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 process[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].

75 Here, we experimentally quantified the consequences of intraspecific variation
76 on ecological processes and subsequent evolutionary trajectories (i.e., eco-
77 evolutionary feedbacks) and then compared these consequences to the ecological and
78 evolutionary consequences of warming. Temperature is a key abiotic factor that
79 strongly varies at the landscape scale, directly affects key ecological functions such
80 primary productivity and ecosystem respiration[17–19], and imposes a strong selective
81 pressure on organism traits[20–22]. We ran a two-phase "common gardening experiment"
82 (*sensu*[8,11], Fig. 1) and manipulated (i) intraspecific variation in a freshwater fish
83 (European minnow, *Phoxinus phoxinus*) by selecting individuals from six
84 evolutionary and functionally distinct populations (i.e., differences in genotypes and
85 functional traits, see Methods and Fig. S1 and S2) and (ii) water temperature by
86 setting mesocosms varying by 2°C throughout the experiment (Fig. S3). An increase
87 in temperature of 2°C represents the general warming expectations for freshwaters
88 over the next 40 years[23]. During the first experimental phase (*ecological effects*, 10-
89 weeks), we compared the strengths of the effects of intraspecific variation among
90 adult minnows, to the strengths of the effects of warming on prey community
91 structure and ecosystem functions (Fig. 1). Adults were then removed from the
92 mesocosms and replaced by juveniles with a common origin for the second
93 experimental phase (*evolutionary effects*, 11-weeks). We tested how the ecological
94 variations induced during the first phase (due to intraspecific variation and/or
95 warming) affected the evolutionary trajectories (fitness and performance) of juveniles.
96

97 **Results**

98 In the first phase, we found that the effects of intraspecific variation in adult
99 minnows on ecological processes (measured over all ecological parameters) were at

100 least as strong as those of warming on ecological processes (mean effect size (MES) ±
101 standard error = 0.103 ± 0.018 and MES ± SE = 0.078 ± 0.036 for intraspecific
102 variation and warming, respectively; t = 0.624, d.f = 18, p = 0.540, Fig. 2).
103 Nonetheless, the effects were heterogeneous across ecological parameters (Fig. 2b,
104 Fig. S4). For instance, intraspecific variation had the strongest ecological effect on the
105 abundance of Cladocera, whereas warming had a particularly strong ecological effect
106 on decomposition rate (Fig. 2b, Fig. S5 and S6). A single interaction term between
107 warming and intraspecific variation was significant (i.e., for benthic primary
108 productivity, F = 10.831, d.f = 5,52, p = 0.022), indicating that the ecological effects
109 of intraspecific variation were not temperature-dependent for most ecological
110 parameters. The body mass and growth rate of minnows, two functionally important
111 traits differing among minnow populations (although the later was also affected by
112 experimental temperature, Fig. S2), were included in a path analysis testing the direct
113 and indirect relationships among trait variation, warming and ecological parameters.
114 We found that intraspecific variation in these two functional traits affected ecological
115 processes as much as warming and that body mass was the most influential functional
116 trait (Fig. 3). We further found that the intraspecific trait variation acted both directly
117 and indirectly on ecological parameters (Fig. 3b). For instance, adult body mass
118 affected the abundance of Copepoda directly, subsequently leading to an indirect
119 effect on the abundance of Cladocera (Table 1, Fig. 3a). The ecological effects of
120 warming were mainly direct (67%), although some indirect effects were also observed
121 (Fig. 3b). For instance, warming directly increased Bivalvia abundance, positively
122 affecting the abundance of Copepoda and the size of Cladocera, hence representing an
123 indirect effect of warming on the zooplankton community (Fig. 3).

