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A cascade of evolutionary change alters consumer-resource dynamics and ecosystem function

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It is becoming increasingly clear that intraspecific evolutionary divergence influences the properties of populations, communities and ecosystems. The different ecological impacts of phenotypes and genotypes may alter selection on many species and promote a cascade of ecological and evolutionary change throughout the food web. Theory predicts that evolutionary interactions across trophic levels may contribute to hypothesized feedbacks between ecology and evolution. However, the importance of 'cascading evolutionary change' in a natural setting is unknown. In lakes in Connecticut, USA, variation in migratory behaviour and feeding morphology of a fish predator, the alewife (*Alosa pseudoharengus*), drives life-history evolution in a species of zooplankton prey (*Daphnia ambigua*). Here we evaluated the reciprocal impacts of *Daphnia* evolution on ecological processes in laboratory mesocosms. We show that life-history evolution in *Daphnia* facilitates divergence in rates of population growth, which in turn significantly alters consumer-resource dynamics and ecosystem function. These experimental results parallel trends observed in lakes. Such results argue that a cascade of evolutionary change, which has occurred over contemporary timescales, alters community and ecosystem processes.

Keywords: life-history evolution; local adaptation; eco-evolutionary dynamics

1. INTRODUCTION

There has been considerable interest in the potential for evolutionary diversification to impact ecological properties and promote reciprocal interactions between ecological and evolutionary forces, or eco-evolutionary feedbacks [1–3]. A requirement of eco-evolutionary dynamics is that evolutionary change, occurring on contemporary timescales (i.e. years to decades), has differential impacts on the environment. A link between genetics and ecology is evident from research showing that genotypes or genetic diversity can influence ecological processes [4–12]. Recent work has also shown that intraspecific diversification can impact the properties of communities and ecosystems [13–17]. However, this body of research has focused on feedbacks between variation in one organism and the rest of the environment. This is important because natural systems are inherently complex, and evolutionary changes in one organism, and associated ecological impacts of these changes, may alter the selective landscape and promote a series of evolutionary changes that propagate throughout the food web. Theory mimicking relatively simple communities predicts that evolutionary interactions among organisms could be an important component of eco-evolutionary dynamics [18–20], but the significance of such a 'cascade of evolutionary change' is unknown.

The zooplanktivorous fish the alewife (*Alosa pseudoharengus*) and water fleas (*Daphnia* sp.) have strong ecological impacts in lakes. Alewives structure the zooplankton community [13,21], while *Daphnia* sp. regulate phytoplankton abundance and nutrient cycling [22–23]. In lakes in Connecticut, USA, the presence or the absence of passages to the coastal ocean lead to lakes with anadromous alewives that migrate seasonally between marine and freshwater environments or lakes with permanent populations of landlocked alewives, respectively. These populations of alewives differ genetically as landlocked alewives diverged from a common anadromous ancestor as recently as 300 years ago [24]. In addition to lakes with landlocked or anadromous alewives, there are lakes without any alewife. All three lake types are comparable ecologically (size, depth and productivity) and contain identical compositions of non-alewife zooplanktivorous fish [13].

Adult anadromous alewives migrate into lakes to spawn during March–May, and young-of-the-year (YOY) alewives spend approximately six months in freshwater before migrating back to the ocean each autumn. In these lakes, *Daphnia* are abundant each spring, but are eliminated by YOY alewife predation in early summer [13]. Conversely, landlocked alewives are present in lakes year-round, and therefore *Daphnia* abundance is consistently low. Small-bodied zooplankton dominate the zooplankton community in lakes with landlocked alewives [13,21], and this has promoted morphological divergence of landlocked alewives from anadromous alewife [25]; anadromous alewives have a larger gape and larger spacing between gill rakers, and target larger prey (e.g. *Daphnia*), than landlocked alewives [13,15].

We recently demonstrated that variation in alewives selects for evolutionary divergence in the life histories of *Daphnia*. *Daphnia* from lakes with anadromous alewife

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grow faster, mature earlier (but at the same size) and produce larger clutches of offspring than *Daphnia* from lakes with landlocked or no alewives [26]. Because *Daphnia* in lakes with anadromous alewives are present only during the spring, and also because lakes in Connecticut are colder during the spring than summer, these evolutionary changes are best explained as an adaptation to a very short growing season and colder environment (i.e. countergradient variation) [27] that are an indirect effect of predation by anadromous alewives. There were no significant life-history differences in *Daphnia* between lakes with landlocked and no alewives, despite differences in predation pressure [13]. Hypothesized explanations include selection by landlocked alewife on other components of fitness (i.e. behaviour), trade-offs associated with shifts in growth and development, or enhanced gene flow between these lakes [26].

