mesocosm, which roughly corresponds to the density of guppies in HP sites (Reznick and Endler 1982, Reznick et al. 2001). The initial biomass of guppy populations was constant across treatments (~ 1.3 g wet mass). The average initial body size of guppies in each mesocosm was the same (~14 mm). The light treatment boxes were erected on the same day as the guppies were introduced.

Response variables

Guppy life history, demographic rates and fitness

At the end of the experiment (28 days) guppies were removed with dipnets, and were sacrificed in an overdose of MS-222, then preserved. Guppies were then weighed, and measured for standard length. We analyzed the responses of life history and demographic rates to the experimental treatments using general linear models and model selection procedures. We then used the parameter estimates from these models to parameterize an integral population projection model (IPM). The IPM modeled demographic rates as functions of continuous traits such as body size to provide an estimate of population growth rates (λ), which in the context of this experiment was interpreted as a measure of absolute fitness (Easterling et al. 2000). Details of this modeling approach were described previously in Bassar et al. (2013).

Demographic rates needed to parameterize the IPM included the mean (and variance) of somatic growth rate, mean (and variance) of offspring size, fecundity (defined as offspring number), probability of reproduction over the interval, and the probability of survival as estimated from field studies (Bassar et al. 2013). Somatic growth rate was defined as the change in standard length from the beginning to the end of the experiment. Because guppies reproduce every 22–25 days, fecundity was estimated by counting the number of offspring in each dissected female after the end of the experiment. Offspring size was calculated as the dry mass of all developing embryos, which was converted to a size measurement based on known length-mass regressions of guppy embryos. Female size at maturity was estimated as the smallest size of females that became pregnant during the experiment. Reproductive allotment, an important life history trait that was not used in the IPM, was calculated as the proportion of body mass dedicated to embryos.

A generalized linear mixed model framework was used to obtain parameter estimates for each demographic rate. Spatial block, light, phenotype and the interaction between light and phenotype were entered as fixed effects. Standard length at the beginning of the experiment and all interactions between length and the treatment variables were entered as fixed covariates. When estimable, mesocosm number was entered as a random effect on the intercept to account for having multiple measures for each experimental unit (mesocosm). Somatic growth and offspring size were modeled with normally distributed errors. Probability of reproduction was modeled as a binomial probability (0 or 1) with a logit link function. Fecundity was modeled as a Poisson distribution. Fecundity and offspring size were natural log transformed. Embryo stage of development (0 to 50) was included as a covariate in the analysis of offspring size and reproductive allotment.

To determine the most parsimonious models the Akaike information criterion (AICc) was for used for models of somatic growth rates and offspring size, while quasi AICc (QAICc) was used for fecundity and probability of reproduction. In cases where there was no best model, parameter estimates of the models that explained a minimum of 95% of the cumulative relative likelihood among models were averaged (Burnham and Anderson 1998). Maximum likelihood estimators were used for the model selection procedures, but restricted maximum likelihood procedures were used to obtain the final model parameters for all models. Results of the model selection procedure were reported in the Supplementary material Appendix 2 Table A1–A4.

The IPM was parameterized using model averaged parameters and the averaged standard errors, which reflected both the uncertainty of each model and of the model selection process (Supplementary material Appendix 1 Table A5). In cases where there was a significant interaction between a predictor variable and body size, parameter estimates were calculated at three sizes: 12, 18 and 24 mm standard length. The sizes were chosen to reflect different life stages of the fish: 12 mm is the size of older immature fish, 18 mm is approximately the size that females reproduce for the first time and 24 mm is the size of older fish that are reproducing for the second or more times. These values did not represent categories, rather they were point estimates at the values of the size covariate to show effects at different values of the covariates.

The IPM was used obtain population growth estimates (λ), stable size distributions, and reproductive values. Stable size distributions and reproductive values were used to calculate sensitivities of λ, but were not discussed further in the manuscript (Supplementary material Appendix 2 Fig. A2–A3). A life table response experiment (LTRE) framework (Caswell 1989) was used to decompose the effect of each treatment on λ in order to understand the relative effects of each size-specific demographic parameter (Supplementary material Appendix 2 Fig. A4) (Bassar et al. 2013).

Ecosystem function

Ecosystem function response metrics were broadly divided into ecosystem structure metrics (e.g. algal and invertebrate biomass) or ecosystem process metrics (e.g. nutrient fluxes, guppy-mediated nutrient recycling, ecosystem metabolism, and leaf litter decomposition). Unless noted, general linear models (GLM) were used to assess the effects of light, phenotype and their interaction on ecosystem function. The models included block, light, phenotype and an interaction between light and phenotype as fixed effects. The block effect was removed from the analysis when not significant ($p > 0.05$).

Algal standing stocks, accrual rates and diversity

On the first day of the experiment, 10 (5 × 5 cm) unglazed ceramic tiles (previously ashed for 2 h at 500°C) were randomly placed in each mesocosm. Two randomly chosen tiles were removed each week to measure algal stocks and diversity. Algal standing stocks (mg chl m^{-2}) were measured from a 5 ml subsample of the algal slurry using fluorescence. The changes in algal biomass through the experiment were analyzed using a linear mixed model approach that is similar to repeated measures ANOVA, but was more powerful because it modeled error terms more accurately (Supplementary material Appendix 1). On the last day of the experiment algae (from a 1 ml slurry subsample preserved in formalin) were then identified to the level of species (or morphospecies), and diversity metrics (species richness, evenness, Shannon–Weiner index) were computed as previously described (Bassar et al. 2010).

Leaf litter decomposition

We assessed how light and phenotype affected the ability of stream ecosystems to process external (allochthonous) subsidies using leaf pack assays. On the first day of the experiment, 10 bagless (i.e. not covered with mesh) leaf packs were randomly placed in each mesocosm. The leaf packs contained ~ 4 g of dried fresh black stick leaves *Pachystachys coccinea* collected from trees in the riparian zone of the Arima River. Two packs, chosen at random were subsampled on five different days during the course of the experiment. They were gently rinsed to remove any settled organic matter or invertebrates, then dried and weighed. Dried masses of the two leaf packs were averaged and corrected for handling loss (Bassar et al. 2010). Leaf litter decomposition (*k*, percent of leaf mass decayed day^{-1}) was analyzed using a non-linear model, and the effects of light and phenotype were tested by constructing contrast matrices (Supplementary material Appendix 1).