124 In the second phase (Fig. 1), we found that the strength of the effect sizes of
125 intraspecific variation and warming on the fitness proxies (survival, growth rate and
126 body condition) were similar (MES ± SE = 0.044 ± 0.004 and MES ± SE = 0.032 ±
127 0.016 for intraspecific variation and warming, respectively, t = 0.665, d.f = 4, p =
128 0.542, Fig. 2). Notably, the average effect sizes of intraspecific variation and warming
129 on the evolutionary parameters were half the intensity of those on ecological
130 parameters (Fig. 2), indicating that evolutionary dynamics were less affected than
131 ecological processes by the initial treatments. Nonetheless, we observed eco-
132 evolutionary feedbacks since the juvenile growth rate was related to the ecological
133 parameters (benthic primary productivity, decomposition rate and Cladocera
134 abundance), which were controlled by intraspecific variation (Fig. 3a). Juvenile
135 survival was also related to juvenile growth rate (density-dependent growth rate) and
136 was indirectly related to warming. We also identified a direct relationship between
137 adult trait variation and juvenile growth rate (Fig. 3), which was unexpected given
138 that the adults were removed from the tanks before the juveniles were introduced.
139 This result indicates interspecific variation had unmeasured indirect effects (mediated
140 by ecological changes) on evolutionary dynamics. Juvenile survival was positively
141 related to the body size of Cladocera and negatively related to temperature (i.e.,
142 survival increased as temperature decreased). Juvenile body condition covaried with
143 both juvenile survival and growth rate and was lower when the abundance of
144 Bivalvia, which was directly affected by temperature, was high (Fig. 3).
145

146 **Discussion**

147 We found that the ecological consequences of intraspecific variation and
148 warming were similar in strength but acted on different ecological processes. Adult

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

168 Here, the eco-evolutionary feedback comprised indirect effects of intraspecific
169 variation among adult minnows on the evolutionary trajectory of juveniles, which
170 were mediated by the direct consequences of adult minnows on the ecological theatre.
171 Currently, very few studies have demonstrated the existence of eco-evolutionary
172 feedback, and most of have focused on model organisms[9–12]. By focusing on a non
173 model organism, our study extends the taxonomic scope of eco-evolutionary feedback

174 loops and suggests that this process does not concern only species with strong eco-
175 evolutionary divergences[8]. We further identified two heritable traits (body mass and
176 growth rate[25,26]) that partially initiate these eco-evolutionary feedbacks and vary
177 between adult minnows originating from environmentally and evolutionary distinct
178 populations. For instance, the zooplankton community was strongly impacted by trait
179 variability, probably through diet specialization. In turn, juveniles performed better
180 (i.e., higher growth rate) in the mesocosms with a higher abundance of zooplankton,
181 confirming that eco-evolutionary feedbacks could arise from a change in prey
182 availability[9]. Previous studies have identified growth rate and body mass as important
183 traits for ecological processes[27–29], and we here provide novel insights into the indirect
184 evolutionary consequences of these traits.

185 Interestingly, intraspecific variation and warming acted additively but not
186 interactively on ecological and evolutionary dynamics. Indeed, we identified only one
187 significant interaction between intraspecific variation and warming on benthic
188 primary productivity, indicating that the effect of intraspecific variation on benthic
189 primary productivity dynamics was temperature-dependent. This finding confirms
190 that the ecological consequences of intraspecific variation are often independent from
191 the abiotic context[15], which might also be the case for eco-evolutionary feedbacks.
192 This independence is surprising, since local adaptation for specific fitness traits and/or
193 for reaction norms often leads to strong context dependency in the responses of
194 organisms to local abiotic conditions[30,31], and we may have observed cascading
195 interactive effects of intraspecific variation on ecological and evolutionary
196 dynamics[32,33]. This finding is important because the absence of strong interactive
197 effects reduces biological complexities and may therefore improve our ability to

198 forecast the ecological and evolutionary consequences of environmental and
199 biodiversity changes[34].

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

215

216 **Methods**

217 *Study species*

218 European minnow (*Phoxinus phoxinus*) was used as the model species. *P. phoxinus* is
219 a small-bodied (maximum length: ~80 mm, mean generation time: ~2 years) cyprinid
220 fish species widely distributed in Western Europe. *P. phoxinus* lives in relatively cold
221 waters, mainly in streams and rivers but also in mountain lakes[24,39]. It is a generalist

222 species that feeds on small invertebrates, algae, zooplankton and small fish larvae[40–
223 42].