Here we ask whether contemporary evolution in *Daphnia* differentially affects consumer-resource dynamics and ecosystem processes. On the basis of the known connection between life-history traits and rates of population growth [28], as well as the established impacts of *Daphnia* grazing on phytoplankton dynamics [22–23], we expect evolution in *Daphnia* to have consequences for community and ecosystem ecology. We evaluated the ecological impacts of *Daphnia* by rearing *Daphnia* from three 'anadromous', three 'landlocked' and three 'no alewife' lakes in a common environment for multiple generations, and then quantifying their impact on phytoplankton dynamics and primary production in laboratory mesocosms. By rearing *Daphnia* in a common environment prior to the experiment and then performing the laboratory experiment under standardized conditions, our experiment allowed us to isolate the impacts of genetically based divergence on ecological processes. We specifically targeted the mechanistic link between evolutionary change and divergent ecological properties by quantifying the influence of population-level effects (rates of *Daphnia* population growth) as well as individual-level effects (*Daphnia* grazing rates) on phytoplankton abundances. We predict that the earlier maturation and larger clutches exhibited by *Daphnia* from lakes with anadromous alewives will facilitate faster rates of population growth, and thereby faster declines in algal biomass and decreased rates of primary production in experimental mesocosms, compared with *Daphnia* from lakes with landlocked alewife or with no alewife. We evaluate the support for these predictions in the previously mentioned laboratory experiment, as well as in multiple years of data on plankton abundances at the whole-lake scale.

2. MATERIAL AND METHODS

We examined the ecological influence of *Daphnia* evolution using *Daphnia ambigua* from three anadromous (Bride, Dodge and Gorton), three landlocked (Amos, Long and Quonnipaug) and three no alewife (Black, Gardner and Wyassup) lakes. We have previously shown that these lake types do not differ significantly in size, depth, productivity or alewife biomass (between landlocked and anadromous lakes only) [13]. All lakes contain similar compositions of non-alewife zooplanktivorous species of fish [13]. These fish species include bluegill (*Lepomis macrochirus*), yellow perch (*Perca flavescens*), golden shiners (*Notemigonus crysoleucas*) and pumpkinseed (*Lepomis gibbosus*).

All clones used in these experiments were established from sexually produced resting eggs (ephippia) collected from lake sediment. Sediment was collected in August–September 2009 using an Ekman Grab. In January 2011, eight genotypes of *Daphnia ambigua* were established per lake. The first laboratory generation consisted of one female per clone reared in 120 ml glass jars containing COMBO media [29] and an abundant supply of algae, *Scenedesmus obliquus* (concentration: >1.0 mg C l^{-1} d^{-1}). The photoperiod for all phases of clone rearing and the mesocosm experiment was 12 L : 12 D cycle. For the second laboratory generation, three individuals were taken from the second clutch of each clone and reared under the same conditions as those of the first generation. Thereafter, each clonal population was allowed to grow to a maximum of 15 adults per container and was maintained at this density for approximately 14 days. This density is not uncommon for experimental rearing of *Daphnia* [30–32]. During this phase of rearing, all beakers were monitored every other day, and clones were transferred to fresh media and algae three times per week. Prior to the experiment, all clonal populations experienced approximately five generations of common garden rearing.

(a) *Laboratory experiment*

We initiated our experiment in March 2011 by filling 56 l rectangular containers with 20 l of COMBO media [29] and added 400 ml of *Scenedesmus obliquus* to yield an initial algal concentration of 0.8 mg C l^{-1} per mesocosm. Four days later, each mesocosm received 32 adult *Daphnia* from a single lake. Our definition of adult *Daphnia* was any individual that contained greater than 2 developing offspring. A clutch size of two is not uncommon for individuals that have released their first clutch into the brood chamber [26]. When initiating this experiment, we recorded the number of individuals that contained their first clutch versus slightly older individuals that contained the third to fifth clutch. Because there are differences in fecundity among our lake types [26], and also because fecundity increases with age (up to clutch no. approx. 5), we used a conservative approach when adding individuals to the mesocosms to minimize initial differences in fecundity. We 'stocked' mesocosms containing *Daphnia* from lakes with anadromous alewives with a higher proportion of individuals that contained their first clutch (electronic supplementary material, table S1). This approach minimized the influence of initial differences in fecundity on population growth in *Daphnia* (electronic supplementary material, table S1).

The initial populations of *Daphnia* in each mesocosm included eight equally represented clones per lake (four individuals per clone). Each lake was replicated three times (nine lakes $\times$ three replicates $=$ 27 mesocosms). The experiment consisted of an additional three units that contained media and algae but no *Daphnia*. All mesocosms were randomly assigned locations in the laboratory and were stirred daily to resuspend algae. We quantified water temperature and light levels weekly.