Invertebrate standing stocks

Invertebrates were collected immediately after guppies were removed on the final day of the experiment. The entire area of mesocosm benthos was agitated thoroughly, and suspended material was collected using a kick net (63 μm mesh) and then preserved. Animals were identified to genus wherever possible (or otherwise, family), and then measured. Biomass was computed using length-mass regressions (Bassar et al. 2010, Heatherly 2012). Invertebrates were analyzed (using a GLM) either as total biomass (mg DM m^2), or as the biomass of two size fractions: small (< 1 mm) or large (> 1 mm). In addition to these whole assemblage analyses, chironomid biomass (either total or size fractionated) was analyzed separately because chironomids are prevalent in guppy diets (Zandona et al. 2011). Details of invertebrate community composition are in Supplementary material Appendix 3.

Ecosystem metabolism

Metabolism, defined as the rate of O_2 production and consumption in each mesocosm, was measured on day 23 of the experiment using the two station method (Hauer and Lamberti 2006). Dissolved O_2 concentration (mg O_2 l^{-1}), water temperature (°C), and barometric pressure (mm Hg) were measured once an hour (for ~ 20 h) using an optical oxygen probe. The measurements were conducted from the downstream end of each mesocosm and from the head-tank inflow beginning one hour after sunrise and continuing hourly until midnight. Gross primary production (GPP) was calculated as the rate of day-time O_2 production, while community respiration (CR-24) was calculated as the daily rate of O_2 consumed per area (Bott 2007). The measurements were corrected for physical evasion of dissolved gasses following Bassar et al. (2010). GPP was expressed either by area (Areal GPP, mg O_2 m^{-2}) or as biomass-specific GPP (mg O_2 mg chl^{-1}). Net daily metabolism (NDM) was calculated as the difference between Areal GPP and CR-24. The responses of these metrics to phenotype and light treatments were analyzed using a GLM on log-transformed data (or raw data for CR-24).

Nutrient fluxes

Nutrient fluxes were defined as the rate of nutrient (nitrogen (N) or phosphorus (P)) movement through the mesocosms, either through uptake by the mesocosm benthos, or by export from the mesocosm. On day 27 of the experiment water samples were collected from the inflow and outflow of each mesocosm, and then were filtered (25 mm, pre-combusted at 450°C Whatman GFF filter) and refrigerated until analysis (within 24 h). Ammonium nitrogen and soluble reactive phosphorus were analyzed using standard methods (Holmes et al. 1999, Parsons et al. 1984, Taylor et al. 2007). Fluxes (μg N or μg P h^{-1} m^{-2}) were calculated by multiplying the differences between inflow and outflow nutrient concentrations by the total water volume in the mesocosms, and then dividing the outcome by the product of residence time and benthic surface area of each mesocosm.

Guppy-mediated nutrient recycling

Nutrient recycling was defined as the rate at which guppies excrete dissolved inorganic nutrients (N or P). On day 27 of the experiment excretion rates (ammonium μg N $fish^{-1}$ h^{-1} and soluble reactive phosphorous μg P $fish^{-1}$ h^{-1}) were measured for three guppies spanning a range of representative sizes from each of mesocosm, as previously described (Bassar et al. 2010). Excretion rate was analyzed as a linear mixed model with spatial block, phenotype, light treatment and the interaction between phenotype and light as categorical fixed effects, and natural log-transformed body mass as a covariate. Mesocosm number was entered as a random effect on the intercept to account for multiple fish being measured from each mesocosm (Supplementary material Appendix 1). Males and females (the female category included immature fish) were analyzed separately because previous experiments have shown that they have different patterns of nutrient recycling (Bassar et al. 2010). Furthermore, female guppies continue to grow throughout their lives while males cease growing at maturation; juvenile guppies were grouped with females because they also are growing and allocate resources similarly to females (Magurran 2005). These models were then used to estimate nutrient excretion rates for all individuals in the populations based on their size as outlined in the IPM section, and the total contribution of guppies to nutrient recycling was estimated as the sum of these individual rates in each of the mesocosms.

The relative contributions of light and phenotypes to the response variables

The relative effects of light and phenotype on each of the response variables were compared using a newly developed method (Ellner et al. 2011). This method calculated the relative contribution of phenotypic and ecological processes to the observed variable as the average of the observed effect of each treatment variable across the other, using the following equations:

$$\text{contribution of light} = 1/2\,[(X_{HLHP} - X_{HLLP}) + (X_{LLHP} - X_{LLLP})]$$

$$\text{contribution of phenotype} = 1/2[(X_{HLHP} - X_{LLHP}) + (X_{HLLP} - X_{LLLP})]$$

Where X was the marginal mean, HP and LP were high and low predation phenotypes, and HL and LL were high and low light, respectively. The relative contributions of light and phenotype for each response variable were calculated as the contribution of each divided by the sum of their contributions. Relative contributions were only estimated for response variables where light and/or phenotype were significant. In cases where size was included as a covariate, the relative contributions were calculated based on marginal means computed for an average body size (18 mm guppy). Marginal means of all response variables are listed in Supplementary material Appendix 4.

Results

Light levels

The light treatment resulted in a four-fold, significant difference in light levels between high and low light treatments (~68×10^6 and ~16×10^6 lumen ft^{-1} day^{-1}, respectively; $p < 0.001$, $F_{1,15} = 38.7$). The light levels in the high light treatment were similar to average light levels observed in the Aripo HP site (~ 82×10^6 lumen ft^{-1} day^{-1}), but levels in the light treatment were lower than observed in the Aripo LP site (~ 35×10^6 lumen ft^{-1} day^{-1}). Despite differences in light, water temperature difference between the high and low light mesocosms were very small at ~ 0.2°C.

Guppy life history traits and absolute fitness

Light significantly increased the somatic growth rates of both LP and HP guppies (Table 1, Supplementary material Appendix 2 Fig. A1). Neither the effect of phenotype nor the interaction between phenotype and light were significant (Table 1, Supplementary material Appendix 2 Fig. A1). High light also increased guppy fecundity (Table 1, Supplementary material Appendix 2 Fig. A1), and HP guppies were significantly more fecund than LP guppies (Table 1, Supplementary material Appendix 2 Fig. A1). The interaction of light and phenotype was not significant (Table 1). Offspring of LP guppies were significantly larger than HP guppies (Table 1, Supplementary material Appendix 2 Fig. A1). Neither the effect of light nor the interaction between light and phenotype were significant (Table 1), although there was a trend towards smaller offspring sizes under high light (Supplementary material Appendix 2 Fig. A1). None of the treatment effects significantly influenced the probability of a reproduction (Table 1), despite observed differences in the means between phenotype treatments, especially at smaller sizes (Supplementary material Appendix 2 Fig. A1). Neither light nor phenotype had a significant effect on reproductive allotment ($p > 0.05$ in all effects, Supplementary material Appendix 1 Table A6).

