The Legacy of Ecosystem Effects Caused by Adaptive Radiation

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There is increasing evidence that closely related species have contrasting ecosystem effects, but very little is known about the temporal scale of these effects. When organisms' ecosystem-effects persist beyond or emerge after their presence in the ecosystem, this might increase the potential for eco-evolutionary feedbacks to accompany evolutionary diversification. Here we studied lab-raised whitefish of a benthic-limnetic species pair from a postglacial adaptive radiation to test whether closely related species have contrasting effects on mesocosm ecosystems (hereafter ecosystem effects). We found that the presence of whitefish (ecological effect) had strong effects on some ecosystem components, for example by reducing snail and mussel abundance and increasing phytoplankton abundance. Whitefish species had contrasting effects (evolutionary effect) on benthic algal cover, dissolved organic carbon, and zooplankton community composition, but these effects only emerged several months after whitefish were removed from the ecosystem. The effects of plasticity and the interactive effects of species and plasticity were relatively weak and, with one exception, not significant. Ecological and evolutionary effect sizes were uncorrelated over both phases of the experiment, as were effect sizes between phases for both ecological and evolutionary contrasts. Overall, our results suggest that adaptive radiation can have effects on the structure and functioning of ecosystems, but that the temporal dynamics and mechanistic basis of these effects are insufficiently understood.

THE process of adaptive radiation typically results in groups of closely related species that are phenotypically and ecologically differentiated and coexist in close physical proximity (Schluter, 2000). Divergent selection is the primary driver of phenotypic diversification during adaptive radiation, and is typically thought to arise from contrasting environmental conditions (Schluter, 2000). However, a complementary view is that adaptive phenotypic diversification itself can modify the fitness landscape through the dynamic emergence of contrasting niches as result of competition and negative frequency dependent selection (Schluter, 1994; Benkman, 1999; Dieckmann, 2004). Previous work has suggested that closely related populations or species can differentially modify a broad range of ecosystem variables (Harmon et al., 2009; Palkovacs and Post, 2009; Bassar et al., 2010; Des Roches et al., 2013; Simon et al., this volume, 2017; Tuckett et al., this volume, 2017), and this might be an overlooked agent of selection involved with evolutionary diversification (Losos, 2010; Yoder et al., 2010; Matthews et al., 2014; Hendry, 2017). In fact, we know little about how adaptive radiations usually unfold in response to multiple interacting agents of selection that can lead to complex fitness landscapes of high dimensionality (Losos, 2010; MacColl, 2011). It is possible that phenotypic diversification might affect ecosystems and alter the course of evolutionary radiation, particularly because the functional links between an organism's phenotype and its environment are thought to be particularly strong in adaptive radiations (Schluter, 2000).

There are two components of time scale that are important for understanding how interactions between phenotypic diversification and ecosystem dynamics might play out in an adaptive radiation. First, on what time scale does adaptive divergence emerge in traits that cause ecosystem effects? Rates of phenotypic evolution during adaptive radiation are often rapid, and these phenotypic differences might underlie contrasting ecosystem effects of organisms (Hendry, 2017). For example, benthic and limnetic stickleback were shown to have ecological effects on various properties of experimental ecosystems such as zooplankton community structure, gross primary productivity and water clarity (Harmon et al., 2009; Des Roches et al., 2013; Rudman and Schluter, 2016). Such ecosystem effects can be due either to heritable species divergence or to environmentally induced plastic differences, or both (Seehausen, 2009; Lundsgaard-Hansen et al., 2014). If the differences between species that cause different ecosystem effects were mostly environmentally induced (phenotypically plastic) then the ecosystem effects of contrasting phenotypes might emerge before genetic differences and reproductive isolation evolve.

A second important aspect involving the time scales of phenotypic and ecosystem change is whether the phenotypic effects of organisms on ecosystems persist over time and in the face of other external ecosystem drivers (Hendry, 2017). Previous work suggests that the size and persistence of ecosystem effects could be important for understanding how organism-mediated modification of the environment might influence other environmental sources of selection during an adaptive radiation (Odling-Smee et al., 2003; Matthews et al., 2014, 2016; McPeek, 2017). The idea that populations of evolving organisms modify their own selective landscape is a core principle of adaptive speciation theory (Schluter, 2000; Dieckmann, 2004), although most adaptive dynamics models assume that evolutionary dynamics are slower than ecological dynamics and so the two processes are analytically separated (Fussmann et al., 2007). The time scale of interaction between ecological and evolutionary process is also at the core of emerging work in the field of eco-evolutionary dynamics, where a considerable body of work investigates ecosystem effects of contemporary evolution

and recent evolutionary history (Matthews et al., 2011; Schoener, 2011; Thompson, 2013; Hendry, 2017).

