

Experimental Evidence of an Eco-evolutionary Feedback during Adaptive Divergence

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SUMMARY

Differences in how organisms modify their environment can evolve rapidly and might influence adaptive population divergence [1, 2]. In a common garden experiment in aquatic mesocosms, we found that adult stickleback from a recently diverged pair of lake and stream populations had contrasting effects on ecosystem metrics. These modifications were caused by both genetic and plastic differences between populations and were sometimes comparable in magnitude to those caused by the presence/absence of stickleback. Lake and stream fish differentially affected the biomass of zooplankton and phytoplankton, the concentration of phosphorus, and the abundance of several prey (e.g., copepods) and non-prey (e.g., cyanobacteria) species. The adult-mediated effects on mesocosm ecosystems influenced the survival and growth of a subsequent generation of juvenile stickleback reared in the same mesocosms. The prior presence of adults decreased the overall growth rate of juveniles, and the prior presence of stream adults lowered overall juvenile survival. Among the survivors, lake juveniles grew faster than co-occurring stream juveniles, except in mesocosm ecosystems previously modified by adult lake fish that were reared on plankton. Overall, our results provide evidence for reciprocal interactions between ecosystem dynamics and evolutionary change (i.e., eco-evolutionary feedbacks) in the early stages of adaptive population divergence.

RESULTS AND DISCUSSION

In the early stages of adaptive population divergence, ecologically differentiated populations (i.e., ecotypes) can evolve contrasting effects on community structure and ecosystem functions [2–6]. However, very little is known about the identity [7], plasticity [8], and evolutionary rates of the traits underlying the ecosystem effects of organisms [2]. If the contrasting ecosystem effects of organisms are sufficiently large and cause persistent environmental differences during adaptive divergence, then an

eco-evolutionary feedback may emerge where organism-mediated environmental modifications become an important agent of selection that influences fitness relationships between the diverging populations [9].

Eco-evolutionary feedbacks have a long history in ecology and evolution and have been formulated (and reformulated) in many different ways [10–14]. In very general terms, an eco-evolutionary feedback occurs when the ecosystem effects (biotic and abiotic) of a population of organisms reciprocally influences fitness variation in the population, selection pressures, and/or evolutionary responses [9, 15]. Feedback loops can emerge from the effects of individuals on population-, community-, and ecosystem-level processes [16, 17].

We tested for an eco-evolutionary feedback using a two-phase mesocosm experiment. In phase 1, we quantified differences in the modification of mesocosm ecosystems caused by two recently diverged (<150 years) and ecologically differentiated (i.e., lake and stream ecotypes) populations of stickleback [18] (Supplemental Experimental Procedures). In this population pair, both phenotypic plasticity and standing genetic variation are implicated in ecotype formation [19]. Prior to phase 1, we reared individuals of each ecotype to adulthood on a typical resource from their own native habitat and from the habitat of the other ecotype, allowing us to test how interactions between genetic background and phenotypic plasticity might affect mesocosm ecosystems. In phase 2, we replaced the adults in each mesocosm with a mixture of laboratory-reared juveniles from both ecotypes (reared in common garden) in order to test how modifications of mesocosm ecosystems affected the growth and survival of co-occurring juveniles of the same ecotypes.

In our experiment, we tested the following four predictions. We predicted that recently diverged lake and stream ecotypes of stickleback would have contrasting effects on mesocosm ecosystems (prediction 1) that were caused by a combination of both genetic background and plasticity (prediction 2) [3, 8, 19]. We also predicted that modification of mesocosm ecosystems by adults could persist long enough (e.g., via prey depletion or habitat modification) so as to influence the resource environment of a subsequent generation of juveniles (prediction 3). Finally, we predicted that the adult-mediated modification of mesocosm ecosystems could influence either (1) the survival of juvenile stickleback or (2) the differential growth and survival of juvenile ecotypes (prediction 4). Either of these outcomes could increase the likelihood of feedbacks between ecosystem modification and fitness variation during adaptive population divergence.

