Intraspecific variation and warming have comparable effects on eco-evolutionary dynamics.

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Abstract

Rapid evolutionary divergences within species can affect the way organisms shape their environment, which in turn can affect the evolutionary trajectories of species. These eco-evolutionary feedbacks have recently been proved, but their relevance compared to that of key environmental drivers in the dynamics of biological systems is still unknown. Here, we filled this gap in knowledge by quantifying the effects of intraspecific variation on ecological processes and evolutionary trajectories and by comparing these effects to those induced by a 2°C warming. We used a common gardening experiment with simultaneous variations in the genetic and phenotypic characters of a widespread freshwater fish species (the European minnow, *Phoxinus phoxinus*) and in the ecosystem temperature. We showed that intraspecific variation led to eco-evolutionary feedbacks that were as strong as the eco-evolutionary consequences of ecosystem warming. Specifically, we found that variations in two heritable phenotypic traits (body size and growth rate) in adult minnows led to ecological changes in the environment that subsequently modulated the evolutionary trajectories of juvenile minnows. Importantly, the eco-evolutionary consequences of intraspecific variation were different and independent from those induced by warming. We conclude that eco-evolutionary feedbacks are not biologically negligible and that intraspecific variation is an indisputable driver of both ecological and evolutionary dynamics.

Significance statement

Global changes are directly modifying the functioning of ecosystems and the evolution of species. Phenotypic and genetic variation observed within species (intraspecific variation) has recently also been shown to alter biological dynamics and
is threatened by global changes. It is hence of utmost importance to quantify the relative importance of intraspecific variation and global changes (here considering warming) on biological dynamics. Here, we demonstrate that intraspecific variation affects ecosystem functioning as intensively as a warming of 2°C. The ecosystem changes induced by intraspecific variation were strong enough to generate feedbacks in the evolution of organisms, with a magnitude similar to that of warming. Intraspecific variation should be a major target of conservation plans because it affects biological dynamics as much as contemporary warming.
Introduction

Reciprocal interactions between ecological and evolutionary dynamics occurring over contemporary time scales (eco-evolutionary dynamics) have been increasingly studied in the last two decades\(^1\)\(^-\)\(^4\). Theory predicts that evolutionary diversification within a species can affect ecological processes such as primary productivity, resulting in environmental changes that can act as new selective pressures modulating the evolution of organisms\(^5\)\(^-\)\(^7\). These reciprocal interactions can generate eco-evolutionary feedbacks linking species evolution and ecosystem functioning, providing an integrative and temporally dynamic framework for understanding biological systems\(^8\).

Although the study of eco-evolutionary feedback loops has long been conceptual\(^3\)\(^,\)\(^5\)\(^,\)\(^8\), recent experimental studies have demonstrated the existence of these processes\(^9\)\(^-\)\(^12\). However, the relative importance of eco-evolutionary feedbacks in the dynamics of natural ecosystems has been questioned\(^2\)\(^,\)\(^3\).

To answer this question, it is important to determine whether eco-evolutionary feedbacks are negligible compared to key environmental drivers affecting both ecological and evolutionary dynamics, such as temperature, nutrient availability, predation or parasitism\(^2\)\(^,\)\(^13\). Recent investigations have revealed that intraspecific variation (emerging from evolutionary diversification) can affect ecological processes with an intensity similar to that of key environmental drivers\(^14\)\(^-\)\(^16\). However, whether the effects of intraspecific variation on evolutionary dynamics (mediated by the effects of intraspecific variation on ecological processes) are similar to or stronger than those of indisputable environmental drivers is still unknown. Addressing this question is fundamental to determining the relative contribution of eco-evolutionary feedbacks in driving the responses of biological systems to varying environmental conditions\(^13\).
Here, we experimentally quantified the consequences of intraspecific variation on ecological processes and subsequent evolutionary trajectories (i.e., eco-evolutionary feedbacks) and then compared these consequences to the ecological and evolutionary consequences of warming. Temperature is a key abiotic factor that strongly varies at the landscape scale, directly affects key ecological functions such as primary productivity and ecosystem respiration\cite{17-19}, and imposes a strong selective pressure on organism traits\cite{20-22}. We ran a two-phase “common gardening experiment” \textit{(sensu)}\cite{8,11}, Fig. 1) and manipulated (i) intraspecific variation in a freshwater fish (European minnow, \textit{Phoxinus phoxinus}) by selecting individuals from six evolutionary and functionally distinct populations (i.e., differences in genotypes and functional traits, see Methods and Fig. S1 and S2) and (ii) water temperature by setting mesocosms varying by 2°C throughout the experiment (Fig. S3). An increase in temperature of 2°C represents the general warming expectations for freshwaters over the next 40 years\cite{23}. During the first experimental phase (\textit{ecological effects}, 10-weeks), we compared the strengths of the effects of intraspecific variation among adult minnows, to the strengths of the effects of warming on prey community structure and ecosystem functions (Fig. 1). Adults were then removed from the mesocosms and replaced by juveniles with a common origin for the second experimental phase (\textit{evolutionary effects}, 11-weeks). We tested how the ecological variations induced during the first phase (due to intraspecific variation and/or warming) affected the evolutionary trajectories (fitness and performance) of juveniles.