In order to test how recent evolutionary divergence and contemporary plasticity might lead to contrasting ecosystem effects, we used lab-raised benthic and limnetic species (*Coregonus zugensis* and *C.* sp. "Bodenbalchen") from a young sympatric whitefish adaptive radiation in Lake Lucerne, Switzerland (Hudson et al., 2017). We raised families of the two whitefish species on two different food treatments each, resulting in four treatments for our common gardening experiment: the benthic species (B), *C.* sp. "Bodenbalchen," raised on benthic (BB) or limnetic food (BL) and the limnetic species (L), *C. zugensis*, raised on benthic (LB) or limnetic food (LL). This design allowed us to compare the ecosystem effects of whitefish presence (an ecological effect), with those resulting from species divergence (an evolutionary effect), phenotypic plasticity (plasticity effect), and their interaction (interaction effect). To investigate the time scale for persistence and emergence of ecosystem effects, we divided our experiment into two phases. In a first phase, we added fish into each mesocosm ecosystem and measured ten ecosystem components after eight weeks. In the second phase, we removed the fish and quantified the ecosystems 14 weeks later. Such a design can help us assess how important evolutionary processes are for ecosystem dynamics relative to other drivers of ecosystem change (Matthews et al., 2016; Brunner et al., 2017; Hendry, 2017).

MATERIALS AND METHODS

Study species.—We used two whitefish species, *C. zugensis* and *C.* sp. "Bodenbalchen," from a recent sympatric adaptive radiation in Lake Lucerne, Switzerland, that began to form about 15,000 years ago (Hudson et al., 2017). *Coregonus zugensis* corresponds to a limnetic ecomorph and is characterized by slow growth and small adult size, a high number of gill rakers, and a streamlined body shape (Steinmann, 1950). *Coregonus* sp. "Bodenbalchen" corresponds to a benthic ecomorph and is characterized by faster growth and larger adult size, a lower number of gill rakers, and a more deep bodied shape (Steinmann, 1950). The species are strongly differentiated at neutral genetic markers (F_{ST} based on microsatellite loci ~ 0.1) and spawn at different water depths (*C.* sp. "Bodenbalchen: 1–5 m, *C. zugensis*: >25 m; Hudson et al., 2017). Recent experimental work has shown that the two species differ in their feeding efficiency on benthic vs. limnetic food, indicating that *C. zugensis* is better adapted to limnetic (zooplankton) feeding and *C.* sp. "Bodenbalchen" to benthic feeding (Lundsgaard-Hansen et al., 2013; Roesch et al., 2013).

Indoor common garden experiment in aquaria.—For each species, five males and five females were used to breed half-sib families, which were then reared in the laboratory for over two years prior to the mesocosm experiment. The eggs were mixed and simultaneously fertilized by the sperm of the five males, resulting in up to 25 half-sib families per species. In the first year of rearing, all juveniles were raised on zooplankton because whitefish larvae cannot efficiently be raised on benthic food. After one year, we began the plasticity manipulation common garden experiment by evenly splitting the juveniles of each species into two food treatments: red mosquito larvae to represent a benthic feeding environment, and live zooplankton (from Lake Lucerne) to represent a limnetic feeding environment. This

resulted in four treatments for our mesocosm experiment, the benthic species (*C.* sp. "Bodenbalchen") raised on benthic (BB) and on limnetic food (BL) and the limnetic species (*C. zugensis*) raised on benthic (LB) and limnetic food (LL). These fish are from the same set of families that were used for a previous experiment (Lundsgaard-Hansen et al., 2014), but the current study is a separate mesocosm experiment performed in the summer after our first experiment.

Outdoor common gardening experiment in mesocosms.—We set up an outdoor mesocosm experiment with 33 mesocosms (1000 L), with the following treatment combinations and replication: BB (*n* = 7), BL (5), LB (7), LL (7), and seven mesocosms without fish (NF). For each mesocosm ecosystem, we covered the bottom of each tank with a layer (2–3 cm) of gravel and sand originating from Lake Lucerne, and a layer of sediments (3–4 cm) collected from three lakes in the region of Lucerne (Roth, Sempach, and Lucerne) in order to inoculate the mesocosms with a diversity of aquatic organisms. We filled the mesocosms with water from Lake Lucerne, supplemented them with additional zooplankton collected from Lake Lucerne, and added nutrients to stimulate primary production (2.46 g of $NaNO_3$ and 0.18 g NaH_2PO_4). Setting up the tanks was finished by 29 April 2010, and fish were introduced on 12 May 2010. In total 78 fish were distributed across 26 tanks, and the number of fish varied between two and five per tank. Average fish weight per tank was 62 g and did not differ between fish treatments (ANOVA: $F_{3,22} = 0.22$, $P = 0.88$).