Light significantly increased the absolute fitness of both phenotypes as evident from population growth rates (Table 2, Fig. 1). However, HP guppies had significantly higher fitness than LP guppies across both light treatments, and the interaction between phenotype and light was not significant (Table 2, Fig. 1). Fitness estimates were driven primarily by differences in the somatic growth rates of small guppies (12 mm), which were significantly elevated in high light (Supplementary material Appendix 2 Fig. A4), and by fecundity, which increased with light, and which was higher in HP than in LP guppies (Supplementary material Appendix 2 Fig. A4). Total guppy biomass (mg wet weight m^{-2}) was significantly higher under high light compared to low light ($p < 0.001$, $F_{1,12} = 50.29$, Table 3), but neither phenotype ($p = 0.931$), nor the interaction between light and phenotype were significant ($p = 0.511$).

Table 1. Lower (0.025) and upper (0.975) confidence intervals of experimental treatment effects on guppy life history traits at small (12 mm), medium (18 mm) and large (24 mm) sizes. Values that do not overlap zero are considered significant and are represented in bold. Means are reported in the Supplementary material Appendix 2 Table A1 (somatic growth), Table A2 (fecundity), Table A3 (probability of reproduction) and Table A4 (offspring size). Trends are reported in Fig. A1.

Effect	Somatic growth	Fecundity	Probability of reproduction	Offspring size
(a) 12 mm				
Phenotype	(−2.756, 0.461)	**(0.003, 0.023)**	(−0.004, 0.014)	**(−0.926, −0.552)**
Light	**(1.247, 4.178)**	**(0.001, 0.036)**	(−0.002, 0.021)	(−0.387, 0.004)
Interaction	(−0.4, 0.888)	(−0.006, 0.005)	(−0.007, 0.007)	(−0.246, 0.13)
(b) 18 mm				
Phenotype	(−0.525, 0.188)	**(1.126, 2.605)**	(−0.005, 0.112)	**(−0.926, −0.552)**
Light	**(1.609, 2.311)**	**(1.65, 3.116)**	(−0.015, 0.123)	(−0.387, 0.004)
Interaction	(−0.104, 0.604)	(−0.781, 0.698)	(−0.006, 0.091)	(−0.246, 0.13)
(c) 24 mm				
Phenotype	(−0.532, 0.941)	**(2.246, 5.463)**	(−0.001, 0.007)	**(−0.926, −0.552)**
Light	**(0.984, 2.367)**	**(3.272, 6.513)**	(−0.002, 0.007)	(−0.387, 0.004)
Interaction	(−0.162, 0.667)	(−1.589, 1.445)	(−0.001, 0.005)	(−0.246, 0.13)

Table 2. Median and confidence intervals of the effects of phenotype, light and their interaction on fitness, measured as population growth rate (λ). Effects in bold are significant at the 0.05 level, two-tailed (i.e. confidence intervals do not overlap with zero).

	Quantile		
Effect	0.025	Median	0.975
Phenotype	0.058	0.191	0.319
Light	0.472	0.606	0.738
Interaction	−0.173	−0.060	0.057

Algal standing stocks, accrual rates, and diversity

Light had a significant positive effect on algal standing stocks (Light: $p < 0.001$, Table 3, Fig. 2), which were also marginally higher in HP compared to LP treatments (Phenotype: $p = 0.049$, Table 3). The effect of light and phenotype on algal standing stocks both changed through time (Day × Light: $p < 0.01$, Day × Phenotype: $p = 0.049$, Table 3). Phenotypic differences were more apparent in weeks 2 and 3 of the experiment than in week 4 (Table 3, Fig. 2). The interaction between light and phenotype was not significant (Day × Phenotype × Light: $p = 0.266$).

The algal assemblage was composed primarily of diatoms (~70% of the community), green algae and cyanobacteria (combined at~15% of the community). Green algae and cyanobacteria were grouped as a single category for the analysis because they showed similar responses to the experimental treatments. Under high light conditions the proportion of diatoms declined from ~80% to ~60% of the total algal biovolume ($p = 0.02$, Table 3) and the proportion of green algae and cyanobacteria increased from ~10% to ~20% of the total algal biovolume ($p = 0.02$, Table 3). Guppy phenotype did not have a significant effect on the composition of algae, but differences between light treatments were slightly smaller in LP guppies compared to HP guppies (Phenotype × Light: $p = 0.051$)(Table 3).

Invertebrate standing stocks

Dipterans, especially chironomids, dominated the invertebrate community (~80% of the total biomass), followed by odonate larva (Supplementary material Appendix 2).

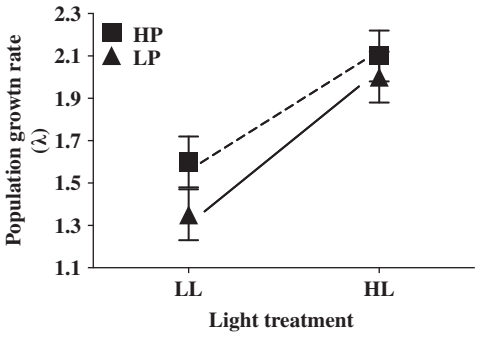

Figure 1. The effect of light and guppy phenotype on guppy absolute fitness, measured as population growth rate (λ). HP refers to high predation guppy phenotype, and LP refers to low predation guppy phenotype. HL is the high light treatment, and LL is the low light treatment.

Under high light conditions total invertebrate biomass and total chironomid biomass both increased (p for both analyses < 0.001, Table 3). Phenotype did not have a significant effect on total invertebrate or chironomid biomass ($p = 0.200$, Table 3). However, some differences were evident between phenotype treatments when the data were divided by size. The biomass of the large (> 1 mm) total invertebrates and large chironomids (> 1 mm) was higher in HP than in LP mesocosms ($p = 0.02$ and 0.038, respectively, Table 3, Fig. 3a). In contrast, phenotype did not affect the biomass of the total smaller invertebrates (< 1 mm) ($p > 0.05$, Fig. 3b) or of the small chironomids (< 1 mm, $p > 0.05$,data not shown). The interaction between light and phenotype was not significant for any of these variables (Table 3).

