Intraspecific variation alters ecosystem and next-generation performance as much as temperature

Allan Raffard[1,2*], Julien Cucherousset[3], Frédéric Santoul[2], Lucie Di Gesu[1] and Simon Blanchet[1,3]

[1] *CNRS, Université Toulouse III Paul Sabatier, Station d'Écologie Théorique et Expérimentale du CNRS à Moulis, UMR-5321, F-09200 Moulis, France.*

[2] *EcoLab, Université de Toulouse, CNRS, INPT, UPS, Toulouse, France.*

[3] *Laboratoire Évolution et Diversité Biologique (EDB UMR 5174), Université de Toulouse, CNRS, UPS, 118 route de Narbonne, Toulouse 31062, France.*

***Corresponding author:** allan.raffard@sete.cnrs.fr / allanraffard@outlook.com

Abstract

Phenotypic or genotypic variation within species affects ecological processes, from populations to ecosystems. However, whether the ecological imprint of intraspecific variation is substantial compared to key environmental drivers, and persistent enough to carry over to next generations is still questioned. Here, we experimentally showed that intraspecific variation manipulated in a freshwater fish (the European minnow, *Phoxinus phoxinus*) led to ecological and transgenerational carry-over effects that were as strong as those of varying temperature by 2°C. Specifically, variation in fish body mass, growth rate and activity altered the size and abundance of prey, which ultimately affected traits and survival of the next fish generation. Temperature variation modulated other ecosystem functions (e.g. litter decomposition) that were also associated to transgenerational carry-over effects. Our results demonstrate that shifting genotypes or phenotypes in wild populations can have substantial and persistent consequences on ecosystems with a similar intensity than climatic variation.

Keywords: biodiversity, climate change, trait-mediated effects, freshwater, ecosystem, community

Introduction

Investigating species trait variability provides a mechanistic framework to predict the links between biodiversity and ecosystem functions (Violle et al. 2007). While trait variation has primarily been quantified at the species level, intraspecific trait variation accounts for a high proportion of the total trait variability in communities (Zhao et al. 2019). Furthermore, intraspecific trait variation has been shown to alter community structure and ecosystem functioning (Rudolf and Rasmussen 2013, Hendry 2016), indicating that intraspecific variation is a significant driver and predictor of ecological dynamics (Des Roches et al. 2018, Raffard et al. 2019b).

Intraspecific trait-mediated ecological effects can sometimes be strong and persist long enough to affect the subsequent generations through 'inheritance' of the surrounding environment (Odling-Smee et al. 2013). Indeed, next generations can experience environmental conditions that have been modified by previous generations, subsequently affecting next-generations performance such as foraging efficiency, growth and survival (Matthews et al. 2016, Best et al. 2017). These "transgenerational carry-over effects" can – under some circumstances – affect patterns of selection and hence the evolutionary dynamics of species (i.e. eco-evolutionary feedbacks, Schoener 2011, Hendry 2016). While these ecological and transgenerational carry-over effects have been the focus of recent experimental and theoretical works (Matthews et al. 2016, Brunner et al. 2017), whether intraspecific variation really matters for the long-term dynamics of complex ecosystems is still questioned (Thompson 1998, Schoener 2011).

50 This issue can be addressed by comparing the intensity of the effects induced
51 by intraspecific variation to those induced by key environmental factors affecting both
52 ecological and evolutionary dynamics, such as temperature (Schoener 2011).
53 Intraspecific variation can affect ecological processes with an intensity similar to that
54 of environmental drivers (El-Sabaawi et al. 2015). However, whether the ecological
55 imprints of intraspecific variation are strong and persistent enough to affect
56 subsequent generations, and whether these transgenerational carry-over effects are
57 similar in strength to those of indisputably important environmental drivers is still
58 unknown. Addressing this question is an important step for determining the relative
59 contribution of intraspecific variation in predicting the responses of ecosystems to
60 global change.
61 Here, we compared the consequences of intraspecific variation on ecosystem
62 properties and on the performance of subsequent generations to those induced by
63 changes in temperature, and assessed which of a series of traits contribute the most to
64 these consequences. Temperature is a key abiotic factor directly affecting ecosystem
65 functions such as primary productivity (Yvon-Durocher et al. 2015), and imposing a
66 strong selective pressure on organism traits (Brown et al. 2004, Rey et al. 2016). We
67 ran a two-phase experiment (Matthews et al. 2011, 2016) (Figure 1) manipulating (i)
68 trait variation in a freshwater fish (European minnow, *Phoxinus phoxinus*) by
69 selecting individuals from populations having evolved distinct genotypes and
70 phenotypes (Figure S1 and S2, see also Raffard et al. 2019a) and (ii) water
71 temperature by setting mesocosms to differ by 2°C throughout the experiment (Figure
72 S3). An increase in temperature of 2°C represents the general warming expectations
73 for freshwaters over the next 40 years (IPCC 2014). During the first experimental
74 phase (*ecological effects*), we compared the strength of the effects of trait variation