The experiment consisted of two phases. Phase 1 ran for 8 weeks, from 12 May to 7 July, and Phase 2 ran for 14 weeks, from 7 July to 13 Oct 2010. During the first eight weeks, four fish died (mortality rate = 0.05), and these were immediately replaced with an individual of a similar weight from the same treatment in the laboratory. On 7 July following several consecutive warm days, 16 of the 78 fish died overnight (deaths were distributed over nine tanks), with all but one individual belonging to the limnetic species. At this point, we terminated phase 1 and removed all the fish from all the mesocosms and began phase 2. This unexpected die-off ended phase 1 two weeks earlier than initially planned, but because we recognized the die-off with six hours of it occurring, there was very little time for the dead fish to decompose and significantly alter ecosystem conditions. Furthermore, in all our analyses in phase 2, the inclusion of dead fish numbers as a co-variable was not significant, and so we disregard this further as a potential source of bias in our analysis.

Measured ecosystem metrics in mesocosms.—We measured a broad array of biological and chemical ecosystem metrics (Table 1) using the same methods described in more detail in a previous study (Lundsgaard-Hansen et al., 2014). In brief, we used a sampling tube to collect 10 L of water that we sieved through a zooplankton net (30 microns), and counted zooplankton in the lab using a dissecting microscope. We filtered water samples to measure algal biomass and the concentration of dissolved organic compounds (DOC). We measured photosynthetic active radiation (PAR) from 400–700 nm to calculate light transmission through the water column. We took photos of the bottom of each tank and used them to estimate benthic algae cover. Gross primary production was measured using diurnal changes in oxygen levels, and sedimentation rate was measured using sediment

Table 1. Effect sizes (Cohen's d) in Phase 1 and 2, resulting from fish presence versus absence (Eco), phenotypic plasticity (Pla), evolutionary divergence (Evo), and from an interaction between plasticity and evolution (Int). Significant effects from ANOVA are indicated in bold (* = $P < 0.05$; ** = $P < 0.01$, *** = $P < 0.001$).

Ecosystem metric	Acronym	Phase	Eco	Pla	Evo	Int
Snail abundance (n/m²)	SNA	1	**1.19****	0.26	0.36	0.17
Dreissena abundance (n/m²)	DRA	1	**1.34****	0.34	0.5	0.48
Macro zooplankton density (n/l)	MAZPD	1	0.82	0.09	0.21	0.11
Micro zooplankton density (n/l)	MIZPD	1	0.49	0.14	0.005	0.42
Phytoplankton concentration (mg/l)	PPC	1	**1***	**0.97***	0.08	0.27
Benthic algae cover (%)	BAC	1	0.45	0.52	0.46	0.13
Photosynthetic active radiation (%)	PAR	1	0.46	0.46	0.44	0.41
Dissolved organic carbon (mg/l)	DOC	1	0.41	0.006	0.37	0.32
Gross primary production (mg O₂/l)	GPP	1	0.2	0.08	0.31	0.11
Sedimentation rate (mg/d)	SED	1	0.49	0.41	0.74	0.13
Snail abundance (n/m²)	SNA	2	0.63	0.73	0.07	0.06
Dreissena abundance (n/m²)	DRA	2	0.50	0.53	0.06	0.3
Macro zooplankton density (n/l)	MAZPD	2	0.08	0.11	0.28	0.5
Micro zooplankton density (n/l)	MIZPD	2	0.5	0.08	0.13	0.45
Phytoplankton concentration (mg/l)	PPC	2	0.11	0.29	0.79	0.1
Benthic algae cover (%)	BAC	2	0.39	0.26	**0.8****	0.02
Photosynthetic active radiation (%)	PAR	2	0.75	0.004	0.16	0.65
Dissolved organic compounds (mg/l)	DOC	2	**1.48****	0.14	**1.46*****	0.27
Gross primary production (mg O₂/l)	GPP	2	0.4	0.09	0.04	0.08
Sedimentation rate (mg/d)	SED	2	0.15	0.45	0.42	0.35

traps. Snails (families of Limnaidae and Planorbidae) and mussels (*Dreissena polymorpha*) were counted on the walls of the tanks.