Ecosystem metabolism

Light enhanced Areal GPP ($p = 0.045$), which was also higher in HP compared to LP mesocosms ($p = 0.040$, Table 3, Fig. 3c). The interaction between light and phenotype was not significant ($p = 0.385$, Table 3). Low light conditions enhanced biomass GPP relative to high light conditions ($p = 0.009$, Table 3, Fig. 3d). The effects of phenotype on biomass GPP were not significant ($p = 0.923$). Community respiration (CR-24) was higher in HP compared to LP mesocosms ($p = 0.037$, Table 3, Fig. 3e), but was not affected by light ($p = 0.143$, Table 3). Interactions between light and phenotype were not significant ($p = 0.220$). Net daily metabolism (NDM) was enhanced by light ($p = 0.031$, Table 3), and was higher in HP compared to LP mesocosms ($p = 0.049$, Table 3). The interaction of light and phenotype was not significant ($p = 0.330$).

Nutrient fluxes

Light did not have a significant effect on N flux ($p = 0.567$, Table 3), but N flux was significantly higher in HP compared to LP mesocosms ($p = 0.020$, Table 3, Fig. 3f). The pattern indicated that HP mesocosms had a stronger tendency towards N export, whereas LP mesocosms had a stronger tendency towards N uptake (i.e it had higher N demand). In contrast, P fluxes were marginally lower in high compared to low light ($p = 0.057$, Table 3, Fig. 3f), and were not affected by phenotype ($p = 0.862$, Table 2, Fig. 3g). The negative sign on P fluxes in high light indicated that there was more mesocosm demand for P under high light compared to low light. There were no significant interactions between phenotype and light in either N flux ($p = 0.279$) or P flux ($p = 0.785$, Table 3).

Leaf litter decomposition

Leaf litter decomposition was faster in HP than in LP treatments ($p = 0.04$, Fig. 3h). Light, and the interaction between light and phenotype were not significant ($p = 0.752$ and $p = 0.651$, respectively).

Guppy-mediated nutrient recycling

Both light and phenotype had significant effects on nutrient excretion, but these effects varied across guppy body sizes

Table 3. The effect of light and phenotype on ecosystem function. Values for all tests except leaf litter decomposion are F ratios with degrees of freedom as subscripts. For leaf litter decomposition the values are t values with degrees of freedom as subscripts. The number of stars indicates significance: $ is $p < 0.10$, * is $p < 0.05$, ** is $p < 0.01$, and *** is $p < 0.001$.

Variable	Light	Phenotype	Light × Phenotype
Guppy biomass	$50.29_{1,12}$***	$0.01_{1,12}$	$0.485_{1,12}$
Algal standing stocks[a]	$118_{1,9}$***	$5.2_{1,9}$*	$0.7_{1,9}$
% diatoms	$6.7_{1,12}$*	$1.5_{1,12}$	$4.6_{1,12}$$
% green algae and cyanobacteria	$6.8_{1,12}$*	$1.5_{1,12}$	$4.5_{1,12}$$
Total invertebrate biomass	$45.1_{1,12}$***	$2.0_{1,12}$	$1.3_{1,12}$
Total chironomid biomass	$38.0_{1,12}$***	$2.0_{1,12}$	$1.2_{1,12}$
Small invertebrate (<1 mm) biomass	$61.8_{1,12}$**	$0.2_{1,12}$	$2.0_{1,12}$
Small chironomid (<1 mm) biomass	$56.3_{1,12}$**	$0.1_{1,12}$	$2.4_{1,12}$
Large invertebrate (>1 mm) biomass	$23.7_{1,12}$**	$7.0_{1,12}$*	$0.2_{1,12}$
Large chironomid (>1 mm) biomass	$7.9_{1,12}$*	$6.9_{1,12}$*	$0.6_{1,12}$
Areal GPP	$4.8_{1,12}$*	$5.3_{1,12}$*	$0.2_{1,12}$
Areal CR_{24}	$2.4_{1,12}$	$5.5_{1,12}$*	$1.6_{1,12}$
Biomass GPP	$4.6_{1,12}$**	$0.0_{1,12}$	$0.2_{1,12}$
NDM	$6.2_{1,12}$*	$4.8_{1,12}$*	$1.1_{1,12}$
N flux	$0.3_{1,12}$	$7.3_{1,12}$*	$1.3_{1,12}$
P flux[b]	$8.8_{1,9}$$	$0.1_{1,9}$	$0.1_{1,9}$
Leaf litter decomposition	$-0.3_{1,61}$	$-2.08_{,61}$*	$0.4_{1,61}$
Total N recycling	$139_{1,12}$***	$69.9_{1,12}$***	$16.8_{1,12}$**
Total P recycling	$45.8_{1,12}$**	$0.2_{1,12}$	$0.6_{1,12}$

[a]This analysis also had a Block effect (F ratio = 4.73,9**), a Day effect ($34.2_{3,25}$***), a Day × Block effect ($4.1_{3,25}$**), a Day × Light effect ($8.2_{3,25}$**), a Day × Phenotype effect ($3_{3,25}$*), and a Day × Phenotype × Light effect ($1.4_{3,25}$) b this analysis also had a significant block effect ($4.7_{3,9}$*)

and between sexes. Large female guppies (>24 mm) excreted N at higher rates than small female guppies (<12 mm) ($p < 0.001$, $F_{1,12} = 58.23$, Fig. 4, Supplementary material Appendix 2 Table A7). The effects of phenotype on female guppy N excretion became more pronounced with increasing body size (Phenotype × Size: $p = 0.057$, $F_{1,11} = 4.53$, Fig. 4a, Supplementary material Appendix 2 Table A7). For larger (>24 mm) guppies HP females excreted more N per fish than LP guppies ($p = 0.027$, $F_{1,12} = 6.38$, Fig. 4, Supplementary material Appendix 2 Table A7), and more at high light compared to low light ($p = 0.006$, $F_{1,12} = 11.29$, Fig. 4a, Supplementary material Appendix 2 Table A7). Large female guppies also excreted P at higher rates than smaller guppies ($p = 0.002$, $F_{1,12} = 16.44$, Fig. 4b, Supplementary material Appendix 2 Table A7), but P excretion was not significantly affected by any other variables (Supplementary material Appendix 2 Table A7). None of the treatments significantly affected N or P excretion in males (Supplementary material Appendix 2 Table A7).