among adult minnows to the strength of the effects of temperature variation on prey community structure and ecosystem functioning (Figure 1). Adults were then removed from the mesocosms and replaced by juveniles with a common origin for the second experimental phase (*transgenerational carry-over effects*). We tested how the ecological variations induced during the first phase (due to intraspecific and/or temperature variation) affected the performance of juveniles.

Material and 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 lentic and lotic waters. It is a generalist species that feeds on small invertebrates, algae and zooplankton.

In September 2016, we collected adult minnows by electrofishing in six rivers in southwestern France (Figure S1). We selected populations that were isolated geographically and had distinct environments (Figure S4) 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). The sampled populations also varied for important functional traits, such as body mass and metabolic rate (Figure S2). Furthermore, we have previously shown that minnow populations in this river system were characterised by unique "functional syndromes" (set of trait variation and covariation) that resulted from a combination of random drift and adaptation to environmental factors (Raffard et al. 2019a). All fish collections and husbandry for adults and juveniles were conducted in accordance with sampling permits obtained from local

100 authorities (25-08-2016, 24-05-2016, 09-273, SA-013-PB-092, A09-3). Fish from
101 different populations were reared at a similar density and separately for ~6 months in
102 1100 L outdoor tanks to minimize prior environmental effects on phenotypes. During
103 rearing, the fish were fed ad-libitum with a mixture of pelletized food and dead
104 chironomids.
105
106 *Phase 1: effects of intraspecific variation and temperature on ecological processes*
107 The experiment consisted of 72 replicated mesocosms placed in a greenhouse with a
108 12:12 h light-dark photoperiod. Mesocosms were filled with 100 L of tap water and 1
109 cm of gravel covering the bottom of each tank. Tanks were covered with a 1 cm
110 plastic mesh net to prevent fish escapes. Nutrients were added to the mesocosms
111 using 5 mL of solution containing nitrogen and phosphorus (ratio N: P: K = 3.3: 1.1:
112 5.8) on December 2nd 2016. Each mesocosm was then inoculated with 200 mL of a
113 concentrated solution of phytoplankton from a unique lake origin (Lake Lamartine,
114 France 43°30'21.5"N, 1°20'32.7"E) on December 12th 2016. Two months later
115 (February 15th 2017), an additional 200 mL of concentrated solution of zooplankton
116 from the same lake was added to each mesocosm. Finally, we inoculated each
117 mesocosm with sediment and macroinvertebrates (i.e., mainly Gastropoda and
118 Bivalvia) from Lake Lamartine.
119 Each tank was assigned to one of twelve treatments (each replicated six times)
120 according to a full-factorial design with intraspecific variation (i.e., population origin,
121 six levels corresponding to each population) and temperature (two levels: low and
122 high temperature) as the main factors (Figure 1). Water temperature was controlled
123 and adjusted using a *Blue Marine*® water chiller and a stainless steel coil placed in
124 each tank through which a flux of water (independent from the water of the tanks)