At the end of phase 2, we unexpectedly discovered ten loaches (*Barbatula barbatula*) distributed across 8 tanks (3*LL, 3*NF, 2*LB). These small benthic fish (weight ranged in mesocosms from 1.7–2.8 g per individual) were unintentionally introduced to the tanks along with the addition of sediments, probably as eggs, fry, or juveniles (loaches start to spawn in April). Since there was an insignificant effect of treatment on their presence (binomial glm: $P = 0.09$), we disregarded them in subsequent analyses.

Statistical analysis.—We used redundancy analysis (RDA) to test for differences among treatments for both zooplankton community composition and ecosystem parameters (Legendre and Gallagher, 2001). For community analyses, we Hellinger transformed the species abundance matrix and used distance-based redundancy analysis with permutations using the function 'anova.cca' in the *vegan* R package (Oksanen et al., 2007). For the suite of ecosystem metrics listed in Table 1, we standardized each ecosystem parameter prior to testing for treatment effects in the RDA analysis. We used linear models for univariate analyses and calculated effect sizes using Cohen's d, which takes the difference in the means of two groups for the variable of interest and corrects for the pooled standard deviation (Cohen, 1988). We compared effect sizes for specific contrasts of interest, namely fish presence/absence (Eco), food treatment (Pla = phenotypic plasticity), species (Evo = evolutionary divergence), and for the interaction of plasticity and divergence (Int; Table 1).

RESULTS

The presence of whitefish had strong effects on the mesocosm ecosystems after eight weeks (Fig. 1A, RDA: $F_{1,29}$ = 3.1, $P = 0.005$), mainly by decreasing the abundance of both mussels ($F_{1,29} = 8.15$, $P = 0.008$) and snails ($F_{1,29} = 11.63$, $P = 0.002$) and increasing the biomass of phytoplankton

($F_{1,29} = 5.3$, $P = 0.03$). At the end of phase 2 (Fig. 1B), 14 weeks after the fish were removed, the overall ecosystem effects of whitefish were less strong (Fig. 1B, RDA: $F_{1,30} = 2.37$, $P = 0.05$), except for the lower concentrations of dissolved organic carbon (DOC) in mesocosms that never received whitefish ($F_{1,30} = 13.22$, $P = 0.001$). At the end of phase 1, we also found that whitefish presence had strong effects on zooplankton community composition (RDA: $F_{1,29} = 7.77$, $P = 0.005$) by shifting it toward smaller plankton species such as rotifers and chydorus (Fig. 2A). However, this effect was no longer significant at the end of phase 2 (Fig. 2B).

In phase 1, we found no effects of whitefish species, plasticity, or their interaction in our multivariate analysis of ecosystem conditions (Fig. 1A: Effects of plasticity, species, and their interaction were not significant, $P > 0.05$) and no effects on zooplankton community composition (Fig. 2A: Pla, Evo, and Int contrasts, $P > 0.05$). From univariate analyses, we found one significant effect of plasticity (Table 1), where phytoplankton biomass was higher in mesocosms with whitefish reared on benthic compared to limnetic prey (ANOVA: $F_{1,22} = 8.9$, $P = 0.02$). In phase 2, however, we found strong species effects on mesocosm ecosystems (Fig. 1B, RDA: $F_{1,22} = 3.0$, $P = 0.02$), where mesocosms that had benthic whitefish (BB and BL) had lower levels of benthic algal cover (ANOVA: $F_{1,21} = 8.3$, $P = 0.009$) and lower DOC levels (ANOVA: $F_{1,21} = 11.8$, $P = 0.002$) than mesocosms that had limnetic whitefish. In phase 2, we found no significant effects of whitefish species, plasticity, or their interaction on the zooplankton community composition (Fig. 2B).