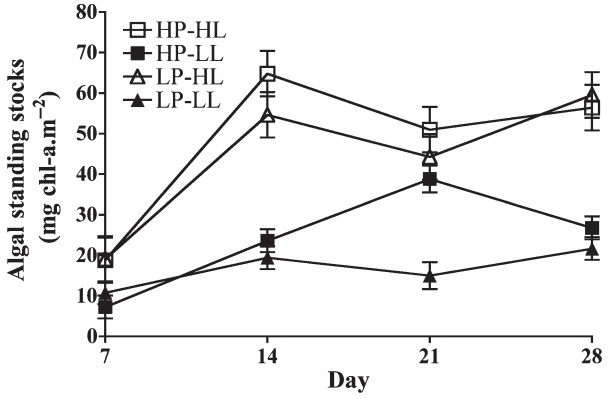

Figure 2. The effects of light and phenotype on algal standing stocks over the duration of the experiment. High predation (HP) phenotypes are in squares and low predation (LP) phenotypes are in triangles. High light (HL) treatments are in white symbols, and low light (LL) treatments are in black symbols. Values are least square (i.e. marginal mean)(standard error).

Both light and phenotype had a significant effect on the total contribution of guppies to N recycling (i.e. total excreted N and P from the entire guppy population in each mesocosm). In general light availability increased total N excretion ($p < 0.001$, Table 3, Fig. 4c), and HP populations excreted more N per hour than LP populations ($p < 0.001$, Table 3). There was a significant interaction between light and phenotype in total N excretion suggesting that the effect of light on total N excretion was stronger for HP guppies than for LP guppies (Phenotype × Light: $p = 0.002$, Table 3). Light significantly enhanced the total contribution of guppies to P recycling ($p < 0.001$, Table 3, Fig. 4d), but neither phenotype ($p = 0.650$, Table 3), nor the interaction between light and phenotype were significant ($p = 0.445$, Table 3).

The relative contributions of light and phenotype to response variables

The responses of guppy somatic growth, population growth (fitness), fecundity, and final biomass to increased light availability were ~2× larger than the phenotypic differences of these traits (Fig. 5). However, phenotypic differences in offspring size were larger than the effect of the light treatment. The effect of light was on average 4× the effect of phenotype on ecosystem structural metrics, but the impact of light and phenotype on the abundance of large invertebrates were nearly equal (Fig. 5). Likewise, the impact of light and phenotype on ecosystem processes were nearly equal, and in some cases (e.g.

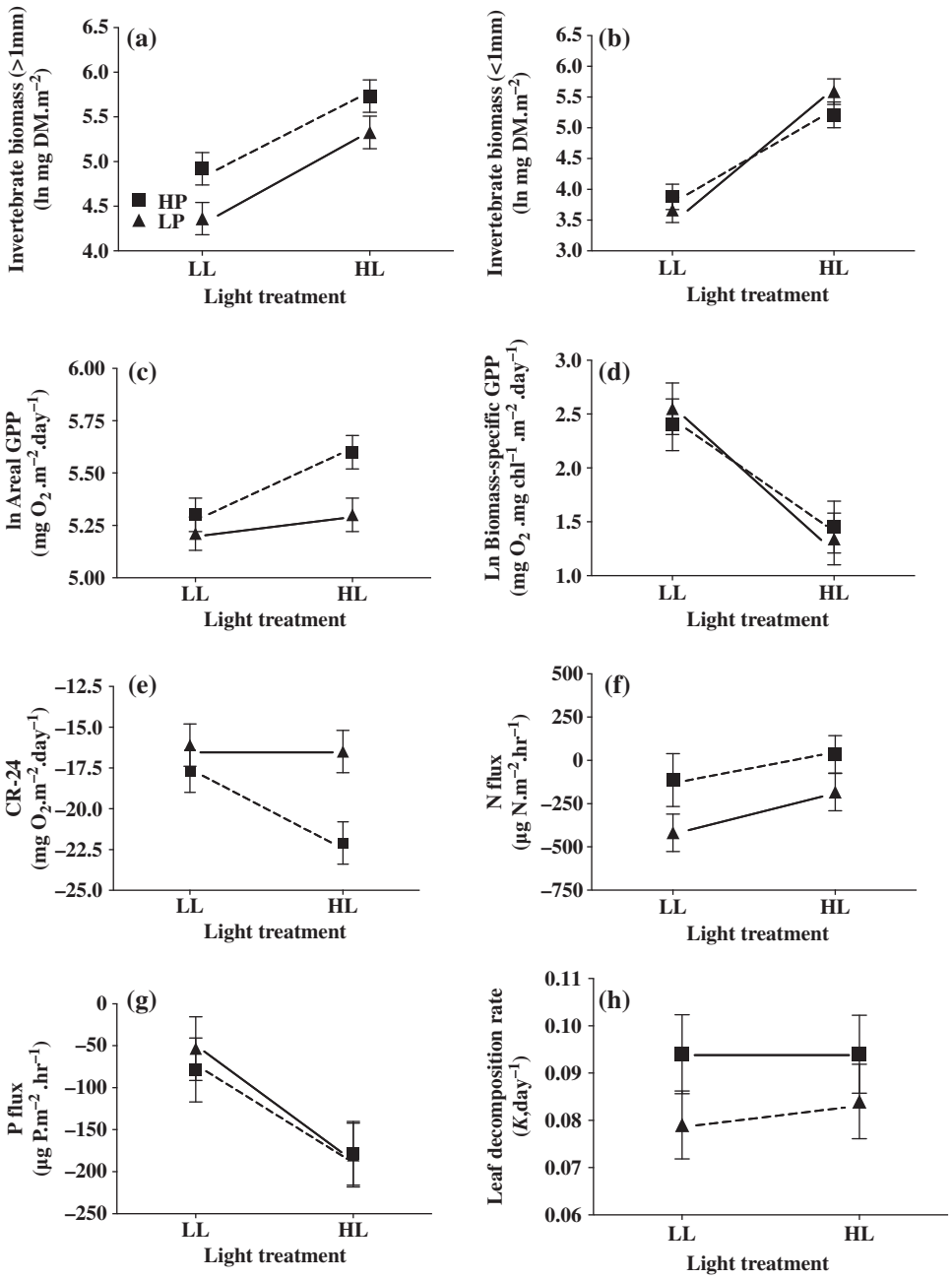

Figure 3. The effects of light and phenotype on ecosystem function. HP is the high predation phenotype, and LP is low predation phenotype. HL is high light, and LL is low light. Values are marginal means (standard error).

leaf decomposition), phenotype had a much stronger effect than light, explaining ~87% of the observed effect (Fig. 5).