224 In September 2016, we collected adult minnows by electrofishing in six rivers
225 in southwestern France (Fig. S1). We selected populations that were isolated
226 geographically (minimal riparian distance among sites = 64 km, mean ± SD = 343 km
227 ± 182) and had distinct environments (Fig. S7) to favor both genetic and phenotypic
228 divergences among populations. Accordingly, the mean genetic divergence among
229 populations was F_{st} = 0.162 (measured using 17 microsatellites, min-max = 0.043-
230 0.313), indicating a high evolutionary distinctiveness among the populations. The
231 body mass (a highly heritable[25,26] and important functional trait[43,44], Fig. S2) of the
232 sampled populations also varied, as did two other important functional traits[20,45–47]:
233 the metabolic (min-max = 0.1388-0.2737 mg $O^2.g^{-1}.h^{-1}$, F = 14.599, d.f = 5,188, $p <$
234 0.001) and ammonium excretion (min-max = 17.02-43.48 µg $NH^{4+}.g^{-1}.L^{-1}.h^{-1}$, F =
235 4.695, d.f = 5,175, $p < 0.001$, unpublished data) rates. All fish collections and
236 husbandry for adults and juveniles were conducted in accordance with sampling
237 permits obtained from local authorities (25-08-2016, 24-05-2016, 09-273, SA-013-
238 PB-092, A09-3). Fish from different populations were reared separately for ~6
239 months in 1100 L outdoor tanks to minimize previous environmental effects on
240 phenotypes. During rearing, the fish were fed with a mixture of pelletized food and
241 dead chironomids until the start of the experiment.

242

243 *Phase 1: effects of intraspecific variation and temperature on ecological processes*
244 The experiment consisted of 72 replicated mesocosms placed in a greenhouse with a
245 12:12 h light-dark photoperiod. Mesocosms were filled with 100 L of tap water and 1

246 cm of gravel covering the bottom of each tank. Tanks were covered with a 1 cm
247 plastic mesh net to prevent fish escapes. Nutrients were added to the mesocosms
248 using 5 mL of solution containing nitrogen and phosphorus (ratio N: P: K = 3.3: 1.1:
249 5.8) on December 2nd 2016. Each mesocosm was then inoculated with 200 mL of a
250 concentrated solution of phytoplankton from a unique lake origin (Lake Lamartine,
251 France 43°30'21.5"N, 1°20'32.7"E) on December 12th 2016. Two months later
252 (February 15th 2017), an additional 200 mL of concentrated solution of zooplankton
253 from the same lake was added to each mesocosm. Finally, we inoculated each
254 mesocosm with sediment and macroinvertebrates (i.e., mainly Gastropoda and
255 Bivalvia) from Lake Lamartine.

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

265 In March 2017, adult fish were weighed to the nearest 0.01 g and a single fish
266 was introduced to each mesocosm. This individual-based approach prevented the
267 experimental ecosystems from collapsing due to the over-density of top consumers
268 and allowed the ecological effects of individual phenotypes to be measured. After 73
269 days (Fig. 1), each fish was removed, weighed and euthanized in a solution of
270 benzocaine at 25 $mg.L^{-1}$. The growth rate ($\%.day^{-1}$) of the adults was calculated

271 as $SGR = \frac{ln(Wf)-ln(Wi)}{T} * 100$, where Wf and Wi are the final and initial body masses,
272 respectively, and T is time interval between two measurements (in days).
273 Concomitantly, we measured multiple community and ecosystem parameters to
274 evaluate differences in ecological processes among treatments.

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

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

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

288 (*iv*) Zooplankton community was assessed by filtering 5 L of water through a
289 200 µm sieve. Samples was conserved in a 70% ethanol solution and subsequently
290 identified to the order or family levels, including Copepoda (i.e., Cyclopoida and
291 Calanoida) and Cladocera (i.e., Daphniidae, Chydoridae and Bosminidae).
292 Zooplankton size was assessed by measuring 10 individuals of each order and family
293 level from each mesocosm to the nearest 0.001 mm using ImageJ®.

294 (*v*) Decomposition rate was measured by quantifying the mass loss of black
295 poplar (*Populus nigra*, a dominant riparian tree in southern France) abscised leaves[48].

296 One day before the start of the experiment, 4 g of air-dried leaves were put in each
297 mesocosm within a coarse mesh (1 x 1 cm) bag. At the end of the phase 1, the
298 remaining leaf material was removed from the mesocosms, rinsed with tap water,
299 oven dried at 60°C for three days and weighed to the nearest 0.001 g to assess the loss
300 of biomass. The decomposition rate was calculated as $k = -\frac{ln\,(X)}{t}$ [48], where X is the
301 proportion of litter remaining after phase 1 and t is the elapsed time in days.