**Results**

In the first phase, we found that the effects of intraspecific variation in adult minnows on ecological processes (measured over all ecological parameters) were at
least as strong as those of warming on ecological processes (mean effect size (MES) ± standard error = 0.103 ± 0.018 and MES ± SE = 0.078 ± 0.036 for intraspecific variation and warming, respectively; $t = 0.624$, d.f = 18, $p = 0.540$, Fig. 2). Nonetheless, the effects were heterogeneous across ecological parameters (Fig. 2b, Fig. S4). For instance, intraspecific variation had the strongest ecological effect on the abundance of Cladocera, whereas warming had a particularly strong ecological effect on decomposition rate (Fig. 2b, Fig. S5 and S6). A single interaction term between warming and intraspecific variation was significant (i.e., for benthic primary productivity, $F = 10.831$, d.f = 5,52, $p = 0.022$), indicating that the ecological effects of intraspecific variation were not temperature-dependent for most ecological parameters. The body mass and growth rate of minnows, two functionally important traits differing among minnow populations (although the later was also affected by experimental temperature, Fig. S2), were included in a path analysis testing the direct and indirect relationships among trait variation, warming and ecological parameters. We found that intraspecific variation in these two functional traits affected ecological processes as much as warming and that body mass was the most influential functional trait (Fig. 3). We further found that the intraspecific trait variation acted both directly and indirectly on ecological parameters (Fig. 3b). For instance, adult body mass affected the abundance of Copepoda directly, subsequently leading to an indirect effect on the abundance of Cladocera (Table 1, Fig. 3a). The ecological effects of warming were mainly direct (67%), although some indirect effects were also observed (Fig. 3b). For instance, warming directly increased Bivalvia abundance, positively affecting the abundance of Copepoda and the size of Cladocera, hence representing an indirect effect of warming on the zooplankton community (Fig. 3).
In the second phase (Fig. 1), we found that the strength of the effect sizes of intraspecific variation and warming on the fitness proxies (survival, growth rate and body condition) were similar (MES ± SE = 0.044 ± 0.004 and MES ± SE = 0.032 ± 0.016 for intraspecific variation and warming, respectively, \( t = 0.665, \text{d.f} = 4, p = 0.542 \), Fig. 2). Notably, the average effect sizes of intraspecific variation and warming on the evolutionary parameters were half the intensity of those on ecological parameters (Fig. 2), indicating that evolutionary dynamics were less affected than ecological processes by the initial treatments. Nonetheless, we observed eco-evolutionary feedbacks since the juvenile growth rate was related to the ecological parameters (benthic primary productivity, decomposition rate and Cladocera abundance), which were controlled by intraspecific variation (Fig. 3a). Juvenile survival was also related to juvenile growth rate (density-dependent growth rate) and was indirectly related to warming. We also identified a direct relationship between adult trait variation and juvenile growth rate (Fig. 3), which was unexpected given that the adults were removed from the tanks before the juveniles were introduced. This result indicates interspecific variation had unmeasured indirect effects (mediated by ecological changes) on evolutionary dynamics. Juvenile survival was positively related to the body size of Cladocera and negatively related to temperature (i.e., survival increased as temperature decreased). Juvenile body condition covaried with both juvenile survival and growth rate and was lower when the abundance of Bivalvia, which was directly affected by temperature, was high (Fig. 3).