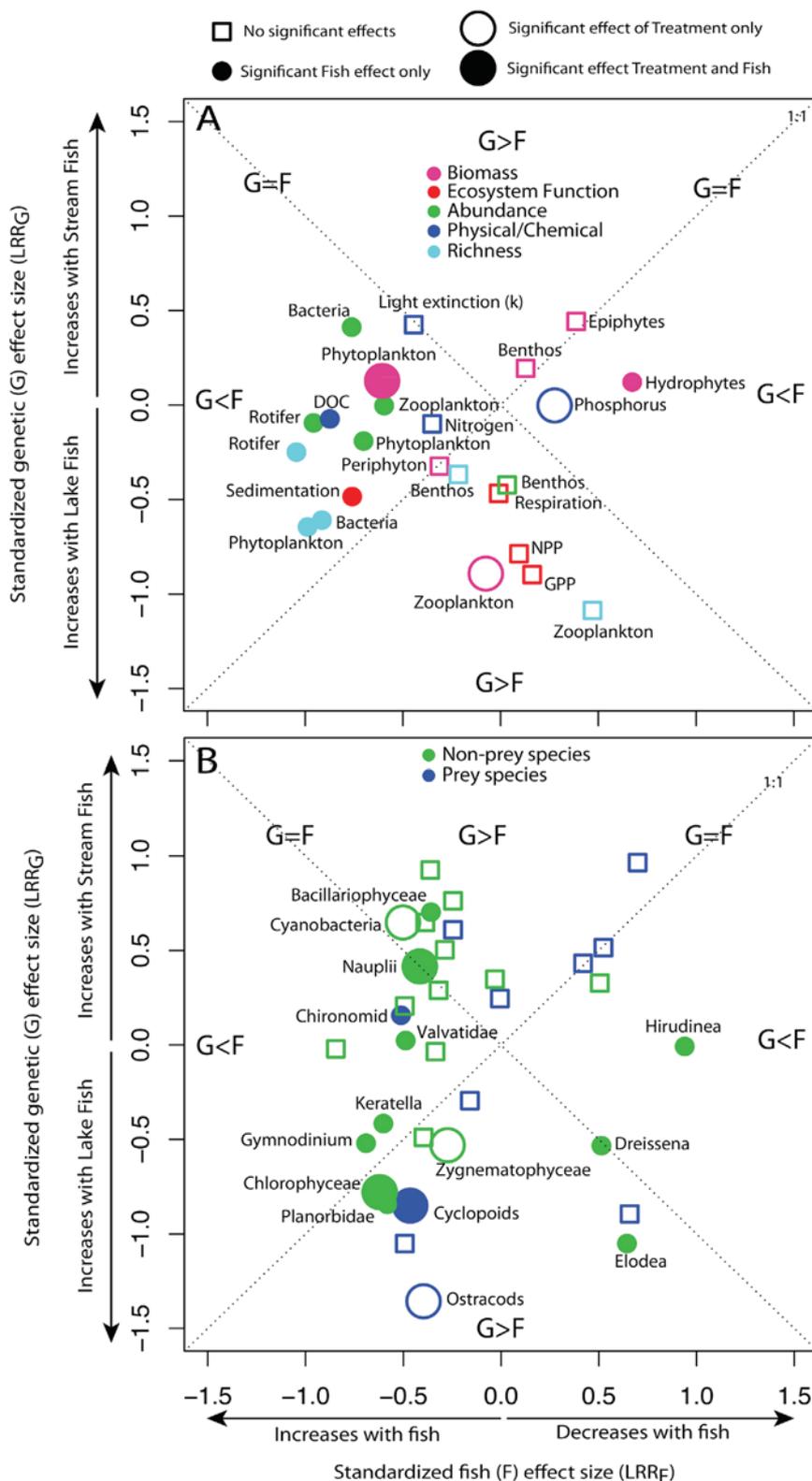


Figure 1. Ecosystem Effects of Stickleback
 Comparison of ecosystem effect contrasts between mesocosms with and without fish (LRR_F ; positive values indicate higher with fish) to those with either lake or stream stickleback (LRR_G ; positive values indicate higher with lake fish) for metrics associated with the structure and functioning (A) and species composition (B) of mesocosm ecosystems. Filled circles indicate a significant fish (F) effect, and large circles indicate a significant treatment (T) effect (i.e., at least one of G, E, or GxE effect is significant). Regions demarcated by the dotted 1:1 lines allow for the comparison of the relative effects sizes of ecology (i.e., fish presence/absence) and evolution (i.e., fish ecotype) on ecosystem metrics. See also Figure S1.

of five mesocosms, consisting of one mesocosm with no fish (NF treatment) and four mesocosms with factorial treatment combinations (LB, LP, SB, and SP) to represent lake (L) and stream (S) fish reared on either plankton (P) or benthic (B) food for 1 year (Supplemental Experimental Procedures). Although we used separate sexes in each block, we did not test for effects of sex because of unintended reproduction in two tanks. Phase 2 of our experiment (September 13 to November 23, 2011) began after we removed the adult fish and introduced 32 juveniles (16 L, 16 S) to each of 20 mesocosms, consisting of four replicate blocks of the same treatment combination from phase 1 (i.e., NF, LB, LP, SB, and SP). We analyzed variation in growth and survival of juveniles using linear mixed-effects models with tank nested within block. Each mesocosm received juveniles from multiple families (i.e., full and half siblings co-occurred within tanks), but we neither measured nor controlled for variation in family specific survival and growth (Supplemental Experimental Procedures).

During phase 1, we measured a wide range of ecosystem metrics (Table S1) and tested for the effects of fish presence/absence (F), as well as for the effects of genetic background of stickleback (G), rearing environment in the lab (E), and their interaction (GxE). We used log response ratios (LRRs) [20] to compare the magnitude of treatment (i.e., G, E, and GxE collectively) and fish

Experimental Design

Phase 1 of our experiment (April 22 to August 18, 2011) was a complete randomized block design with eight replicate blocks

effects across multiple ecosystem metrics (Supplemental Experimental Procedures). This approach allows us to compare the relative importance of recent phenotypic evolution and the