We started monitoring algal and *Daphnia* abundances one week after the introduction of zooplankton. Prior to collecting samples, each mesocosm was stirred to homogenize its contents. Water samples (2–3 ml) were removed from the centre of each mesocosm with a pipette, and algal density was quantified via a laser particle counter (Spectrex PC-2200, Redwood City, CA). The average value of two replicate counts by the laser counter was used as the estimate of

algal cell density per mesocosm per date. *Daphnia* abundances were enumerated by filtering 1 l of water through 80 μm mesh netting and preserving samples in 70 per cent ethanol. All individuals were subsequently counted. The densities of *Daphnia* and algae were quantified three times per week for a total of 15 sampling events over the course of the 41-day experiment.

Our dependent variables included rates of algal decline, rates of *Daphnia* population growth, day of peak algal and *Daphnia* abundances, and net primary production (NPP). The rate of decline of algae was measured for each mesocosm by fitting an exponential decay function ($y = ae^{-bx}$) to the algae density data starting at day 8 through day 20 of the experiment. This period represents the time between the average (across lake types) maximum and minimum densities of algae. We used the rate of decay (parameter b) as the basis of comparison. The exponential decay model produced a strong fit to the data (r^2 mean = 0.95; range = 0.82–0.99). We quantified rates of *Daphnia* population growth using two complementary approaches. First, we calculated rates of exponential growth over the first 10 days following the addition of *Daphnia* using the formula $N_t = N_0e^{rt}$, where N_t is the *Daphnia* density at day 10, N_0 is the initial density of *Daphnia*, r is the rate of increase and t is the time interval. Second, we fitted an exponential function ($y = ae^{bx}$) to the *Daphnia* data for each mesocosm to obtain the parameter b, which describes the rate of increase for a given replicate. We evaluated differences in *Daphnia* growth over longer durations (i.e. the first 16 days of the experiment and from day 1 until peak *Daphnia* population size); the differences in *Daphnia* growth among lake types were similar irrespective of time period, although we did not evaluate differences in growth past day 20.

We evaluated primary production in the mesocosms as one measure of ecosystem function. To calculate primary production, we converted algal cell densities to rates of oxygen production and consumption from a previously established regression. Rates of NPP were then calculated as oxygen production–consumption. We established the relationship between algal cell density and oxygen production–consumption prior to the experiment by sampling the same species of algae in the same mesocosms that were used in the current study. To establish this regression, oxygen consumption was measured with a fluorescent oxygen probe (DO-400, Golden Scientific, Temecula, CA) [33]. We sampled 0.3–0.4 ml from containers containing a range of algal densities similar to those observed in the current experiment. We pulled samples into a 1 ml graduated syringe, and inserted the oxygen probe into the open end of the syringe. We expunged all air from the syringe chamber with the plunger and sealed the tip of the syringe with the probe inside using tacky rubber. The entire system was kept in an incubator to maintain stable temperature and pressure. Oxygen consumption was measured as the change in oxygen concentration over a 20–60 min period, after the probe and sample equilibrated. Oxygen consumption was measured in the dark, with samples wrapped in aluminium foil, and net oxygen production was measured in the light, with rates corrected to the approximate average irradiance (approx. 600 lux). Algal cell density was then converted to oxygen production–consumption by fitting a power function to the data (light measurements $r^2 = 0.76$; dark measurements $r^2 = 0.78$). We used this regression to convert the algal density data collected in each mesocosm to NPP. We compared NPP among lake types with two approaches. First, similar to our measurements of algal decline, we fitted a decay function ($y = ae^{-bx}$) to the date-specific NPP data from day 8 through day 20. Second, we quantified the total amount of (net) primary production over this same period of time by taking the integration of the relationship between NPP and day of the experiment using the trapezoidal rule. This latter approach yields a single estimate of the total amount of oxygen produced over the specified time interval (i.e. mg O_2 l^{-1} per 12 day).

(b) Daphnia *grazing trials*

We performed grazing trials at the completion of the mesocosm experiment to determine whether *Daphnia* from anadromous, landlocked and no alewife lakes differ in their ability to consume algae. This experiment used the same lakes and clones as those used in the mesocosm study. To establish the individuals used in the grazing trials, a single female was removed from existing cultures in the laboratory and was placed in a 90 ml jar containing COMBO medium [29], and fed non-limiting supplies of algae (concentration: >1.0 mg C l^{-1} day^{-1}). The next generation was then established by collecting three neonates per clone and rearing them under the same conditions. Media and algae were changed every other day.

We quantified the algal consumption rates using *Daphnia* that were reared under controlled conditions for two generations. We began this experiment by collecting five neonates (less than 24 h old) from each of six clones per lake (30 individuals per lake). These individuals were taken from clutches 2–4 of the *Daphnia* from the previous generation. We placed six individuals (one individual per clone) into 90 ml jars containing COMBO medium [29]. This density is representative of the maximum abundances of *Daphnia* observed in the mesocosm experiment. Each lake was replicated five times. All phases of *Daphnia* rearing used environmental conditions (photoperiod = 14 L : 10 D cycle, temperature = 20°C) that were similar to those used in the mesocosm experiment, although the photoperiods differed. All animals were provided with algal concentrations similar to the peak algal densities observed in the mesocosm experiment (concentration = 1.03 mg C l^{-1} d^{-1}).