**Discussion**

We found that the ecological consequences of intraspecific variation and warming were similar in strength but acted on different ecological processes. Adult
minnows from evolutionary and phenotypically distinct populations modulated both
the abundance and the size of their prey (zooplankton Cladocera), probably because
these populations have different prey consumption and selectivity characters. In
contrast, warming strongly accelerated leaf litter decomposition, probably because
warmer temperatures stimulate bacterial activity\textsuperscript{18,20}. The evolutionary effects of
intraspecific variation (resulting from eco-evolutionary feedbacks) and warming were
also similar in strength, regardless of the fitness traits investigated. For instance, the
survival of juvenile minnows was higher the low-temperature than the high-
temperature treatment (which is expected given that minnows inhabit relatively cold
rivers\textsuperscript{24}), whereas the growth rate of juveniles differed depending on the adult
minnow population introduced at the onset of the experiment. Notably, the effects of
warming on the evolutionary trajectories of juveniles might be overestimated
compared to the effects of intraspecific variation, since the former represents the
cumulative results of both second-phase direct effects and first-phase indirect effects
mediated by ecological changes. Overall, our results demonstrate that intraspecific
variation can affect the ecological and evolutionary dynamics of biological systems as
much as warming does, although in different directions. Thus, eco-evolutionary
feedbacks occur in this type of biological system and significantly modulate the
whole biological dynamics of ecosystems.

Here, the eco-evolutionary feedback comprised indirect effects of intraspecific
variation among adult minnows on the evolutionary trajectory of juveniles, which
were mediated by the direct consequences of adult minnows on the ecological theatre.
Currently, very few studies have demonstrated the existence of eco-evolutionary
feedback, and most of have focused on model organisms\textsuperscript{9−12}. By focusing on a non
model organism, our study extends the taxonomic scope of eco-evolutionary feedback
loops and suggests that this process does not concern only species with strong eco-evolutionary divergences. We further identified two heritable traits (body mass and growth rate) that partially initiate these eco-evolutionary feedbacks and vary between adult minnows originating from environmentally and evolutionary distinct populations. For instance, the zooplankton community was strongly impacted by trait variability, probably through diet specialization. In turn, juveniles performed better (i.e., higher growth rate) in the mesocosms with a higher abundance of zooplankton, confirming that eco-evolutionary feedbacks could arise from a change in prey availability. Previous studies have identified growth rate and body mass as important traits for ecological processes, and we here provide novel insights into the indirect evolutionary consequences of these traits.

Interestingly, intraspecific variation and warming acted additively but not interactively on ecological and evolutionary dynamics. Indeed, we identified only one significant interaction between intraspecific variation and warming on benthic primary productivity, indicating that the effect of intraspecific variation on benthic primary productivity dynamics was temperature-dependent. This finding confirms that the ecological consequences of intraspecific variation are often independent from the abiotic context, which might also be the case for eco-evolutionary feedbacks. This independence is surprising, since local adaptation for specific fitness traits and/or for reaction norms often leads to strong context dependency in the responses of organisms to local abiotic conditions, and we may have observed cascading interactive effects of intraspecific variation on ecological and evolutionary dynamics. This finding is important because the absence of strong interactive effects reduces biological complexities and may therefore improve our ability to
forecast the ecological and evolutionary consequences of environmental and biodiversity changes\textsuperscript{34}.

In conclusion, we demonstrated for the first time that the magnitude of eco-evolutionary feedbacks was as strong as the effects of warming on ecological and evolutionary dynamics; thus, eco-evolutionary feedbacks are not biologically negligible. Intraspecific variation in major heritable traits such as growth rate or body mass is commonplace in the wild and can arise via various evolutionary processes including natural selection and genetic drift\textsuperscript{35}. Our study proves that intraspecific variation is an indisputable driver of biological dynamics (at both the ecological and evolutionary scale) that should not be considered noise in ecosystems. Current environmental changes are rapid and can directly affect ecosystem functioning\textsuperscript{18}. These changes can also directly modulate the distribution of intraspecific variation in landscapes and thereby indirectly effect the eco-evolutionary dynamics of biological systems\textsuperscript{10,11}. These results reinforce recent reports that changes in intraspecific variations of wild populations (e.g., harvest\textsuperscript{36} or pollution\textsuperscript{37}) could be as harmful as considerable environmental changes (e.g., warming) to biological dynamics and that this facet of biodiversity should therefore be conserved adequately\textsuperscript{38,39}.