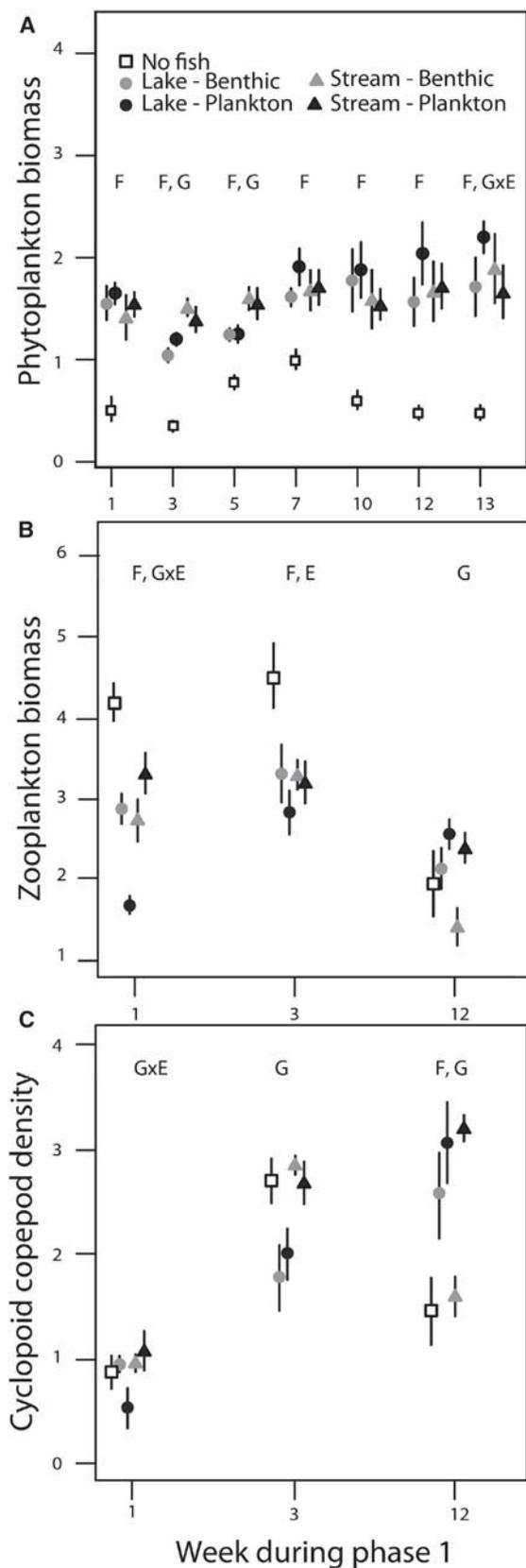


Figure 2. Temporal Dynamics of Ecosystem Effects

Temporal dynamics of selected ecosystem metrics (left y axis; all in log units) during phase 1. (A) Phytoplankton biomass (log chlorophyll a $\mu\text{g/l}$), (B) zooplankton biomass (log mg/l), and (C) cyclopoid copepod density (log N/l) are shown. Significant contrasts are labeled as in the main text, and all error bars indicate ± 1 SE. See also [Figure S2](#).

presence/absence of stickleback for explaining variation in community and ecosystem structure in mesocosms [14, 21, 22].

Effects on Mesocosm Ecosystems

At the end of phase 1, we measured 59 ecosystem metrics and found 24 significant fish effects and nine significant treatment effects (i.e., at least one of the G, E, or GxE effects was significant). The fish effects were widespread among our ecosystem metrics ([Figure 1](#), filled-in circles; [Table S1](#)) and had greater multivariate effect sizes (MVESs, measured as centroid distances from a non-metric multidimensional scaling analysis) than the treatment effects ($MVES_F = 0.83$ [SD = 0.61], $MVES_G = 0.21$ [0.21], $MVES_E = 0.25$ [0.22], $MVES_{GxE} = 0.14$ [0.23]; all paired t tests comparing fish and treatment effects had $p < 0.05$; [Table S2](#)). However, there were also several significant treatment effects ([Figure 1](#)), including those on zooplankton biomass (G), phytoplankton biomass (GxE), dissolved nutrients (GxE), and abundances of both zooplankton (cyclopoids, E; ostracods, G) and phytoplankton (*Cyanobacteria*, GxE; *Chlorophyceae*, G; *Zygnematophyceae*, E).

Treatment effects varied both in their magnitude and significance during phase 1 ([Figure 2](#); [Table S1](#)) and often occurred in the absence of significant fish effects (e.g., large open circles in [Figures 1](#) and [S2](#)). There was no correlation between the relative magnitudes of fish and treatment effects ([Figure S2](#)). For example, tanks with fish always had a smaller average size of zooplankton and lower abundance of certain species (e.g., *Daphnia*, Calanoid copepods, and *Bosmina*) compared to tanks without fish ([Figure S3](#)), but the significance of treatment effects varied both among and within zooplankton species over time ([Figure S3](#)). The frequency (albeit low), magnitude, and independent occurrence of significant treatment effects relative to fish effects ([Figures 1](#), [2](#), [S2](#), and [S3](#)) suggests that considering both the origin (e.g., genetics or plasticity) and amount (e.g., degree of trait divergence) of recent phenotypic divergence might help us explain variation in community structure and ecosystem conditions that is unaccounted for by fish presence/absence [14, 21, 22].