The ecological effect sizes (i.e., whitefish presence/absence) were not correlated with the evolutionary effect sizes (i.e., different species) in either phase of the experiment (Fig. 3A). For the most part, significant ecological and evolutionary effects occurred independently, and effect sizes were not correlated between the two phases of the experiment. For the two largest evolutionary effects (Fig. 3), one occurred with a significant and similarly large ecological effect (i.e., DOC
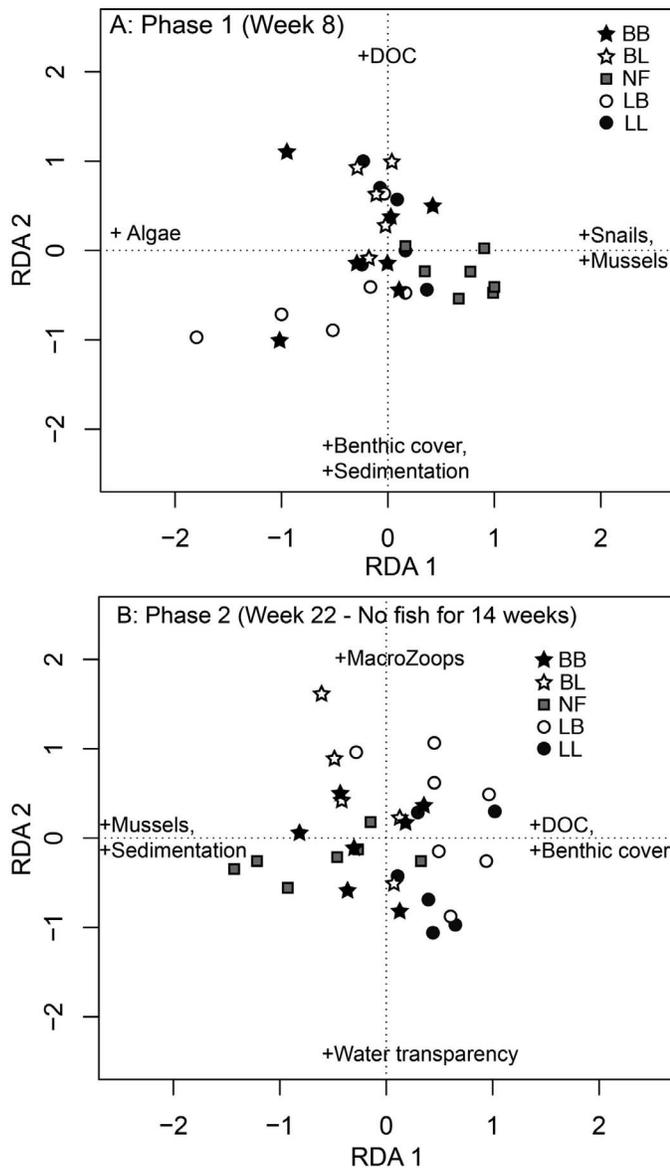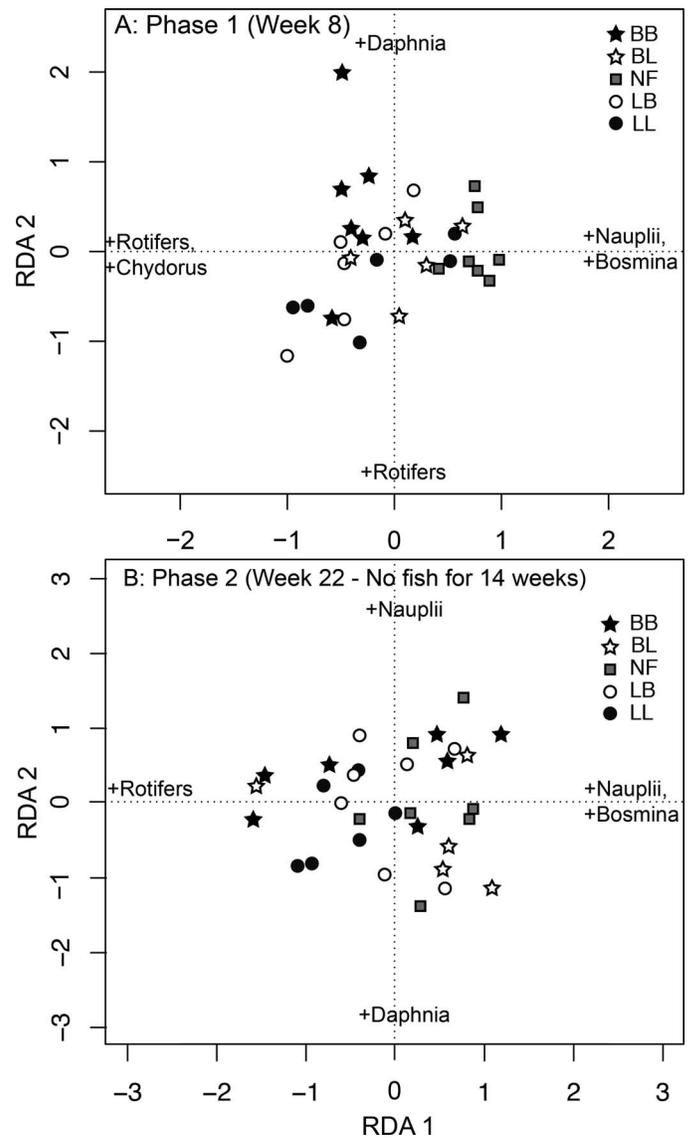
Fig. 1. Variation in ecosystem metrics (Table 1) among treatments for both phases of the experiment. Each dot is a mesocosm, and the five treatment combinations are Benthic whitefish raised on either benthic (BB) or limnetic (BL) food, Limnetic whitefish reared on either benthic (LB) or limnetic food (LL), and no fish (NF). In phase 1, the effect of fish presence/absence was significant (squares vs. stars and circles), and in phase 2, the species effect was significant (stars vs. circles) and the effect of fish presence/absence was marginally significant (P = 0.05).