We estimated the grazing rates of *Daphnia* by evaluating declines in algae over a 24 h period. Algal consumption rates were determined by transferring all *Daphnia* to fresh media and algae on day 4, measuring algal concentrations via a laser counter (see description above), and then re-evaluating algal concentration 24 h later. Algal consumption rate was then measured as (algal concentration on day 4 − algal concentration on day 5)/time elapsed.

(c) *Statistical analyses*

We analysed our data using linear mixed models (SAS v. 9.1, SAS Institute, Cary, NC) implemented with restricted maximum-likelihood estimation. For each variable, lake type was entered as a fixed effect, and replicate lake populations were nested within lake type as a random effect. Temperature and light level of each mesocosm were included as covariates. Our design used between-within subjects degrees of freedom (Proc mixed, ddfm = bw) to determine the denominator degrees of freedom. A likelihood ratio test was used for tests of significance of the random effects. Post hoc Tukey tests followed significant ($p < 0.05$) lake type effects.

(d) Daphnia *and phytoplankton biomass in lakes*

To compare the results of our laboratory experiment with the patterns observed in lakes, we sampled *Daphnia* and phytoplankton abundances in lakes. We sampled for plankton in April because zooplankton and, to a lesser extent,

phytoplankton are abundant in our lakes in April [13], and YOY alewife are absent from anadromous lakes during this period. We sampled zooplankton on one date (between 1 and 15 April 2005) in three anadromous (Bride, Dodge and Gorton), four landlocked (Amos, Long, Quonnipaug and Rogers) and four no alewife (Black, Gardner, Hayward and Linsley) lakes. Zooplankton were collected from the deepest point in each lake with an 80 μm mesh plankton net [13]. Each sample was preserved in 70 per cent ethanol, and *Daphnia* were subsequently counted after samples were split with a plankton splitter. Zooplankton biomass (microgram per litre) was quantified for each lake via length–mass regressions [13]. The evaluation of *Daphnia* biomass among lake types, as opposed to the abundances of *Daphnia*, represents a proxy for total grazing pressure on phytoplankton. Differences in *Daphnia* biomass (log-transformed) were analysed using a one-way ANOVA, with lake type entered as a fixed effect.

Phytoplankton biomass was estimated from chlorophyll *a* concentrations. Chlorophyll *a* was quantified in three anadromous lakes (Bride, Dodge and Gorton), three landlocked lakes (Amos, Quonnipaug and Rogers) and three lakes without alewives (Linsley, Gardner and Hayward). All sampling occurred between 31 March and 15 April over at least two separate years. Sampling occurred in 2005–2006 and 2008–2009 in Bride, Dodge, Quonnipaug, Rogers and Linsley, and in 2005–2006 in Gorton, Amos, Gardner and Hayward. We sampled over multiple years to determine the consistency of any variation in phytoplankton abundance among lake types. Water samples were filtered onto Whatman GF/F filters (Whatman, Brentford, UK) and analysed for chlorophyll *a* concentrations on a Turner Designs TD-700 fluorometer (Turner Designs, Sunnyvale, CA) following Environmental Protection Agency method 445.0. We evaluated the mean epilimnetic chlorophyll concentration for the total plankton community. Differences in chlorophyll *a* concentration among lake types were analysed with a one-way analysis of variance. We used the mean chlorophyll concentration for each lake in the analysis.

3. RESULTS

(a) *Mesocosm experiment*

We observed significant differences in algal population dynamics and NPP among lake types (figure 1 and table 1; electronic supplementary material, table S2). Algal densities in mesocosms with *Daphnia* from anadromous lakes declined at rates that were 41 and 42 per cent faster (over days 8–20) than algae in mesocosms with *Daphnia* from landlocked or no alewife lakes, respectively (electronic supplementary material, tables S2 and S3; figure 1). NPP was 32 to 36 per cent lower during this same time period in mesocosms with *Daphnia* from anadromous versus landlocked and no alewife lakes (table 1 and figure 1). Post-hoc Tukey tests showed that anadromous lakes differed significantly from landlocked and no alewife lakes (figure 1). The results for primary production are similar if we evaluate the rate of decline of NPP over days 8–20; significant differences among lake types were observed as NPP declined at rates that were 51 and 56 per cent faster in mesocosms with *Daphnia* from anadromous lakes than NPP in mesocosms with *Daphnia* from landlocked or no alewife lakes, respectively (table 1; electronic supplementary material, tables S2 and S3). There were no significant differences in NPP among lake types over days 20–41 as all mesocosms converged on low algal densities (average NPP days 20–41 in mg O_2 l^{-1} d^{-1}: anadromous = 0.199 ± 0.011, landlocked = 0.243 ± 0.011, no alewife = 0.219 ± 0.0106; $F_{2,6} = 3.65$, $p = 0.092$). There were also no significant differences in algae cell size at the peak abundances of *Daphnia* (average cell size in μm ± 1 s.e.: anadromous = 5.25 ± 0.28, landlocked = 5.09 ± 0.1, no alewife = 4.92 ± 0.18; $F_{2,6} = 0.79$, $p = 0.49$).