The independent occurrence of significant treatment and fish effects ([Figures S2](#) and [S3](#)) makes it difficult to disentangle the mechanisms underlying the effects of genetic and plastic differences between lake and stream populations on mesocosm ecosystems. For example, in the first five sampling weeks of phase 1, the G effects on phytoplankton biomass ([Figure 2A](#)) might have resulted from the treatment effects on zooplankton biomass and copepod density observed during the same period ([Figures 2B](#) and [2C](#)). However, this G effect was transient, and a new GxE effect on phytoplankton emerged at the end of phase 1 ([Figure 2A](#)), along with a significant G effect but insignificant fish effect on zooplankton biomass ([Figure 2B](#)). Variation in the occurrence of significant treatment and fish effects through time ([Figure 2](#)) could reflect weak, transient, or attenuating

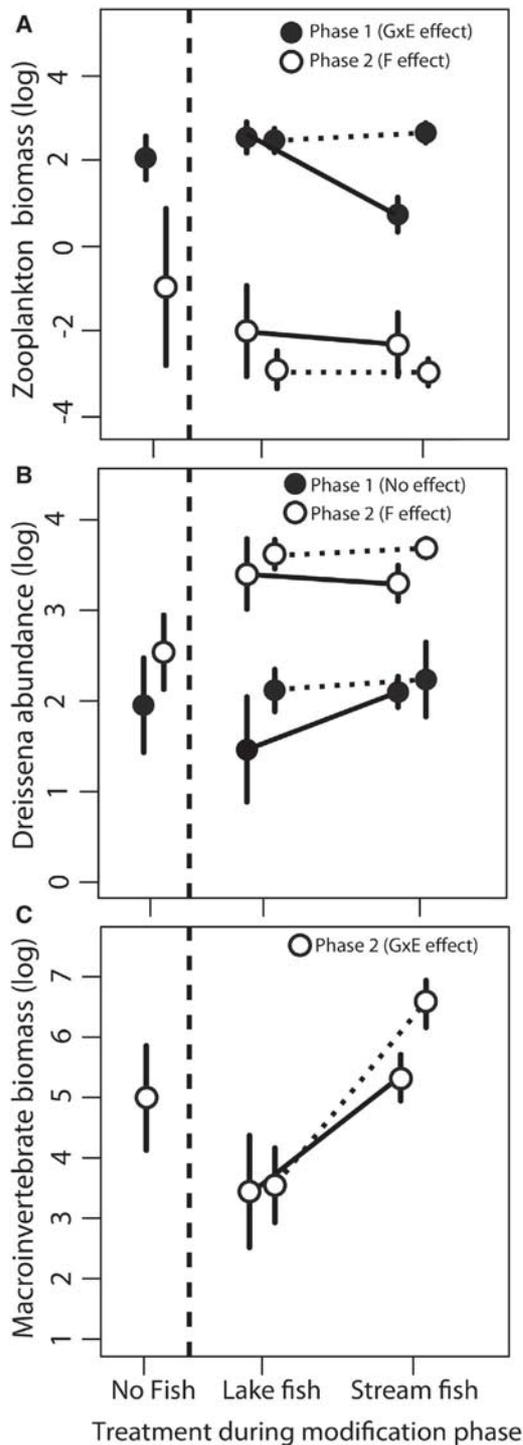


Figure 3. Effects of Adult Stickleback on the Environment of Juveniles
Biomass variation in relation to the treatments established during phase 1, only including data from the 20 mesocosms used during phase 2 (Supplemental Experimental Procedures). Treatments during phase 1 are mesocosms with either no fish (NF) or lake or stream fish. Lines connect treatments where fish were reared on either benthic chironomids (solid lines) or pelagic zooplankton (dotted lines). All error bars indicate ± 1 SE.

(A) Zooplankton biomass measured at the end each phase.