125 flowed at either 18°C or 21°C. On average, the low and high water temperature
126 treatments differed by 2.08°C according to natural seasonal variations (Figure S3).
127 In March 2017, adult fish were weighed to the nearest 0.01 g and a single fish
128 was introduced to each mesocosm. This individual-based approach prevented the
129 experimental ecosystems from collapsing due to the over-density of top consumers
130 and allowed the ecological effects of individual trait variation to be measured. After
131 73 days (Figure 1), each fish was removed and phenotyped. We measured six traits on
132 each individual including body mass, growth rate, metabolic rate, activity, aspect ratio
133 and gut length (see supplementary method for details). Concomitantly, we measured
134 multiple community and ecosystem parameters to evaluate differences in ecological
135 processes among treatments: Pelagic and benthic algae stocks, filamentous algae,
136 decomposition rate, abiotic parameters, Copepoda and Cladocera abundances and
137 size, and macroinvertebrates (Bivalvia and Gastropoda) abundance (see
138 supplementary method for details).
139
140 *Phase 2: transgenerational effects of ecological differences on juvenile performance*
141 After the removal of adult fish on June 13th 2017, 45 juvenile minnows were
142 introduced to each mesocosm. We used juveniles from a single origin (i.e., fish farm,
143 *Amorvif EURL*) to control for potential genetic effects. Juveniles were introduced as
144 soon as possible after hatching to increase the possibility of differential mortality
145 and/or ontogenetic plasticity. Therefore, juveniles were introduced when they were
146 only two weeks old as stage III larvae (Figure S5). They were not manipulated (i.e.,
147 weighted and/or measured) before being randomly introduced in the mesocosms to
148 limit potential mortality. The juveniles were removed from the mesocosms 79 days
149 later, and we measured several proxies for their fitness (i.e. performance). Individuals

150 were counted to assess survival, weighed to the nearest 0.001 g to assess growth rate
151 (assuming all juveniles had the same initial body mass, we used the final body mass
152 of juveniles as a measure of growth rate), and measured in length to the nearest 0.1
153 mm (using ImageJ) to assess the body condition, which was calculated as the
154 residuals of the relationship between individual body mass and length.
155
156 *Statistical analyses*
157 Two adult individuals died before the end of phase 1, so we discarded these two
158 replicates from the analyses. Moreover, we identified six tanks in which crayfish had
159 been inadvertently introduced; we discarded these six replicates because crayfish are
160 known to have disproportionally strong impacts on ecosystems (Alp et al. 2016). As
161 such, the final analyses were run on 64 replicates.
162 First, we compared the magnitude of the effects of intraspecific variation and
163 temperature increase on ecological (phase 1) and evolutionary (phase 2) dynamics. To
164 do so, we used a meta-analytic approach consisting of first running linear models
165 linking each ecological or evolutionary parameter (dependent variables) to the
166 explicative variables, i.e., intraspecific variation (categorical factor, six levels),
167 temperature (categorical factor, two levels) and the resulting two-term interaction.
168 The interaction term was removed when not significant because it prevents the
169 interpretation of simple terms (Nakagawa and Cuthill 2007). From these linear
170 models, we calculated the standardized effect sizes eta squared (Levine and Hullett
171 2002) (η^2) as follows: $\eta^2 = SS_x/SS_{tot}$, where SS_x is the sum of squares for the effect of
172 interest (intraspecific variation, temperature or the interaction term, if significant) and
173 SS_{tot} is the total sum of squares. Sums of squares were extracted from type II analysis
174 of variance when the interaction was not in the model and from type III analysis of

175 variance when the interaction was significant (Langsrud 2003). Finally, the mean
176 effect size (MES) values of intraspecific variation and temperature across the
177 ecological or evolutionary parameters were compared using t-test.

178 Next, we assessed which individual trait contributed the most to ecological
179 differentiations and subsequently to carry-over effects to the next generation using a
180 causal analysis. Since we aimed at identifying the mechanisms by which the
181 mesocosms diverged, we included the six traits measured on adult fish from phase 1
182 because these traits can drive ecological processes (Hildrew et al. 2007). We used
183 path analyses (Grace 2006) to set a full model based on biologically rational paths and
184 the visual inspection of the variance-covariance matrix, and all variables were scaled
185 to the mean to facilitate the comparison. We first ran a model linking individual traits
186 and temperature to ecological parameters. A full model was constructed and
187 simplified by removing sequentially weak and/or nonsignificant paths until reaching a
188 model that was correct statistically (i.e., a model that best fit the observed covariance
189 matrix based on the maximum likelihood χ^2 statistic (Grace 2006), while leading to
190 the lowest Akaike Information Criteria (AIC) value. We finally extracted the absolute
191 values of path coefficients from the final model to tease apart the direct and indirect
192 effects of individual traits and temperature on the ecological parameters. We then ran
193 a second path-analysis linking ecological parameters to performance parameters of
194 juveniles, while fixing the links found in the first model (i.e. traits to ecological
195 parameters) so as not to over-fit the model. Statistical analyses were performed using
196 R software (R Core Team 2013), and path analyses were run using Amos (Arbuckle
197 2014).