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

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

312

313 *Phase 2: effect of ecological differences on juvenile evolution*

314 After the removal of adult fish on June 13th 2017, 45 juvenile minnows were
315 introduced to each mesocosm. We used juveniles from a unique origin (i.e., fish farm,
316 *Amorvif EURL*) to control for potential genetic effects. Juveniles were introduced as
317 soon as possible after hatching to increase the possibility of differential mortality
318 and/or ontogenetic plasticity. Therefore, juveniles were introduced when they were
319 only two weeks old as stage III larvae[50] (Fig. S8). They were not manipulated (i.e.,
320 weighted and/or measured) before being randomly introduced in the mesocosms to

321 limit potential mortality. The juveniles were removed from the mesocosms 79 days
322 later, and we measured several proxies for their fitness. Individuals were counted to
323 assess survival, weighed to the nearest 0.001 g to assess growth rate (assuming all
324 juveniles had the same initial body mass, we used the final body mass of juveniles as
325 a measure of growth rate), and measured in length to the nearest 0.1 mm (using
326 ImageJ) to assess the body condition, which was calculated as the residuals of the
327 relationship between individual body mass and length.
328
329 *Statistical analyses*
330 Two adult individuals died before the end of phase 1, so we discarded these two
331 replicates from the analyses. Moreover, we identified six tanks in which crayfish had
332 been inadvertently introduced; we discarded these six replicates because crayfish are
333 known to have disproportionally strong impacts on ecosystems[48]. As such, the final
334 analyses were run on 64 replicates.
335 First, we compared the magnitude of the effects of intraspecific variation and
336 temperature on ecological (phase 1) and evolutionary (phase 2) dynamics. To do so,
337 we used a meta-analytic approach consisting of first running linear models linking
338 each ecological or evolutionary parameter (dependent variables) to the explicative
339 variables, i.e., intraspecific variation (categorical factor, six levels), temperature
340 (categorical factor, two levels) and the resulting two-term interaction. The interaction
341 term was removed when nonsignificant because it prevents the interpretation of
342 simple terms[51]. From these linear models, we calculated the standardized effect sizes
343 eta squared[52] (η^2) as follows: $\eta^2 = SS_x/SS_{tot}$, where SS_x is the sum of squares for the
344 effect of interest (intraspecific variation, temperature or the interaction term, if
345 significant) and SS_{tot} is the total sum of squares. Sums of squares were extracted from

346 type II analysis of variance when the interaction was not in the model and from type
347 III analysis of variance when the interaction was significant[53]. Finally, the MES
348 values of intraspecific variation and temperature across the ecological or evolutionary
349 parameters were compared using t-test.

350 Next, we assessed the direct and indirect links between intraspecific variation,
351 temperature, and the ecological and evolutionary parameters using a causal analysis.
352 Since we aimed at identifying the mechanisms by which the mesocosms diverged, we
353 included the body mass and the growth rate of adult fish from phase 1 because these
354 two traits are known to drive ecological processes[43]. We used path analyses[54–56] to set
355 a full model based on biologically rational paths and the visual inspection of the
356 variance-covariance matrix, and all variables were scaled to the mean to facilitate the
357 comparison. This full model was then simplified by removing sequentially weak
358 and/or nonsignificant paths until reaching a model that was correct statistically (i.e., a
359 model that best fit the observed covariance matrix based on the maximum likelihood
360 χ^2 statistic[55]), while leading to the lowest Akaike Information Criteria (AIC) value.
361 We finally extracted the absolute values of path coefficients from the final model to
362 tease apart the direct and indirect effects of body mass, growth rate and temperature
363 on the ecological and evolutionary parameters. Statistical analyses were performed
364 using R software[57], and path analyses were run using Amos[58].

365

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515 **Authors' contributions:** A.R and S.B conceived the study. A.R and L.DG carried out
516 the experiment with contributions from S.B and J.C. A.R performed the statistical
517 analyses. A.R, S.B and J.C interpreted and discussed the results. A.R, S.B and J.C
518 wrote the article, and all authors made corrections.