(B) Total abundance of *Dreissena* on the walls of each mesocosm at the end of each phase.

effects of top predators on lower trophic levels. Alternatively, it could reflect predators having a combination of direct and indirect effects on material cycling and biogeochemical processes in ecosystems through a wide variety of mechanisms [23], including both trophic and non-trophic interactions [24]. Regardless of the mechanisms driving ecosystem modifications, our results support our first two predictions: mesocosm ecosystems differed among treatments at the end of phase 1 due to a combination of genetic effects, rearing environment effects (i.e., plasticity), and their interaction (Figures 1 and S2).

To test our third prediction, we investigated whether the effects on mesocosm ecosystems of adults (phase 1; Figures 1 and 2) influenced three indicators of the resource environment experienced by juveniles in the next generation (phase 2; Figure 3), specifically, zooplankton communities, *Dreissena* abundance, and macroinvertebrates associated with macrophytes (Figure 3; Table S1).

First, at the end of phase 1, zooplankton biomass was lowest in tanks with stream fish reared on benthic food (GxE effect: $F_{1,10} = 12.53$, $p < 0.001$) but did not differ between tanks with and without fish (fish effect: $F_{1,16} = 0.40$, $p = 0.53$). In contrast, by the end of phase 2, there was a clear fish effect but no treatment effects on zooplankton biomass (Figure 3A; fish effect: $F_{1,16} = 5.62$, $p = 0.018$; treatment effects: all $p > 0.05$), suggesting a legacy effect of fish presence during phase 1 on resources available for juveniles in phase 2 (Figure 3A).

Second, we found that the fish effects on *Dreissena* differed between phases. In phase 1, we saw no difference in *Dreissena* abundance in mesocosms with or without fish (Figure 3B; fish effects, phase 1: $F_{1,16} = 0.40$, $p = 0.53$), but in phase 2, we observed more *Dreissena* in those mesocosms that previously had fish during phase 1 (phase 2: $F_{1,16} = 9.47$, $p = 0.002$). *Dreissena* were common in our mesocosms (Figure 3B; phase 1: mean = 7/tank, SD = 5.5; phase 2: mean = 30/tank, SD = 17) and can be very important grazers of plankton communities in natural ecosystems, reaching densities of >100 individuals/ m^2 and feeding rates up to 100 ml/hr [25]. *Dreissena* can have strong effects on zooplankton and phytoplankton communities [26], but further experiments would be necessary to test for competition between *Dreissena* and juvenile stickleback.

Third, we found a GxE effect (caused by adults in phase 1) on the biomass of macroinvertebrates associated with macrophytes at the end of phase 2 (Figure 3C; $F_{1,10} = 3.93$, $p = 0.047$). The interactive effects of genetic background and plasticity on trait variation (e.g., body shape and morphology) [19, 27] might account for the treatment effects of adults on resources in phase 2. However, the link between trait variation and feeding behavior is highly uncertain [27], and it is difficult to predict divergence in ecosystem effects from morphological and shape divergence between populations [1, 28–30]. In general, we need a better understanding of the functional significance of morphological variation [31] over a range of timescales (e.g., lab foraging trials and mesocosm experiments) and environmental conditions (e.g., natural environments).

(C) Biomass of macroinvertebrates associated with macrophytes at the end of phase 2.

See also Figure S3.