**Methods**

**Study species**

European minnow (*Phoxinus phoxinus*) was used as the model species. *P. phoxinus* is a small-bodied (maximum length: \(~80\) mm, mean generation time: \(~2\) years) cyprinid fish species widely distributed in Western Europe. *P. phoxinus* lives in relatively cold waters, mainly in streams and rivers but also in mountain lakes\textsuperscript{24,39}. It is a generalist
species that feeds on small invertebrates, algae, zooplankton and small fish larvae\textsuperscript{40-42}.

In September 2016, we collected adult minnows by electrofishing in six rivers in southwestern France (Fig. S1). We selected populations that were isolated geographically (minimal riparian distance among sites = 64 km, mean ± SD = 343 km ± 182) and had distinct environments (Fig. S7) to favor both genetic and phenotypic divergences among populations. Accordingly, the mean genetic divergence among populations was $F_{st} = 0.162$ (measured using 17 microsatellites, min-max = 0.043-0.313), indicating a high evolutionary distinctiveness among the populations. The body mass (a highly heritable\textsuperscript{25,26} and important functional trait\textsuperscript{43,44}, Fig. S2) of the sampled populations also varied, as did two other important functional traits\textsuperscript{20,45-47}:

the metabolic (min-max = 0.1388-0.2737 mg O\textsubscript{2}.g\textsuperscript{-1}.h\textsuperscript{-1}, $F = 14.599$, d.f = 5,188, $p < 0.001$) and ammonium excretion (min-max = 17.02-43.48 µg NH\textsubscript{4+}.g\textsuperscript{-1}.L\textsuperscript{-1}.h\textsuperscript{-1}, $F = 4.695$, d.f = 5,175, $p < 0.001$, unpublished data) rates. All fish collections and husbandry for adults and juveniles were conducted in accordance with sampling permits obtained from local authorities (25-08-2016, 24-05-2016, 09-273, SA-013-PB-092, A09-3). Fish from different populations were reared separately for ~6 months in 1100 L outdoor tanks to minimize previous environmental effects on phenotypes. During rearing, the fish were fed with a mixture of pelletized food and dead chironomids until the start of the experiment.

Phase 1: effects of intraspecific variation and temperature on ecological processes

The experiment consisted of 72 replicated mesocosms placed in a greenhouse with a 12:12 h light-dark photoperiod. Mesocosms were filled with 100 L of tap water and 1
cm of gravel covering the bottom of each tank. Tanks were covered with a 1 cm plastic mesh net to prevent fish escapes. Nutrients were added to the mesocosms using 5 mL of solution containing nitrogen and phosphorus (ratio N: P: K = 3.3: 1.1: 5.8) on December 2nd 2016. Each mesocosm was then inoculated with 200 mL of a concentrated solution of phytoplankton from a unique lake origin (Lake Lamartine, France 43°30'21.5"N, 1°20'32.7"E) on December 12th 2016. Two months later (February 15th 2017), an additional 200 mL of concentrated solution of zooplankton from the same lake was added to each mesocosm. Finally, we inoculated each mesocosm with sediment and macroinvertebrates (i.e., mainly Gastropoda and Bivalvia) from Lake Lamartine.

Each tank was assigned to one of twelve treatments according to a full-factorial design with intraspecific variation (i.e., population origin, six levels corresponding to each population) and temperature (two levels: low and high temperature) as the main factors (Fig. 1). Each treatment was replicated six times. Water temperature was controlled and adjusted using a Blue Marine® water chiller and a stainless steel coil placed in each tank through which a flux of water (independent from the water of the tanks) flowed at either 18°C or 21°C. Natural seasonal temperature variations occurred; on average, the low and high water temperature treatments differed by 2.08°C according to seasonal variations (Fig. S3).