Discussion

Our study shows that both light and guppy phenotype can significantly affect ecosystem function. Whereas light has a much stronger effect on ecosystem structure (e.g. standing stocks) than phenotype, light and phenotype are equally important in shaping many ecosystem processes such as nutrient recycling and primary production. These findings indicate that phenotypic differences within a species, which are typically ignored in ecosystem studies, can affect ecosystem processes as much as variability in abiotic conditions that limit numerous aspects of the ecosystem. The absence of interaction between light and phenotype for ecosystem function, life history traits, and absolute guppy fitness suggests that the effects of guppy phenotype on ecosystem function are not influenced by light availability, and that light does not modify the ecosystem effects of guppy life history phenotype by modifying guppy traits or fitness.

The difference in light between the high light and low light levels in the experiment is comparable to difference in light levels observed in HP and LP locations in the Aripo River. The effect of light on algal standing stocks,

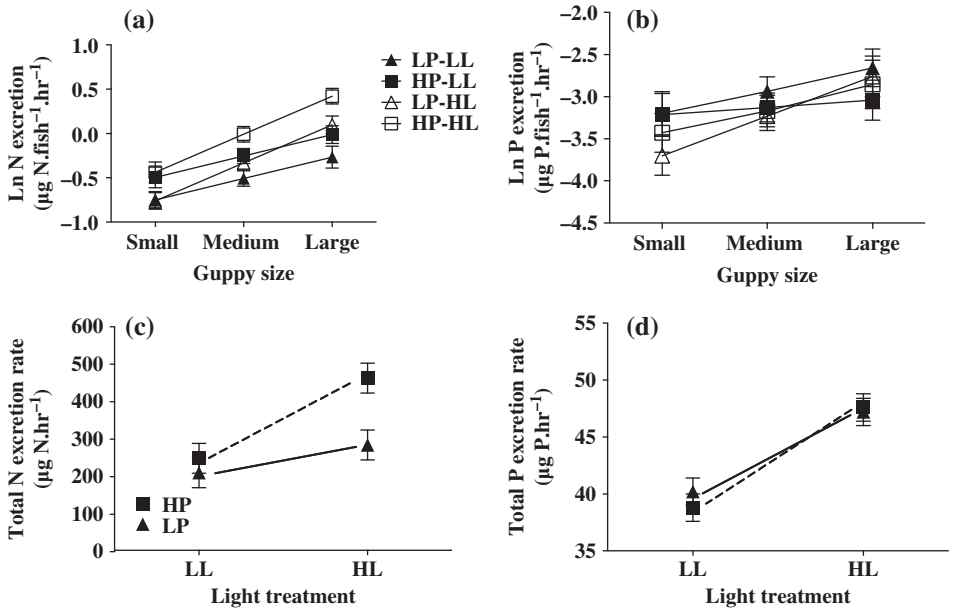

Figure 4. The effects of light and phenotype on individual nutrient recycling rates (a and b) and total (i.e. population level) nutrient recycling rates (c and d). Panel a represents ammonium N excretion rates by female guppies. Panel b represents soluble reactive P excretion rates by female guppies. Panel c represents total contribution of guppies in each treatment to N recycling. Panel d represents the total contribution of guppies in each treatment to P recycling. High predation (HP) phenotypes are in squares and low predation (LP) phenotypes are in triangles. High light (HL) treatments are in white symbols, and low light (LL) treatments are in black symbols. Values are least square means (plus standard error). Because of significant interactions between body size and the experimental treatments, least square means were estimates by centering the general linear models at three different size classes (small guppies < 12 mm, medium guppies (~18 mm), and large guppies (> 24 mm)).

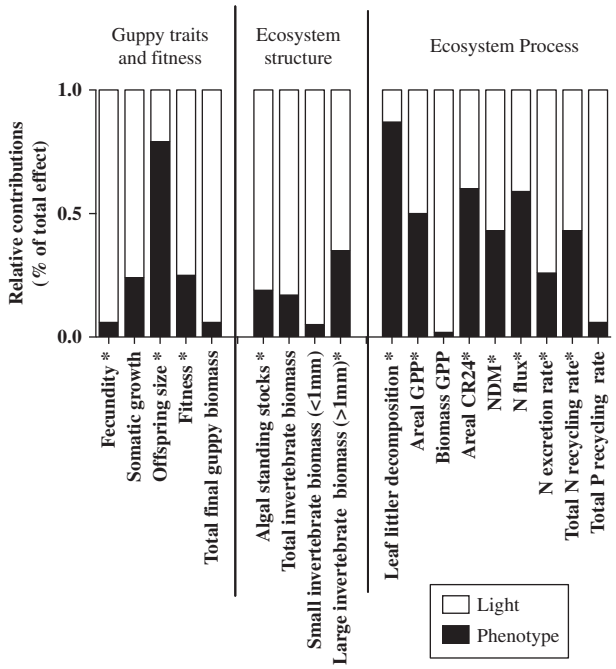

Figure 5. The relative contributions of light and guppy phenotype to observed differences in guppy traits, fitness and ecosystem function (structure and process metrics) as specified on the x-axis. Response variables are defined in the method section. Only response variables with a significant effect of either light or phenotype are shown. Stars indicate a significant phenotype effect. The relative contributions are calculated using marginal means, which were estimated at body size = 18 mm for N excretion and fecundity. The relative contribution was averaged across all four days of algal sampling for the algal standing stock metric.

algal composition, GPP, invertebrate biomass, consumer-mediated N recycling and P fluxes are largely consistent with previous studies (Grether et al. 2001, Kiffney et al. 2004, Moslemi et al. 2012). Likewise, the effect of guppy phenotype on algal standing stocks, GPP, and nutrient recycling is consistent with other studies, and with a scenario where LP guppies consume more algae and recycle less N than HP guppies (Bassar et al. 2010, Zandona et al. 2011). Our results for invertebrate biomass and leaf litter decomposition differ from some previous experiments, which showed a reduction of invertebrate biomass and leaf decomposition rates in HP mesocosms (Bassar et al. 2010). However, the effects of guppy phenotype on these variables are generally inconsistent, with some studies reporting no effects of phenotype on invertebrate or leaf litter (Palkovacs et al. 2009). Currently we do not understand why the effects of guppies on invertebrates and leaves differ between experiments, but one potential candidate is differences in invertebrate diversity within the artificial channels, which can be driven by differences in light shading methods, differences in the timing of the experiments (dry versus wet season), or by differences between the locations of invertebrate assemblages used to seed the experiments (example St. Patrick's creek (this experiment) versus Ramdeen stream (Palkovacs et al. 2009)).