Fig. 2. Variation in zooplankton species composition among treatments for both phases of the experiment, with the same treatment combinations as in Figure 1. In phase 1 (Panel A), there was only a strong effect of fish presence/absence (squares vs. stars and circles), and in phase 2 (Panel B), none of the contrasts were significant.

concentration in phase 2) and one occurred independently of an ecological effect (i.e., Benthic algae cover: Fig. 3B).

DISCUSSION

We found strong short-term effects (after eight weeks) of whitefish presence/absence (ecological effect) on mesocosm ecosystems (Figs. 1A, 2A), as well as strong contrasting effects of closely related species (evolutionary effect) that emerged after whitefish had been removed from the mesocosms for 14 weeks (Fig. 1B, Table 1: Evo column). Overall, this provides additional evidence that evolutionary differentiation between either young species (Harmon et al., 2009; Lundsgaard-Hansen et al., 2014) or recently diverged populations (Matthews et al., 2016; Brunner et al., 2017) can have

contrasting effects on ecosystems, and builds on previous work showing that phenotypically differentiated populations of the same species can induce ecosystem divergence (Palkovacs and Post, 2009; Bassar et al., 2010; Fryxell and Palkovacs, this volume, 2017; Simon et al., this volume, 2017; Tuckett et al., this volume, 2017). However, our observation of evolutionary effects that emerge independently of, and over different time scales as, ecological effects (Fig. 3), suggests a potentially complex set of mechanisms underlying how differences between closely related species can affect ecosystem processes. Regardless of the specific mechanisms, the emergence of ecosystem effects beyond either the presence or lifetime of an organism could increase the likelihood for feedbacks between ecological dynamics and selection pressures (Matthews et al., 2014).

The presence of whitefish had strong short-term ecological effects (Figs. 1A, 2A) that are consistent with cascading trophic interactions (Carpenter et al., 1985). Whitefish have been previously implicated in cascading trophic interactions
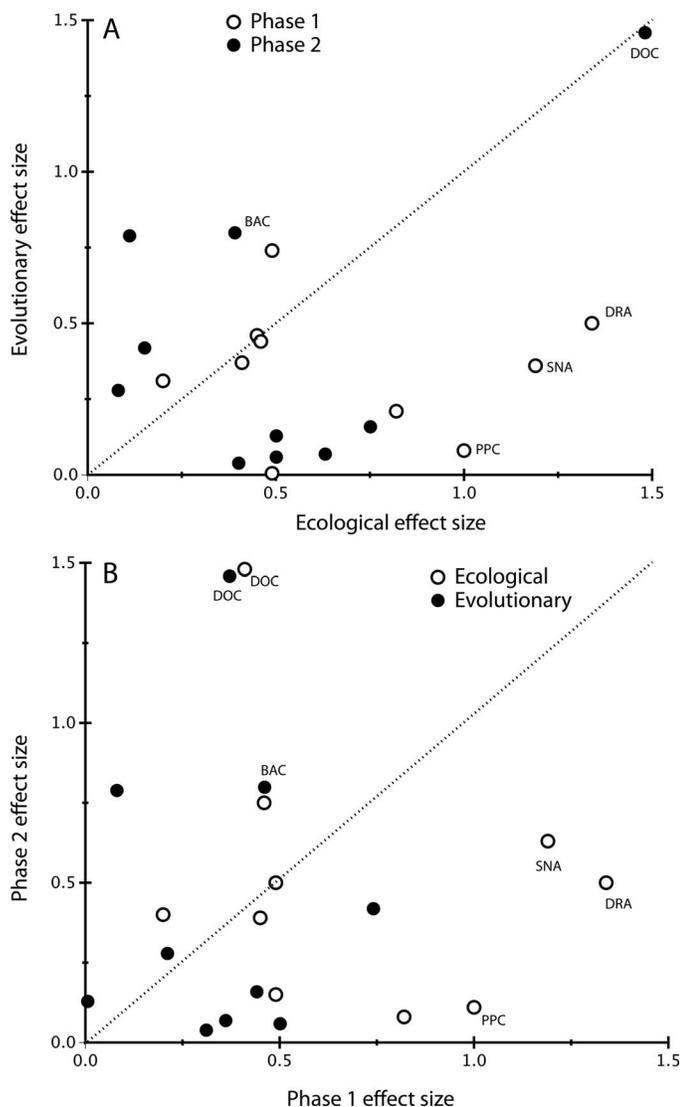
Fig. 3. Comparison of effect sizes between (A) the presence/absence of whitefish (Ecological effect) versus the species of whitefish (Evolutionary effect), and between (B) ecosystem metrics from phase 1 and phase 2. Metrics with significant differences for either contrast are labeled with codes found in Table 1.