In March 2017, adult fish were weighed to the nearest 0.01 g and a single fish was introduced to each mesocosm. This individual-based approach prevented the experimental ecosystems from collapsing due to the over-density of top consumers and allowed the ecological effects of individual phenotypes to be measured. After 73 days (Fig. 1), each fish was removed, weighed and euthanized in a solution of benzocaine at 25 mg.L⁻¹. The growth rate (% day⁻¹) of the adults was calculated
as $SGR = \frac{\ln(W_f) - \ln(W_i)}{T} \times 100$, where $W_f$ and $W_i$ are the final and initial body masses, respectively, and $T$ is time interval between two measurements (in days).

Concomitantly, we measured multiple community and ecosystem parameters to evaluate differences in ecological processes among treatments.

(i) Pelagic algae stock was assessed as a proxy of pelagic primary productivity. Measurements were performed using a portable spectrometer (AlgaeTorch, bbe Moldaenke®) to assess the chlorophyll-a concentration ($\mu$g/L) in the water column. Two measurements were taken in each mesocosm and were averaged for the analyses.

(ii) Benthic algae stock was assessed as a proxy of the benthic primary productivity using a portable spectrometer (BenthoTorch, bbe Moldaenke®). The chlorophyll-a concentration ($\mu$g/cm$^2$) was measured on two tiles (20 x 20 cm) placed in the mesocosms the day before the start of the experiment. These measurements were averaged for analyses.

(iii) The abundance of filamentous algae was quantified. Filamentous algae cover (%) was visually estimated by two operators, and values were averaged for analyses.

(iv) Zooplankton community was assessed by filtering 5 L of water through a 200 $\mu$m sieve. Samples was conserved in a 70% ethanol solution and subsequently identified to the order or family levels, including Copepoda (i.e., Cyclopoida and Calanoida) and Cladocera (i.e., Daphniidae, Chydoridae and Bosminidae). Zooplankton size was assessed by measuring 10 individuals of each order and family level from each mesocosm to the nearest 0.001 mm using ImageJ®.

(v) Decomposition rate was measured by quantifying the mass loss of black poplar ($Populus nigra$, a dominant riparian tree in southern France) abscised leaves$^{48}$. 
One day before the start of the experiment, 4 g of air-dried leaves were put in each mesocosm within a coarse mesh (1 x 1 cm) bag. At the end of the phase 1, the remaining leaf material was removed from the mesocosms, rinsed with tap water, oven dried at 60°C for three days and weighed to the nearest 0.001 g to assess the loss of biomass. The decomposition rate was calculated as $k = -\frac{\ln(X)}{t}$, where $X$ is the proportion of litter remaining after phase 1 and $t$ is the elapsed time in days.

(vi) Macroinvertebrates (> 1 mm, essentially molluscs) were collected from the mesh bags used to measure decomposition rates, conserved in a 70% ethanol solution, and identified as Bivalvia or Gastropoda.

(vii) Abiotic parameters of the water [pH, specific conductance ($\mu$S), oxygen concentration (mg.L$^{-1}$) and turbidity (NTU)] were measured with a multiparameters probe (YSI Pro DSS Water Quality Meter®). We summarized these parameters using principal component axis (PCA) (package ade4 in R$^{49}$). We selected the first axis of the PCA as the synthetic variable. This axis explained 60% of the variance and was correlated to the oxygen concentration (loading component: -0.95), pH (-0.93), specific conductance (0.70) and, to a lesser extent, turbidity (0.25).

Phase 2: effect of ecological differences on juvenile evolution

After the removal of adult fish on June 13$^{th}$ 2017, 45 juvenile minnows were introduced to each mesocosm. We used juveniles from a unique origin (i.e., fish farm, Amorvif EURL) to control for potential genetic effects. Juveniles were introduced as soon as possible after hatching to increase the possibility of differential mortality and/or ontogenetic plasticity. Therefore, juveniles were introduced when they were only two weeks old as stage III larvae$^{50}$ (Fig. S8). They were not manipulated (i.e., weighted and/or measured) before being randomly introduced in the mesocosms to
limit potential mortality. The juveniles were removed from the mesocosms 79 days later, and we measured several proxies for their fitness. Individuals were counted to assess survival, weighed to the nearest 0.001 g to assess growth rate (assuming all juveniles had the same initial body mass, we used the final body mass of juveniles as a measure of growth rate), and measured in length to the nearest 0.1 mm (using ImageJ) to assess the body condition, which was calculated as the residuals of the relationship between individual body mass and length.