Nonetheless we found that whereas both light and phenotype altered primary production rates, only phenotypes affected leaf litter decomposition. This suggests that whereas light acts primarily on autochthonous (internal or algal based) pathways, guppy phenotype acts on both autochthonous and allochthonous (external or leaf litter based) pathways. External subsidies are a significant source of energy for stream

communities, and characterizing how streams are connected to adjacent systems through subsidies is an important goal for stream ecologists (Allan and Castillo 2007). Phenotypic differences can potentially alter connections between stream systems and adjacent environments by changing the rates at which external subsidies (i.e. leaves) are processed.

Species effects on ecosystem function are thought to be context specific, meaning that their strength can be modulated by background environmental conditions or disturbance events (Kurle and Cardinale 2011). In contrast to this we find that the interactions of light and phenotype for all ecosystem response variables are either not statistically significant or relatively weak. Likewise, although light has a large effect on life history traits, there are no interactions between phenotype and light in life history traits and fitness. Guppy life history traits are affected by the availability of light, indicating that there is some plasticity in guppy phenotypes that allowed their traits to vary with environmental conditions (Table 1). However, one reason interactions between light and phenotype are largely absent is that life history traits, ecosystem-effect traits (e.g. nutrient recycling rates), and fitness of both LP and HP guppies show similar and equal responses to light variability (Fig. 2, 3).

The lack of interaction between phenotype and light when it comes to guppy fitness is particularly interesting because it clarifies the processes that cause the evolution of the LP phenotype. Life history traits characteristic of LP guppies evolve when HP guppies are transplanted from HP sites to upstream sites that are free from guppies and guppy predators (Reznick et al. 1997). The mechanism that causes the evolution of the LP phenotype is currently unknown (Reznick et al. 2012, Bassar et al. 2013). Early studied assumed that predators in HP sites were thought to feed primarily on large guppies, while *R. hartii* in LP sites was thought to feed primarily on juvenile guppies (Reznick et al. 1996a). A shift in size specific mortality from large guppies (in HP sites) to small guppies (in LP sites) would cause LP-like life history traits to evolve, but mark–recapture studies showed that size specific mortality did not differ between LP and HP sites (Reznick et al. 1996a). Since the LP phenotype predictably evolves when HP guppies are transplanted into previously guppy-free environments (Reznick et al. 1990,1997), and since they do so while also retaining ample genetic variation (Carvalho 1993), something in nature must tip the balance in favor of the LP phenotype. One candidate is per capita resource availability, which is lower in LP compared to HP populations. Not only is light availability, which limits guppy food items (algal and invertebrate standing stocks), lower in LP compared to HP environments, but guppy density is also typically higher in LP compared to HP communities (Reznick et al. 1996a, 2001). If LP phenotypes are fitter than HP phenotypes under reduced resources, then such conditions might cause the LP phenotype to evolve when HP guppies are transplanted into guppy free, upstream locations.

Two recent findings generally support an interaction between resource availability and fitness as a mechanism for the evolution of LP guppies: The trophic morphology and feeding behavior of LP guppies suggests that they are more efficient at acquiring resources than HP guppies (Palkovacs et al. 2011), and while the fitness of LP guppies is higher than HP guppies at high population densities. This fitness advantage disappears at low population densities (Reznick et al. 2012, Bassar et al. 2013). Had we observed a significant interaction between light (which controls resources) and phenotype in guppy fitness we would have provided support for the hypothesis that LP guppies were fitter under low light conditions compared to HP guppies. Instead we found that HP guppies retain their fitness advantage at varying levels of resource supply (controlled by light) however, guppy density in this experiment was low, comparable to guppy density in HP environments, and likely similar to the density guppies in the early stages of introduction from HP to guppy-free, LP sites. Our data show that lower per capita resources produced by lower light conditions might not tip the balance in favour of LP guppies in the early stages of guppy introduction when guppy densities are low. However it is possible that light availability becomes more important as densities increase. A better understanding of the mechanisms driving guppy evolution will require mesocosm experiments to compare the effects of light availability on the fitness of HP and LP guppies under high and low guppy density conditions.

Our study demonstrates that intraspecific differences in life history phenotype, which are largely ignored in ecosystem studies, can affect key ecosystem processes as much as meaningful changes in abiotic variability, and that assessing how the ecological effects of phenotypes vary across environmental gradients can help us clarify evolutionary mechanisms. Our findings therefore motivate for a stronger integration between evolutionary biology and ecosystem science in experiments and field studies.

Acknowledgements – R. W. El-Sabaawi and R. D. Bassar contributed equally to this work. We thank J. Travis, K. MacNeil, J.-P. Zagarola, G. Ng, C. Tse, C. Morris, J. Heinen, T. N. Heatherly, T. Kohler, E. Palkovacs and E. Zandona for their help with experimental design and field collection, and for comments on early versions of this manuscript. We thank the Ramdeen family, the Ramlal family, Simla Research Station and The Asa Wright Centre for logistical assistance. This work was funded by Frontiers In Biological Research (FIBR) National Science Foundation grant (EF0623632). Animal use protocol number: l A-20110007 – Univ. of California, Riverside.

References

Allan, J. D. and Castillo, M. M. 2007. Stream ecology: structure and function of running waters. – Springer.

Arendt, J. D. and Reznick, D. N. 2005. Evolution of juvenile growth rates in female guppies (*Poecilia reticulata*): predator regime or resource level? – Proc. R. Soc B. 272: 333–337.

Bailey, J. K. et al. 2009. From genes to ecosystems: an emerging synthesis of eco-evolutionary dynamics. – New Phytol. 184: 746–749.