198 **Results**

199 In the first phase (Figure 1), we found that the effects of intraspecific variation in
200 adult minnows on ecosystem properties (measured over all ecological parameters) had
201 a similar intensity than those induced by temperature increase (mean effect size
202 (MES) ± standard error = 0.103 ± 0.018 and MES ± SE = 0.078 ± 0.036 for
203 intraspecific variation and temperature, respectively; $t = 0.624$, d.f = 18, $p = 0.540$,
204 Figure 2). Nonetheless, the effects differed between ecological parameters (Figure 2b,
205 Figure S6). For instance, intraspecific variation had the strongest effect on abundance
206 and size of the fish prey community (Cladocera, Copepoda and Gastropoda), whereas
207 increasing temperature had a particularly strong effect on decomposition rate (Figure
208 2b, see also Figure S7, S8 and Table S1 for details). The interaction term between
209 temperature and intraspecific variation was significant only for benthic algae stock (F
210 = 10.831, d.f = 5,52, $p = 0.022$), indicating that the ecological effects of intraspecific
211 variation were temperature-independent for most ecological parameters.
212 We found that intraspecific variation in fish body mass and activity were the
213 most influential functional traits and that variation in each of these two traits had
214 similar –although weaker- ecological effects than temperature variation (Figure 3a).
215 We further found that trait variation acted mainly directly on ecological parameters,
216 and minor indirect effects were detected (Figure 3a). For instance, adult body mass
217 positively affected the abundance of Copepoda directly, subsequently leading to an
218 indirect effect on the abundance of Cladocera (Table S2). The ecological effects of
219 temperature were both direct and indirect (Figure 3a). For instance, temperature
220 directly increased Bivalvia abundance, which positively affected the abundance of
221 Copepoda and the size of Cladocera, hence representing an indirect effect of
222 temperature on the zooplankton community (Table S2). The covariance structure of

223 the simplified path model did not differ from that of the data (χ^2 = 87.064, d.f = 114, p
224 = 0.971), indicating that the data were well supported by the model.
225 In the second phase (Figure 1), we found that the strength of the effect sizes of
226 intraspecific variation and temperature on the performance of juveniles (survival,
227 growth rate and body condition) were similar (MES ± SE = 0.044 ± 0.004 and MES
228 ± SE = 0.032 ± 0.016 for intraspecific variation and temperature, respectively, *t* =
229 0.665, d.f = 4, *p* = 0.542, Figure 2). The average effect sizes of intraspecific and
230 temperature variations on the performance of juveniles were half the intensity of those
231 on ecological parameters (Figure 2), indicating that transgenerational carry-over
232 effects induced by the initial treatments were weaker in average than ecological
233 effects observed in the first phase. Nonetheless, we found evidence for
234 transgenerational carry-over effects of intraspecific variation since juvenile survival,
235 growth rate and body condition were influenced by ecological parameters (e.g.
236 benthic algae stock, Copepoda and Gastropoda abundance) that were themselves
237 controlled by intraspecific variation (Figure 3b, Table S3). Amongst the adult traits,
238 activity, growth rate and body mass contributed the most to the carry-over effects on
239 juvenile performances (Figure 3c). For instance, active individuals decreased the
240 abundance of Gastropoda, which subsequently affected juvenile survival and growth
241 rate (Tables S2 and S3). Temperature increase mainly impacted -negatively- juvenile
242 survival (i.e., survival increased as temperature decreased, Table S3). Also, juvenile
243 survival was related to juvenile growth rate (density-dependent growth rate), leading
244 to an indirect effect of temperature on juvenile growth rate (Table S3). Finally,
245 juvenile body condition covaried with both juvenile survival and growth rate, and was
246 affected by multiple ecological parameters (Table S3) which were directly affected by
247 trait variation and temperature (Table S2). The covariance structure of the simplified

248 path model for the phase 2 did not differ from that of the data (χ^2 = 148.875, d.f =
249 196, p = 0.995), indicating that the data were well supported by the model.