in natural lakes (Berg et al., 1994; Hansraj, 2000; Ellis et al., 2011) mainly because of their planktonic foraging behavior (Berg et al., 1994). In our experiment, the presence of whitefish reduced the number of snails and mussels and shifted the planktonic community toward species that are smaller and less efficient grazers (e.g., bosmnia, copepod nauplii). These modifications of grazer community coincided with an increase in algal biomass, consistent with expectation from trophic cascade theory (Carpenter et al., 1985). However, we found no evidence for variation in the strength of trophic cascades between whitefish species after eight weeks (phase 1). In phase 2, after fish were removed from the system, the effects of whitefish presence/absence on grazer and phytoplankton communities disappeared.

In the first phase of the experiment, we only found effects of whitefish presence and of previously environmentally induced plastic differences on ecosystems (Table 1). The evolutionary effects of heritable species differences only emerged 14 weeks after the whitefish were removed from the system. The short-term ecological effects might reflect

cascading trophic interactions, specifically that higher algal abundances are caused by reductions of grazer biomass (i.e., snails, mussels) (Carpenter et al., 1985) and by shifts in grazer community composition (i.e., zooplankton; Polis et al., 2000). However, these ecological effects did not persist by the end of phase 2, and new evolutionary effects emerged (i.e., on DOC and benthic algal cover) that may not have been the product of trophic cascades.

Several previous studies have found clear evolutionary effects of differences between predators on prey community structure (Harmon et al., 2009; Palkovacs and Post, 2009; Des Roches et al., 2013; Lundsgaard-Hansen et al., 2014), but in this experiment we found no such effects. In a previous experiment, using the same populations of whitefish that were raised in the same common garden experiment, but performed in a different season, we found that the benthic species (reared on benthic food) more strongly reduced both mussels and snails, and the limnetic species (reared on plankton) more strongly reduced zooplankton density (Lundsgaard-Hansen et al., 2014). A lack of congruence between the results of mesocosm experiments that use the same species, reared in the same environments, but are performed in different environmental contexts (e.g., seasons, inoculum of species, habitat structure, etc.) suggests strong context-dependency of the phenotypic effects of organisms (Fryxell and Palkovacs, this volume, 2017; Hendry, 2017; Pérez-Jvostov et al., this volume, 2017; Tuckett et al., this volume, 2017). This is not entirely surprising, because differential effects of organisms on their resources could strongly depend on the species composition (Harmon et al., 2009) and trait variation among prey genotypes (Pantel et al., 2011), and these would have been somewhat different between experiments.

The only evolutionary effects of differences between whitefish species we observed were on non-prey components of the ecosystem, and they were detected only 14 weeks after fish were removed from the mesocosms. We are unaware of any previous experiments that test for the ecosystem effects of differences between closely related populations or species long after they have been removed from the ecosystem. In one previous stickleback experiment with a similar two phase design, differential ecosystem effects of adult lake and stream stickleback were present several months after the adults had been removed from the system and replaced with a standardized population of juvenile stickleback (Matthews et al., 2016). However, these "legacy effects" were primarily associated with changes in community structure (e.g., zooplankton, mussels, and macroinvertebrates), whereas in the current experiment we found effects on dissolved organic carbon (DOC) and benthic algal cover.