We observed significant ($p < 0.05$) differences in rates of population growth of *Daphnia* among lake types (table 1; electronic supplementary material, tables S2 and S3); rates of exponential growth during the first 10 days were 23 to 28 per cent faster in mesocosms with *Daphnia* from anadromous versus landlocked or no alewife lakes (figure 1). *Daphnia* from anadromous lakes were approximately 2.5 times more abundant by day 10 of the experiment than *Daphnia* from the other lakes (figure 1), and peak abundances of *Daphnia* occurred significantly earlier (approx. 6 days; table 1, electronic supplementary material, tables S2 and S3; figure 1) in mesocosms with *Daphnia* from anadromous lakes. Post hoc Tukey tests revealed that *Daphnia* from anadromous lakes exhibited significantly faster rates of population growth and significantly earlier timing of peak abundances than *Daphnia* from landlocked and no alewife lakes (electronic supplementary material, table S2). There were no significant differences in the size-structure of the *Daphnia* populations (average proportion of juveniles ± 1 s.e.: anadromous = 0.57 ± 0.01, landlocked = 0.6 ± 0.014, no alewife = 0.58 ± 0.01; $F_{2,6} = 0.56$, $p = 0.6$).

(a) *Grazing trials*

We performed separate but complementary experiments using the same clones used in the mesocosm experiment to evaluate the ability of *Daphnia* to graze upon algae at an equal density. Our consumption experiments revealed no significant differences in *Daphnia* grazing rates among lake types (mean change in algal cells ml^{-1} ± 1 s.e.: anadromous = 72.4 ± 17.1, landlocked = 95.1 ± 17.4, no alewife = 67.4 ± 13.0; $F_{2,6} = 1.67$, $p = 0.27$).

(b) Daphnia *and phytoplankton biomass in lake*

We evaluated *Daphnia* and phytoplankton abundances at the whole-lake level in April to compare trends among lakes. We found marginally non-significant differences in the biomass of *Daphnia* ($F_{2,8} = 3.26$, $p = 0.092$; figure 2). *Daphnia* from lakes with anadromous alewives were more abundant than *Daphnia* from lakes with landlocked alewives (317×) or no alewives (2.4×). The differences were significant ($F_{2,7} = 6.12$, $p = 0.029$) following the removal of one statistical outlier (standardized residual more than 2). We found significant whole-lake differences in the biomass of phytoplankton (chlorophyll) among lakes types ($F_{2,5} = 7.07$, $p = 0.035$; figure 2). Phytoplankton biomass in lakes with anadromous alewife was 31 and 21 per cent lower than landlocked lakes and those with no alewives, respectively.

4. DISCUSSION

Our experimental results demonstrate that contemporary life-history evolution in *Daphnia* can significantly affect phytoplankton population dynamics and ecosystem