Statistical analyses

Two adult individuals died before the end of phase 1, so we discarded these two replicates from the analyses. Moreover, we identified six tanks in which crayfish had been inadvertently introduced; we discarded these six replicates because crayfish are known to have disproportionately strong impacts on ecosystems. As such, the final analyses were run on 64 replicates.

First, we compared the magnitude of the effects of intraspecific variation and temperature on ecological (phase 1) and evolutionary (phase 2) dynamics. To do so, we used a meta-analytic approach consisting of first running linear models linking each ecological or evolutionary parameter (dependent variables) to the explicative variables, i.e., intraspecific variation (categorical factor, six levels), temperature (categorical factor, two levels) and the resulting two-term interaction. The interaction term was removed when nonsignificant because it prevents the interpretation of simple terms. From these linear models, we calculated the standardized effect sizes eta squared as follows: $\eta^2 = \frac{SS_x}{SS_{tot}}$, where $SS_x$ is the sum of squares for the effect of interest (intraspecific variation, temperature or the interaction term, if significant) and $SS_{tot}$ is the total sum of squares. Sums of squares were extracted from
type II analysis of variance when the interaction was not in the model and from type III analysis of variance when the interaction was significant. Finally, the MES values of intraspecific variation and temperature across the ecological or evolutionary parameters were compared using t-test.

Next, we assessed the direct and indirect links between intraspecific variation, temperature, and the ecological and evolutionary parameters using a causal analysis. Since we aimed at identifying the mechanisms by which the mesocosms diverged, we included the body mass and the growth rate of adult fish from phase 1 because these two traits are known to drive ecological processes. We used path analyses to set a full model based on biologically rational paths and the visual inspection of the variance-covariance matrix, and all variables were scaled to the mean to facilitate the comparison. This full model was then simplified by removing sequentially weak and/or nonsignificant paths until reaching a model that was correct statistically (i.e., a model that best fit the observed covariance matrix based on the maximum likelihood $\chi^2$ statistic), while leading to the lowest Akaike Information Criteria (AIC) value. We finally extracted the absolute values of path coefficients from the final model to tease apart the direct and indirect effects of body mass, growth rate and temperature on the ecological and evolutionary parameters. Statistical analyses were performed using R software, and path analyses were run using Amos.

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Authors’ contributions: A.R and S.B conceived the study. A.R and L.DG carried out the experiment with contributions from S.B and J.C. A.R performed the statistical analyses. A.R, S.B and J.C interpreted and discussed the results. A.R, S.B and J.C wrote the article, and all authors made corrections.
Table 1: Causal pathways between variations in intraspecific traits (body mass_{adults} and growth rate_{adults}), temperature and ecological and evolutionary parameters obtained from path analyses.