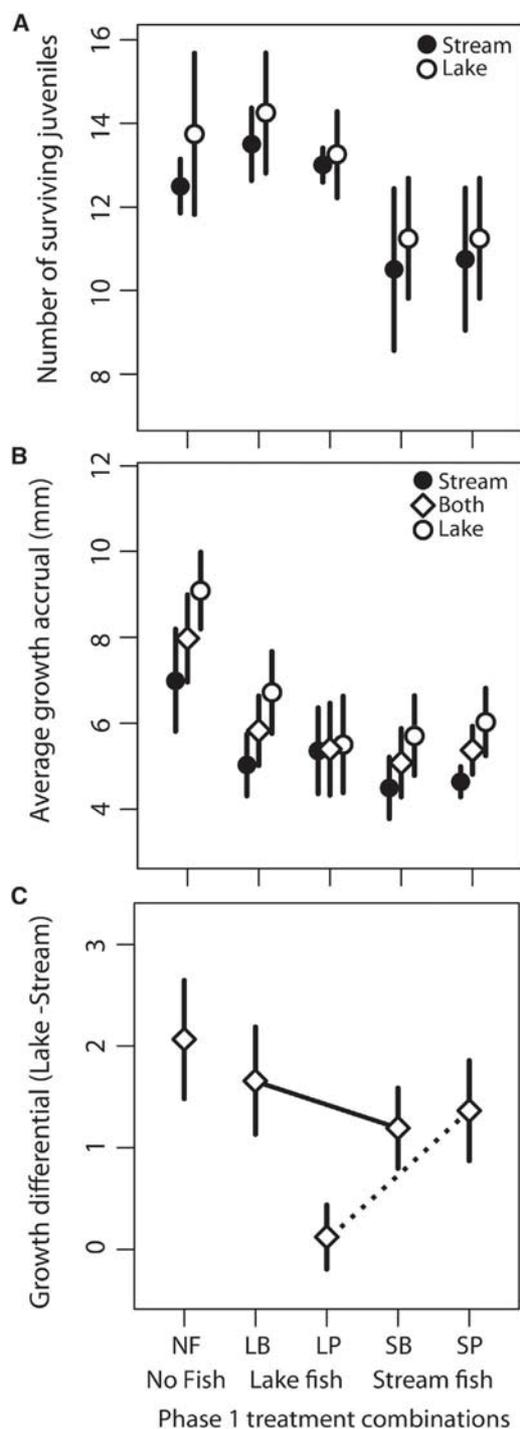


Figure 4. Effects of Adult Stickleback on Juvenile Growth and Survival
 (A) The number of surviving juveniles of lake and stream at the end of phase 2 based on the treatment of their mesocosm in phase 1.
 (B) Average increase in juvenile length during phase 2 for the entire juvenile population (diamonds) or for stream (filled circles) and lake (open circles) juvenile populations separately.
 (C) Mesocosm-specific growth differentials (in mm) calculated as the lake minus stream growth accruals. Lines connect treatments during phase 1 where adult fish were reared on either benthic chironomids (solid lines) or pelagic zooplankton (dotted lines).
 All error bars indicate ± 1 SE. See also Tables S3–S5.

Overall, these three results (Figure 3) support our third prediction: adults can alter the biomass of communities (e.g., zooplankton and macroinvertebrates) and the abundance of species (e.g., *Dreissena*) that are known to have profound and durable impacts on ecosystems [32]. Transmitting environmental conditions across generations has previously been shown to alter the relationship between trait variation and fitness among environments [33]. In our case, ecosystem differences persisted well beyond the presence of the adults, and this might increase the likelihood of eco-evolutionary feedbacks.

Do the Ecosystem Modifications of Adults Affect Juvenile Growth and Survival?