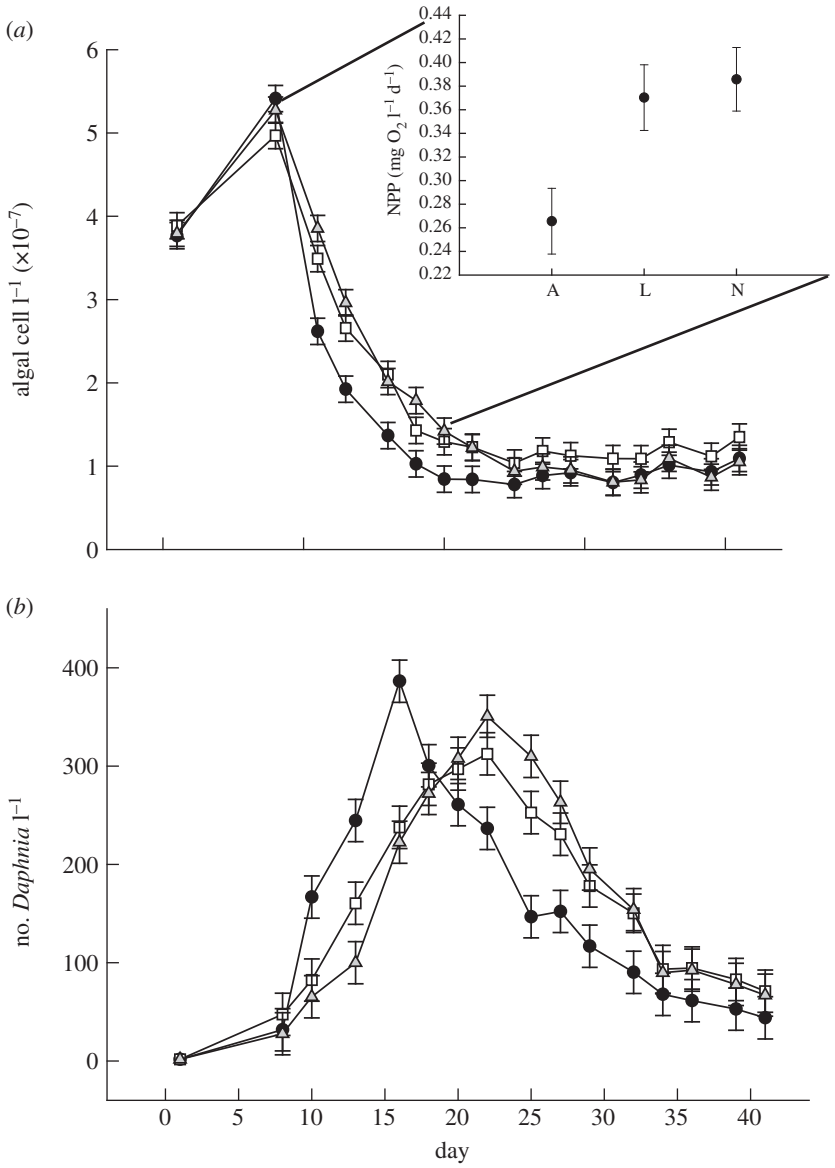


Figure 1. Algal and *Daphnia* population dynamics. Black circles denote anadromous lakes; white squares, landlocked lakes; grey triangles, no alewife lakes. Error bars = ± 1 s.e. (*a*) Algal density. We observed a significantly ($p < 0.05$) faster rate of decline of algae in mesocosms with *Daphnia* from anadromous lakes versus *Daphnia* from landlocked or no alewife lakes. Inset: rates of net primary production. A, anadromous; L, landlocked; N, no alewife. Significant ($p < 0.05$) differences among lake types were observed. (*b*) *Daphnia* density (all individuals). *Daphnia* from anadromous lakes exhibited significantly ($p < 0.05$) faster rates of population growth and earlier timing of peak abundances than *Daphnia* from landlocked or no alewife lakes.

Table 1. Analyses of algal and *Daphnia* dynamics. Parameters were analysed using linear mixed models, with lake type entered as a fixed effect, lake nested within lake type as a random effect, and individual mesocosm temperature and light level included as covariates. When a covariate was not significant ($p > 0.05$), it was removed from the model and the data were reanalysed. b, rate of exponential decay; d, days; r, intrinsic rate of increase.

factor	d.f.	rate of algal decline (b)	NPP (mg O_2)	rate of NPP decline (b)	timing of algal max. (d)	*Daphnia* pop. growth (*r*)	timing of *Daphnia* max. (d)	max. *Daphnia* density (no. l^{-1})
covariates:								
light	1,16	5.03*	10.84**	11.6**	0.17††	0.07††	0.28††	0.35††
temperature	1,16	0.36††	0.09††	0.04††	0.41††	<0.001††	3.5†	32.0***
fixed effects:								
lake type	2,6	7.72*	5.18*	6.16*	4.35†	8.78*	6.41*	0.2††
random effects:								
lake	1	0.29††	0.19††	0.08††	1.37††	0.29††	0.71††	0.34††

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; $^{\dagger}0.05 < p < 0.1$; $^{\dagger\dagger}p > 0.1$ (n.s.).