519 **Table 1:** Causal pathways between variations in intraspecific traits (body $mass_{adults}$
520 and growth $rate_{adults}$), temperature and ecological and evolutionary parameters
521 obtained from path analyses.
522

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	0.11	0.002
Size Cladocera	Bivalve abundance	0.428	0.114	< 0.001
Copepoda 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
Bivalvia 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
	Copepoda 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$_{juveniles}$	Body mass$_{adults}$	0.479	0.130	< 0.001
	Growth rate$_{adults}$	0.725	0.125	< 0.001
	Prod. benthic	0.332	0.092	< 0.001
	Cladocera abundance	0.250	0.089	0.005
	Survival$_{juveniles}$	-0.566	0.084	< 0.001
	Decomposition rate	-0.234	0.093	0.012
Body condition$_{juveniles}$	Bivalve abundance	-0.175	0.073	0.016
	Survival$_{juveniles}$	0.556	0.087	< 0.001
	Growth rate$_{juveniles}$	0.941	0.083	< 0.001

523

Fig. 1. Experimental design used to test the ecological (phase 1) and evolutionary (phase 2) effects of intraspecific variation among adult minnows (*Phoxinus phoxinus*) and warming.

Fig. 2. Comparison of the ecological and evolutionary effects of intraspecific variation and warming. (a) Eta squared (η^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 (η^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 β 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 β 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.*

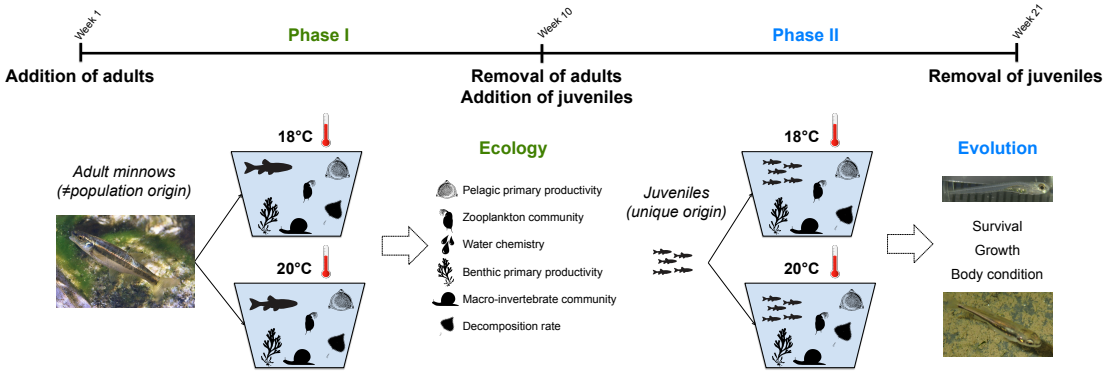
Week 1
Phase I
Week 10
Phase II
Week 21
Addition of adults
Removal of adults
Addition of juveniles
Removal of juveniles
Adult minnows
(≠population origin)
18°C
20°C
Ecology
Pelagic primary productivity
Zooplankton community
Water chemistry
Benthic primary productivity
Macro-invertebrate community
Decomposition rate
Juveniles
(unique origin)
18°C
20°C
Evolution
Survival
Growth
Body condition

Fig. 1.