| Response                  | Effect                        | Path coefficient | S.E.  | p-value |
|---------------------------|-------------------------------|------------------|-------|---------|
| Growth rate_{adults}      | Body mass_{adults}            | -0.674           | 0.093 | < 0.001 |
| Cladocera abundance       | Growth rate_{adults}          | -0.341           | 0.111 | 0.002   |
|                           | Copepod abundance             | 0.339            | 0.111 | 0.002   |
| Size Cladocera            | Bivalve abundance             | 0.428            | 0.114 | < 0.001 |
| Copepod abundance         | Growth rate_{adults}          | 0.37             | 0.153 | 0.016   |
|                           | Bivalve abundance             | 0.311            | 0.113 | 0.006   |
|                           | Body mass_{adults}            | 0.477            | 0.153 | 0.002   |
| Bivalvvia abundance       | Temperature                   | 0.441            | 0.113 | < 0.001 |
| Abiotic parameters        | Body mass_{adults}            | -0.289           | 0.124 | 0.019   |
|                           | Filamentous algae             | -0.644           | 0.092 | < 0.001 |
|                           | Growth rate_{adults}          | -0.194           | 0.124 | 0.116   |
| Pelagic prod.             | Prod. benthic                 | 0.244            | 0.12  | 0.043   |
| Benthic prod.             | Growth rate_{adults}          | -0.522           | 0.139 | < 0.001 |
|                           | Bivalvia abundance             | -0.228           | 0.118 | 0.054   |
|                           | Body mass_{adults}            | -0.486           | 0.139 | < 0.001 |
|                           | Temperature                   | 0.292            | 0.132 | < 0.001 |
|                           | Filamentous algae             | 0.239            | 0.12  | 0.047   |
| Decomposition rate        | Body mass_{adults}            | 0.375            | 0.132 | < 0.001 |
|                           | Temperature                   | 0.532            | 0.096 | < 0.001 |
| Filamentous algae         | Temperature                   | 0.554            | 0.118 | < 0.001 |
|                           | Bivalvia abundance             | -0.207           | 0.123 | 0.092   |
|                           | Copepod abundance             | -0.168           | 0.110 | 0.126   |
| Survival_{juveniles}      | Size Cladocera                | -0.195           | 0.123 | 0.112   |
|                           | Temperature                   | -0.183           | 0.123 | 0.135   |
|                              |                        |        |        |       |
|------------------------------|------------------------|--------|--------|-------|
| Growth rate\textsubscript{juveniles} | Body mass\textsubscript{adults} | 0.479  | 0.130  | < 0.001 |
| Growth rate\textsubscript{adults}  |                        | 0.725  | 0.125  | < 0.001 |
| Prod. benthic                |                        | 0.332  | 0.092  | < 0.001 |
| Cladocera abundance          |                        | 0.250  | 0.089  | 0.005  |
| Survival\textsubscript{juveniles} |                        | -0.566 | 0.084  | < 0.001 |
| Decomposition rate           |                        | -0.234 | 0.093  | 0.012  |
| Body condition\textsubscript{juveniles} | Bivalve abundance | -0.175 | 0.073  | 0.016  |
| Survival\textsubscript{juveniles} |                        | 0.556  | 0.087  | < 0.001 |
| Growth rate\textsubscript{juveniles} |                        | 0.941  | 0.083  | < 0.001 |
Fig. 1. Experimental design used to test the ecological (phase 1) and evolutionary (phase 2) effects of intraspecific variation among adult minnows (<i>Phoxinus phoxinus</i>) and warming.

Fig. 2. Comparison of the ecological and evolutionary effects of intraspecific variation and warming. (a) Eta squared ($\eta^2$) effect size of the intraspecific variation among adults and temperature on ecological (green) and evolutionary (blue) dynamics. Error bars represent ± 1 SE. (b) Delta of effect sizes ($\eta^2$) of intraspecific variation and temperature on ecological and evolutionary parameters. Positive values indicate a higher effect of intraspecific variation, and negative values indicate a higher effect of temperature.

Fig. 3. Effects of intraspecific trait variation and warming on ecological and evolutionary dynamics. (a) Representation of the simplified path analysis linking intraspecific trait variation among adult minnows, temperature, and ecological and evolutionary dynamics. The covariance structure of this simplified path model, which contains both ecological and evolutionary dynamics, did not differ from that of the data ($\chi^2 = 65.373$, d.f. = 72, $p = 0.696$), indicating that the data were well supported by the model. The arrow line width is proportional to the $\beta$ path coefficients (brown and pink arrows represent positive and negative values, respectively), and the dotted lines represent indirect effects of intraspecific variation on evolutionary parameters. (b) Cumulated absolute $\beta$ path coefficients extracted from the simplified path analysis depicting the direct (filled) and indirect (hatched) relationships between intraspecific trait variation among adult minnows, temperature, ecological dynamics (green) and evolutionary dynamics (blue). Note that the direct effects of intraspecific variation on
evolutionary dynamics are not true direct effects (because the adult fish were removed before phase 2 of the experiment) but instead reveal unmeasured causal relationships.

# = abundance.
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553 Fig. 1.
Fig. 2.
Fig. 3.