There is ample evidence that predators can have strong ecosystem effects that extend well beyond their prey communities (Schmitz et al., 2004, 2010) and thereby regulate key biogeochemical processes associated with carbon cycling (Schmitz et al., 2013). Typically the amount and composition of dissolved organic carbon is thought to influence fish communities either by direct effects on water clarity (Seehausen et al., 1997; Marques et al., 2017) or by indirect effects on the resources that determine prey community composition (Yan et al., 2008). However, there is also evidence that fish can indirectly alter the composition of DOC, and hence water transparency, by altering the balance between multiple sources of DOC (e.g., algal, terrestrial inputs, sediments; Harmon et al., 2009). In our experiment, DOC levels might have been higher in the

treatments with the limnetic whitefish species due to the increased biomass of benthic algae, which could have significantly contributed to the overall DOC pool over the course of the experiment. DOC is a complex mixture of carbon that is derived from multiple sources (e.g., algae, macrophytes, sediments) that vary widely in their persistence due to differential reactivity with bacterial communities and ultraviolet radiation (Mopper et al., 1991; Koehler et al., 2012). The lower benthic cover of algae in mesocosms with benthic whitefish might have been caused by effects on grazer communities (e.g., snails and mussels), but although this would be consistent with evolutionary effect on grazers that we found in a previous experiment (Lundsgaard-Hansen et al., 2014), we did not detect any such effects on grazers in this experiment.

Previous work has suggested that plasticity might influence the ecosystem effects of organisms (Lundsgaard-Hansen et al., 2014; Matthews et al., 2016), but we find very little evidence of this in our experiment (Table 1). Plasticity can generate rapid within-population adjustments of trait distributions (West-Eberhard, 2003), and so plasticity cannot be neglected when studying eco-evolutionary dynamics (Fischer et al., 2014). Plasticity effects can result in at least two different types of feedbacks: If environmental fluctuations affect the expression of a developmentally plastic trait and if this trait also affects environmental fluctuations, a reciprocal interplay between the expression of an organism's plastic phenotype and its environment might emerge (Agrawal, 2001). Phenotypic plasticity can also be involved in true eco-evolutionary feedbacks, if ecosystem effects that result from phenotypic plasticity affect subsequent evolution in a genetically heritable trait, including the genetic basis of plasticity itself (Yamamichi et al., 2011). More theory, as well as more experiments and empirical case studies, will help to achieve a better understanding of how developmental plasticity affects ecosystems and the characteristics and likelihood of eco-evolutionary dynamics that emerge from such effects.

The whitefish species we studied here belong to a monophyletic adaptive radiation that has happened in Lake Lucerne after the last glacial maximum, with species starting to form no longer than 15,000 years ago (Hudson et al., 2017). While the endemic species evolved within the lake in geographical sympatry, their genetic variation derives from two distantly related glacial lineages that formed a hybrid swarm shortly before or just after colonization of the Alpine region (Hudson et al., 2011). This suggests that whitefish standing genetic variation was high from the onset of colonization, which may have allowed for fast responses to selection during early diversification (Seehausen, 2004; Barrett and Schluter, 2008). Natural selection during whitefish speciation was likely multi-dimensional, as species differentiation included spawning depth and time (Vonlanthen et al., 2009, 2012), life history (Vonlanthen et al., 2012), and foraging traits and behavior (Vonlanthen et al., 2009; Roesch et al., 2013). Further, some traits with an important functional role for benthic vs. limnetic feeding have been shown to be genetically heritable in whitefish (Lundsgaard-Hansen et al., 2013), and fast changes in trait means, most likely through contemporary evolution, have been documented in several Swiss whitefish species (Bittner et al., 2010; Vonlanthen et al., 2012). All these characteristics of the whitefish species complex, in combination with our previous and current results of contrasting ecosystem effects resulting from evolutionary differentiation of whitefish

species (Lundsgaard-Hansen et al., 2014), suggests the possibility for eco-evolutionary feedbacks, but this remains to be tested experimentally.

In order to increase our understanding of the potential for eco-evolutionary interactions in speciation and adaptive radiation, future experiments should test at what stage of phenotypic divergence ecosystem effects begin to arise (Hendry et al., 2013; Hendry, 2017). Further, they should quantify whether ecosystem contrasts induced by differences between populations result in differences in the fitness landscapes experienced by the populations of environment modifying organisms themselves (Matthews et al., 2016). Because the same factors that constrain adaptive evolution in general can also constrain eco-evolutionary feedbacks, future studies should also measure evolutionary responses to selection in this context.

Conclusions.—Our findings of ecosystem effects resulting from evolutionary differentiation between young sympatric species in an adaptive radiation provides additional evidence that phenotypic differentiation can affect ecosystems (Post et al., 2008; Harmon et al., 2009, Bassar et al., 2010). Our findings that, at the end of our experiment, effects of evolutionary divergence were comparable in magnitude to those of ecology, highlights the necessity to take evolutionary history and process into account when attempting to understand variation in ecosystem structure and functioning. That differences in ecosystem state, which emerged as a result of differentiation among species, were observed several weeks after removal of the organisms is at least consistent with potential for eco-evolutionary feedbacks to emerge in and perhaps influence the course of adaptive radiation.

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