Survival did not differ among mesocosms with and without fish (fish effect: $p = 0.49$; Table S4); however, mesocosms previously modified by adult stream fish had lower overall juvenile survival (genetic effect: $p = 0.002$; Table S4). The prior presence of adult stream fish reduced the overall survival of both stream and lake juveniles, but this was only significant for stream juveniles (Figure 4A; Table S4). Growth accrual measured in a common environment is a useful proxy of variation in relative performance between juveniles of different fish ecotypes, because attaining larger body sizes over the growing season can improve overwintering survival [34], reduce predation risk [35], and increase adult female fecundity [36]. To compare variation in growth among the surviving juveniles, we calculated (1) an average growth accrual ($GA = \text{Length}_{\text{Nov}} - \text{Length}_{\text{Sept}}$) for each ecotype in each mesocosm and (2) an average growth accrual differential ($GA_{L-S} = GA_{\text{Lake}} - GA_{\text{Stream}}$) between co-occurring ecotypes in each mesocosm. We found that the differential growth between ecotypes (GA_{L-S}) depends on the interaction between the ecotype and rearing environment (i.e., GxE effect) of the adult that was present in phase 1 (Figure 4C; Table S5; $GA_{L-S} = 1.71$ mm, SE = 0.72, $p = 0.04$). Lake juveniles entirely lost their growth advantage over stream juveniles in ecosystems previously modified by lake fish that were reared to adulthood on lake-like food (i.e., plankton) (Figure 4C). This result provides our strongest evidence of an eco-evolutionary feedback (prediction 4) because the interaction between the genotype and rearing environment of adults causes differential modification of ecosystems (evolutionary effect on ecosystems) and this subsequently affects the relative growth (proxy of fitness variation) of co-occurring ecotypes (feedback on differential growth of co-occurring ecotypes).

Existing theory suggests that phenotypic plasticity can either facilitate or constrain adaptive divergence, depending on how plasticity affects the relationship between phenotype and fitness in a given environmental context [37, 38]. In our lake-stream pair, the extent of plasticity varies among traits [19], but we are unsure which traits underlie the ecosystem effects of stickleback. Our results support one additional study [3] showing that plasticity can alter ecosystem conditions in mesocosms (Figure 1), but we additionally find that the interactive effects of rearing environment and genetic background can have a bigger impact on growth differentials between lake and stream juveniles than does the prior presence/absence of adult fish (Figure 4C). Future work should identify the plasticity of traits underlying ecosystem effects and quantify which traits are related to fitness variation in the modified environmental conditions.

Our experiment provides evidence for multiple components of an eco-evolutionary feedback, but at least two significant uncertainties remain. First, does growth accrual adequately reflect variation in relative fitness between ecotypes? Our primary evidence of an eco-evolutionary feedback (i.e., [Figure 4C](#)) relies on the assumption that growth rate is a useful proxy of fitness variation both within and between ecotypes [34, 39, 40]. However, survival differences between lake and stream juveniles did not depend on the presence/absence, ecotype, or prior rearing history of the adults in the previous generation ([Figure 4A](#)).

Second, what is the consequence of ecosystem modification for adaptive divergence in this population pair? Our observation that growth differentials were never less than zero ([Figure 4C](#)) suggests that lake juveniles would often outcompete stream juveniles, particularly in environments that are modified by adults that are reared in, or that originate from, streams. However, our experiment was performed in mesocosms, which neither emulate the full range of environmental conditions experienced by natural populations nor reflect any one environmental (e.g., lake or stream) condition more than another. As a result, very little is known about what types of similar modifications might be present in nature and how they might interact with other agents of selection (e.g., competition, predation, parasitism, etc.) in more natural environments.

More work is needed to determine which traits underlie the ecosystem effects of organisms in natural settings [2] and how such ecosystem modifications might influence evolutionary responses [9]. Our results highlight the ecosystem consequences of very recent phenotypic and genetic divergence that can occur over fewer than 100 generations [19, 30]. The lake-stream pair that we used is much less divergent in its shape and morphology than many other well studied lake-stream pairs [30, 41], and so we might expect a greater divergence in the ecosystem effects of different ecotypes as phenotypic divergence between them increases [1]. If our experimental results can be transferred to more natural settings, then considering a broader range of mechanisms underlying eco-evolutionary feedbacks may be useful for ecological theories of adaptive divergence and speciation.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, three figures, and five tables and can be found with this article online

AUTHOR CONTRIBUTIONS

B.M., B.L.-H., T.A., and O.S. conceived of the experiment. T.A., K.E.S., B.L.-H., and B.M. carried out the experiment. B.M. did the analysis and wrote the first draft of the manuscript. All authors edited and contributed to the writing.

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