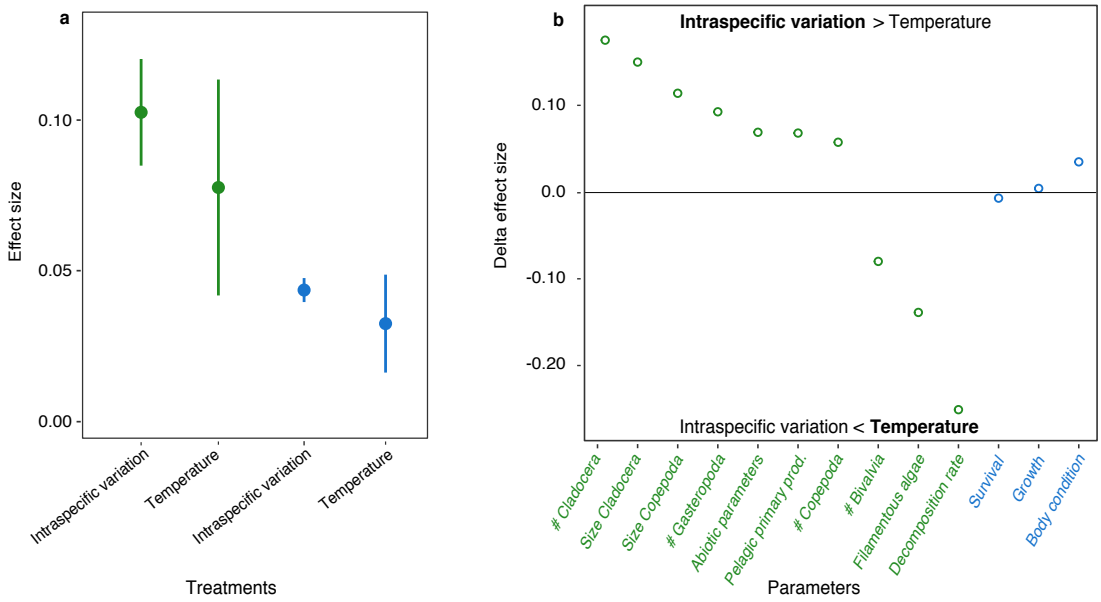
a
Effect size
0.10
0.05
0.00
Intraspecific variation
Temperature
Intraspecific variation
Temperature
Treatments
b
Intraspecific variation > Temperature
Intraspecific variation < Temperature
Delta effect size
0.10
0.0
-0.10
-0.20
Cladocera
Size Cladocera
Size Copepoda
Gasteropoda
Abiotic parameters
Pelagic primary prod.
Copepoda
Bivalvia
Filamentous algae
Decomposition rate
Survival
Growth
Body condition
Parameters

Fig. 2.

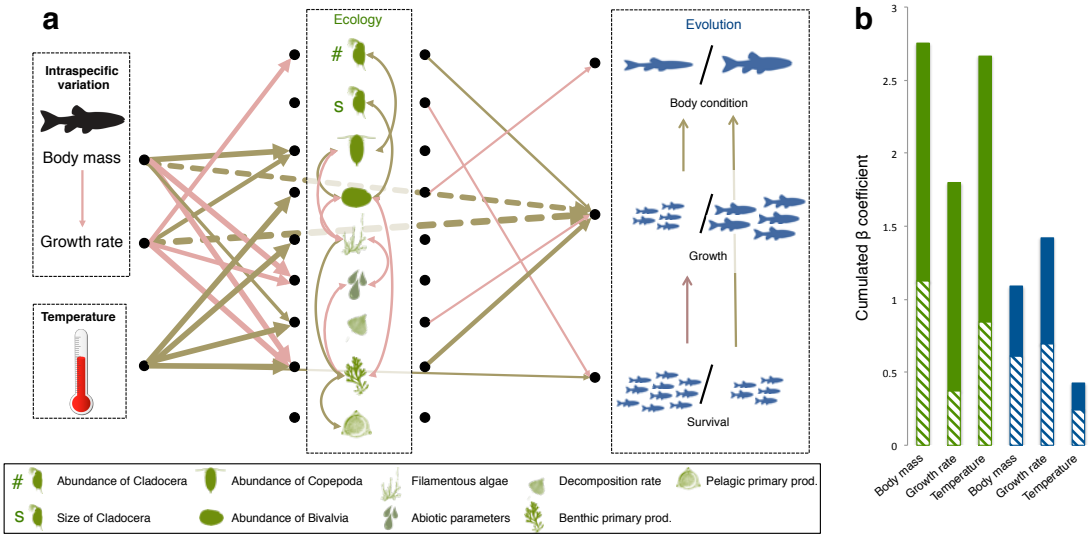
a
Intraspecific variation
Body mass
Growth rate
Temperature
Ecology
#
S
Evolution
Body condition
Growth
Survival
Abundance of Cladocera
Abundance of Copepoda
Filamentous algae
Decomposition rate
Pelagic primary prod.
Size of Cladocera
Abundance of Bivalvia
Abiotic parameters
Benthic primary prod.
b
Cumulated β coefficient
0
0.5
1
1.5
2
2.5
3
Body mass
Growth rate
Temperature
Body mass
Growth rate
Temperature

Fig. 3.