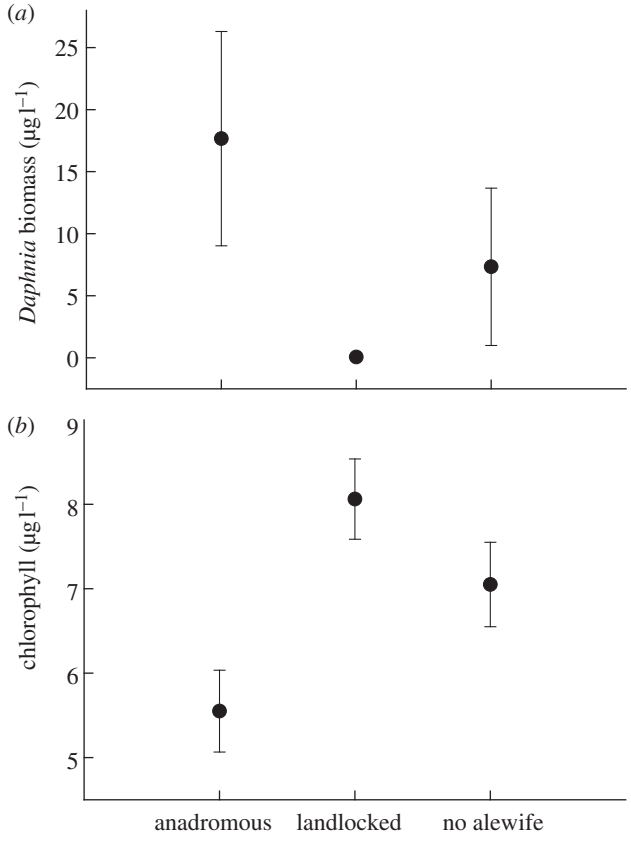


Figure 2. Phytoplankton and *Daphnia* biomass in lakes in April. (*a*) *Daphnia* biomass. Zooplankton sampling occurred in the three anadromous (Bride, Dodge and Gorton), four landlocked (Amos, Long, Quonnipaug and Rogers) and four no alewife (Black, Gardner, Hayward and Linsley) lakes in April 2005. Differences among lake types were marginally non-significant ($F_{2,8} = 3.26$, $p = 0.092$). (*b*) Phytoplankton biomass. Chlorophyll *a* was quantified in three anadromous (Bride, Dodge and Gorton), three landlocked (Amos, Quonnipaug and Rogers) and three no alewife (Gardner, Hayward and Linsley) lakes. The biomass of total chlorophyll differed significantly ($p < 0.05$) among lake types. Error bars = ± 1 s.e.

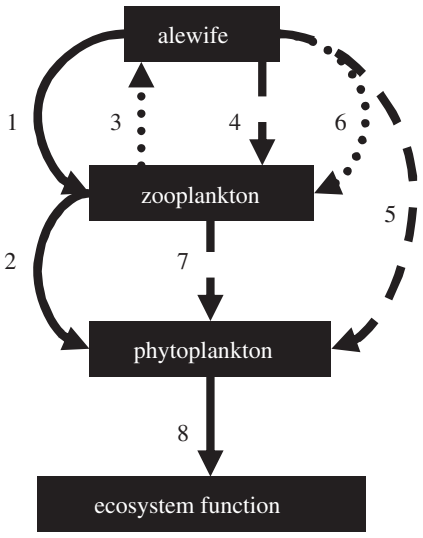
function (table 1 and figure 1). In mesocosms that contained *Daphnia* from lakes with anadromous alewives, algal abundance declined significantly faster while rates of NPP were significantly lower than mesocosms with *Daphnia* from landlocked or no alewife lakes (table 1 and figure 1; electronic supplementary material, table S2). These differences in phytoplankton dynamics and primary production were probably driven by a link between life-history traits and population growth; *Daphnia* from lakes with anadromous alewives exhibited significantly faster rates of population growth than *Daphnia* from landlocked or no alewife lakes (table 1 and figure 1; electronic supplementary material, table S2) and there was no evidence for differences in grazing rates among *Daphnia* genotypes (i.e. trait- or individual-level impacts) or in the size-structure of the experimental populations (see §3). Much recent work has shown that phenotypic or genetic variation in one community member can significantly influence ecological properties [4–17]. Given that (i) landlocked and anadromous populations differ genetically [24], (ii) morphological differences among juvenile alewives are maintained in a common garden for several months [25], (iii) morphological traits are highly heritable [34–36], and (iv) intraspecific variation in alewives drives evolutionary divergence in *Daphnia* [26], our results argue that evolutionary interactions across trophic levels, or a cascade of evolutionary change, impact phytoplankton dynamics and ecosystem function (figure 3).

(a) *Field versus laboratory*

For there to be an ongoing feedback between ecological and evolutionary processes, evolutionary divergence must have significant and observable effects on ecological properties in a natural setting, and this link from evolution to ecology needs to be apparent at the scale at which selection operates. To gain insights into the importance of our laboratory experiment from the perspective of natural ecosystems, we evaluated *Daphnia* and phytoplankton abundances at the whole-lake scale over multiple years. This data allow us to ask whether our laboratory results are congruent with whole-lake data.

At the whole-lake scale, the differences in the biomass of plankton among lake types in April are similar to those observed in the laboratory experiment. *Daphnia* in lakes with anadromous alewives consistently reach abundances in April that are higher than *Daphnia* in lakes without alewives and at least two orders of magnitude greater than *Daphnia* populations in lakes with landlocked alewives [13] (figure 2*a*). These differences in the biomass of *Daphnia* in lakes are correlated with divergence in phytoplankton abundances. The biomass of phytoplankton in April is significantly lower in lakes with anadromous alewives than in lakes with landlocked alewives or lakes without alewives (figure 2*b*). These trends in plankton abundances are transient because the onset of intense predation by anadromous alewives in late spring alters plankton community structure in summer [13].