Bassar, R. D. et al. 2010. Local adaptation in Trinidadian guppies alters ecosystem processes. – Proc. Natl Acad. Sci. USA. 107: 3616–3621.

Bassar, R. D. et al. 2013. Experimental evidence for density-dependent regulation and selection on Trinidadian guppy life histories. – Am Nat. 181: 25–38.

Bott, T. L. 2007. Primary productivity and community respiration. – In: Hauer, F. R. and Lamberti, G. A. (eds), Methods in stream ecology. Elsevier, pp. 663–690.

Burnham, K. P. and Anderson, D. R. 1998. Model selection and multimodel inference: a practical information-theoretic approach. – Springer.
Carvalho, G. R. 1993. Evolutionary aspects of fish distribution: genetic variability and adaptation. – J. Fish Biol. 43: 53–73.
Caswell, H. 1989. The analysis of life table response experiments. I. Decomposition of treatment effects on population growth rate. – Ecol. Modell. 46: 221–237.
Easterling, M. R. et al. 2000. Size-specific sensitivity: applying a new structured population model. – Ecology 81: 694–708.
Ellner, S. P. et al. 2011. Does rapid evolution matter? Measuring the rate of contemporary evolution and its impacts on ecological dynamics. – Ecol. Lett. 14: 603–614.
Gosselin, M. et al. 1990. Light and nutrient limitaton of sea-ice microalgae (Hudson Bay, Canadian Arctic). – J. Phycol. 26: 220–232.
Grether, G. F. et al. 2001. Rain forest canopy cover, resource availability, and life history evolution in guppies. – Ecology 82: 1546–1559.
Harmon, L. J. et al. 2009. Evolutionary diversification in stickleback affects ecosystem functioning. – Nature 458: 1167–1170.
Hauer, F. R. and Lamberti, G. A. 2006. Methods in stream ecology. – Academic Press/Elsevier.
Heatherly, T. N. 2012. Flow regime, guppy introduction and light manipulation influence invertebrate assemblages in Trinidadian streams. – School of National Resources, Univ. of Nebraska.
Hill, W. R. et al. 1995. Light limitation in a stream ecosystem: responses by primary producers and consumers. – Ecology 76: 1297–1309.
Holmes, R. M. et al. 1999. A simple and precise method for measuring ammonium in marine and freshwater ecosystems. – Can. J. Fish Aquat. Sci. 56: 1801–1808.
Karlsson, J. et al. 2009. Light limitation of nutrient-poor lake ecosystems. – Nature 460: 506–509.
Kiffney, P. M. et al. 2004. Establishing light as a causal mechanism structuring stream communities in response to experimental manipulation of riparian buffer width. – J. N. Am. Benthol. Soc. 23: 542–555.
Kohler, T. J. et al. 2012. Flow, nutrients, and light availability influence Neotropical epilithon biomass and stoichiometry. – Freshwater Sci. 31: 1019–1034.
Kurle, C. M. and Cardinale, B. J. 2011. Ecological factors associated with the strength of trophic cascades in streams. – Oikos 120: 1897–1908.
Magurran, A. E. 2005. Evolutionary ecology: the Trinidadian guppy. – Oxford Univ. Press.
Moslemi, J. M. et al. 2012. Impacts of an invasive snail (*Tarebia granifera*) on nutrient cycling in tropical streams: the role of riparian deforestation in Trinidad, West Indies. – Plos ONE 7: e38806.
Palkovacs, E. P. et al. 2009. Experimental evaluation of evolution and coevolution as agents of ecosystem change in Trinidadian streams. – Phil. Trans. R. Soc. B 364: 1617–1628.
Palkovacs, E. P. et al. 2011. Eco-evolutionary trophic dynamics: loss of top predators drives trophic evolution and ecology of prey. – Plos ONE 6: e18879.
Parsons, T. R. et al. 1984. A manual of chemical and biological methods for seawater analysis. – Pergamon Press.
Post, D. M. and Palkovacs, E. P. 2009. Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. – Phil. Trans R. Soc. B 364: 1629–1640.
Reznick, D. N. 2013. A critical look at reciprocity in ecology and evolution: introduction to the symposium. – Am. Nat. 181: S1–S8.
Reznick, D. and Endler, J. A. 1982. The impact of predation on life-history evolution in Trinidadian guppies (*Poecilia reticulata*). – Evolution. 36: 160–177.
Reznick, D. N. and Bryga, H. A. 1996. Life-history evolution in guppies (*Poecilia reticulata*: Poeciliidae). 5. Genetic basis of parallelism in life histories. – Am. Nat. 147: 339–359.
Reznick, D. A. et al. 1990. Experimentally induced life history evolution in a natural population. – Nature 346: 357–359.
Reznick, D. N. et al. 1996a. Life-history evolution in guppies (*Poecilia reticulata*). 6. Differential mortality as a mechanism for natural selection. – Evolution 50: 1651–1660.
Reznick, D. N. et al. 1996b. Life-history evolution in guppies (*Poecilia reticulata*: Poeciliidae). 4. Parallelism in life-history phenotypes. – Am. Nat. 147: 319–338.
Reznick, D. N. et al. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). – Science. 275: 1934–1937.
Reznick, D. et al. 2001. Life-history evolution in guppies. VII. The comparative ecology of high- and low-predation environments. – Am. Nat. 157: 126–140.
Reznick, D. N. et al. 2012. Life history evolution in guppies VIII: the demographics of density regulation in guppies (*Poecilia reticulata*). – Ecology 66: 2903–2915.
Taylor, B. W. et al. 2007. Improving the fluorometric ammonium method: matrix effects, background fluorescence, and standard additions. – J. N. Am. Benthol. Soc. 26: 167–177.
Torres Dowdall, J. et al. 2012. Fine-scale local adaptation in life histories along a continuous environmental gradient in Trinidadian guppies. – Funct. Ecol. 26: 616–627.
Vannote, R. L. et al. 1980. River continuum concept. – Can. J. Fish Aquat. Sci. 37: 130–137.
Zandona, E. et al. 2011. Diet quality and prey selectivity correlate with life histories and predation regime in Trinidadian guppies. – Funct. Ecol. 25: 964–973.

Supplementary material (available online as Appendix oik.01769 at <www.oikosjournal.org/readers/appendix>). Appendix 1–2.