What explains the trends at the whole-lake level? In April, *Daphnia* are not subjected to predation by anadromous alewives, but landlocked alewives are present. Alewives are strong predators on *Daphnia* [21], and *Daphnia* are known as important consumers of phytoplankton [22–23]. As a result, differences in *Daphnia* and phytoplankton biomass between lakes with landlocked and anadromous alewives are likely to be influenced by variation in alewife predation pressure. Conversely, lakes with anadromous alewives and lakes without alewives do not differ in non-alewife zooplanktivorous fish community composition in April. Yet *Daphnia* abundances are higher and phytoplankton abundances are consistently lower in lakes with anadromous alewives than in those without alewives (figure 2). These results suggest that the observed differences in plankton biomass do not simply reflect variation in the strength of a fish-mediated trophic cascade. If this was the case, then *Daphnia* and phytoplankton abundances should be similar in lakes with anadromous alewives and no alewives in the spring. Many biotic and abiotic factors can influence plankton abundances in lakes, but we suggest that the whole-lake differences in plankton abundance we observe could signal the impact of evolution in *Daphnia* on the ecology of these lakes. This speculation is supported by similar magnitudes of divergence in the field and in laboratory; *Daphnia* are 147 per cent (field) and 141 per cent (laboratory) more abundant in lakes with anadromous



past research:

1, 2. Alewives structure zooplankton community [13,21]. *Daphnia* influence phytoplankton abundance [22,23].

3. Zooplankton community structure drives divergence between anadromous and landlocked alewives [15,24,25].

4, 5. Phenotypic differences in alewives have differential impacts on zooplankton and phytoplankton [13,15].

6. Variation in alewives drives evolution in zooplankton [26].

current study:

7. Evolution in zooplankton has divergent impacts on phytoplankton.

8. Divergent impacts of zooplankton evolution on phytoplankton alter ecosystem function.

Figure 3. A conceptual model illustrating key ecological and evolutionary pathways in the alewives–zooplankton system. Ecological interactions are depicted by solid arrows. Evolutionary interactions are depicted by dotted arrows. Pathways from evolution to ecology are depicted by dashed arrows.

alewives, while phytoplankton biomass is 21 per cent (field) and 27 per cent (laboratory) lower in lakes with anadromous alewives.

(b) *Link from evolution to ecology*

The effect of evolution on ecology, and the potential for ecology and evolution to interact via reciprocal feedbacks, is a rapidly growing field of research [1–3]. There is evidence for a pathway from evolution to ecology from multiple perspectives. For instance, research has shown that specific genotypes or genetic diversity can differentially alter the properties of populations, communities and ecosystems [4–12]. Such work provides a clear link between genetics and ecology, and indicates the potential for contemporary evolution to influence ecology. Furthermore, laboratory experiments exploring interactions between rotifers (predator) and algae (prey) demonstrated that the evolution of prey can significantly alter the population dynamics of predator and prey [36,37]. Finally, recent studies of contemporary evolution in natural populations of guppies, sticklebacks and alewives illustrated the ecological importance of adaptive divergence [13–17]. For example, Bassar *et al.* [17] showed that populations of guppies (*Poecilia reticulata*) adapted to environments that differ in predation intensity alter variables such as algal standing stocks, primary production and nutrient fluxes. In all three species of fish, there is evidence for genetic differentiation [24,38,39], and in guppies and sticklebacks trait differences are maintained after multiple generations of laboratory rearing [40,41]. However, these experiments [13–17] all used wild-caught individuals to demonstrate the community and ecosystem impacts of intraspecific variation, which potentially confound environmental and genetic influences.

Our results build upon previous studies [4–17] by using laboratory-reared populations of locally adapted *Daphnia* to show that contemporary evolution can significantly influence prey population dynamics and one measure of ecosystem function (see also [10]). This common garden approach is important because it demonstrates the impact of genetically based variation on phytoplankton abundances and NPP, and identifies difference in life-history traits and population growth as an important mechanism. Collectively, it is becoming increasingly clear that recent evolutionary change could represent a significant agent of ecological change.

5 CONCLUSIONS

Explorations of feedbacks between ecology and evolution have primarily focused on the interplay between changes in one organism and the rest of the environment. Here we take a significant step in characterizing how diversification in multiple organisms in a community could alter the functioning of ecosystems. Prior work in this system showed that divergence in alewives has direct effects on community and ecosystem processes [13,15], which, in turn, drives life-history evolution in *Daphnia* [26] (see figure 3). Here we evaluated the impact of these alewife–*Daphnia* interactions on lower trophic levels and showed that this connection between alewife diversification and life-history evolution in *Daphnia* further alters phytoplankton dynamics and primary production (figure 3). Our results argue that intraspecific evolutionary divergence among organisms and across trophic levels can have consequences that ultimately impact the functioning of ecosystems. The extent to which these interactions may involve more than two trophic levels remains to be seen. Given that natural systems typically contain multiple trophic levels and also that linkages among trophic levels are common, our results indicate that a cascade of evolutionary change could be a key contributor to feedbacks between ecology and evolution.

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