250 **Discussion**

251 We found that the ecological consequences of intraspecific and temperature variations
252 were similar in strength but acted independently on different ecological parameters.
253 Adult minnows from distinct populations modulated both the abundance and the size
254 of their prey (zooplankton and Gastropoda), and these effects were predicted by
255 variation among individuals in functional traits. In contrast, temperature variation
256 strongly accelerated leaf litter decomposition, probably because warmer temperatures
257 stimulate bacterial activity. These ecological imprints led to transgenerational carry-
258 over effects on the performance of the next generation, which were also similar in
259 strength between intraspecific variation and temperature. For instance, the survival of
260 juveniles was higher in the low-temperature than in the high-temperature treatment,
261 whereas the growth rate of juveniles differed depending on the trait characteristics of
262 adult minnows introduced at the onset of the experiment. Overall, our results
263 demonstrate that intraspecific variation can substantially affect ecosystem properties,
264 which fosters ecological legacy to the next generations as much as temperature does.

265 Using a fine phenotypic screening of individual functional traits, we identified
266 the traits contributing the most to the ecological effects of intraspecific variation. We
267 revealed that multiple traits mediated the top-down control of minnows on prey
268 community structure, ecosystem processes and subsequent transgenerational carry-
269 over effects. Some of these traits were different among populations (e.g. body mass,
270 metabolic rate), and both genetic (adaptive or not) and environmental factors
271 underlined these trait differences among these populations (Raffard et al. 2019a).
272 Body mass and metabolic rate are functional traits affecting the energetic needs and

273 assimilation of individuals (Brown et al. 2004, Hildrew et al. 2007), leading to trophic
274 differences among individuals. Our results demonstrate that population differences on
275 these traits can strongly contribute to subsequent ecosystem differentiations. We
276 further identified traits, such as activity, that mainly varied within populations but that
277 also contributed to changes in ecosystem functioning. Behavioural variation in
278 populations allows individuals to increase their performance through niche
279 partitioning, ultimately affecting communities and ecosystems (e.g. Gastropoda
280 abundance, Wolf and Weissing 2012). This confirms that individuals are not
281 functionally equal neither among nor within populations (Wolf and Weissing 2012,
282 Royauté and Pruitt 2015), and that –as recently shown in another fish species (Schmid
283 et al. 2019)- it is possible to use these trait values to predict changes in important
284 ecological properties.

285 Furthermore, we provide novel insights by demonstrating that these traits can
286 also generate substantial transgenerational carry-over effects. The carry-over effects
287 that we detected on subsequent generations are important as they suggest that the
288 ecological effects of intraspecific variation in minnow are strong and long-lasting
289 enough to modulate the whole dynamics of ecosystems. These effects correspond to
290 indirect effects of trait variation among adult minnows on the performance of
291 juveniles, which were mediated by the direct consequences of adult minnows on the
292 ecological theatre. Multiple ecological parameters affected the performance of
293 juveniles, such as the resource of juveniles (e.g. size of Cladocera) or the abiotic
294 composition of their environment (e.g. pH or oxygen). Unsurprisingly, adult traits that
295 have the highest ecological effects foster the highest transgenerational carry-over
296 effects on juvenile performance, meaning that variation in these traits can be used to
297 predict both direct ecological effects and indirect transgenerational effects of

298 intraspecific variation. Currently, very few studies have demonstrated the existence of
299 transgenerational carry-over effects, and most of them have focused on model
300 organisms (e.g. Turcotte et al. 2013, Matthews et al. 2016). Our study extends the
301 taxonomic scope of transgenerational effects, and suggests that this process does not
302 concern only species with strong evolutionary divergences (Matthews et al. 2011).
303 Interestingly, intraspecific and temperature variations acted additively but not
304 interactively on ecosystem properties and on the performance of next generation.
305 Indeed, we identified only one significant interaction term between intraspecific
306 variation and temperature on benthic algae stock. This finding confirms that the
307 ecological consequences of intraspecific variation are often independent from the
308 abiotic context (El-Sabaawi et al. 2015), which also seems to be the case for the
309 transgenerational carry-over effects induced by intraspecific variation. This
310 independence is surprising, since local adaptation for specific fitness traits and/or for
311 reaction norms often leads to strong context dependency in the responses of
312 organisms to local abiotic conditions (Kawecki and Ebert 2004), and we may have
313 observed cascading interactive effects of intraspecific variation on ecological and
314 evolutionary dynamics (Rosenblatt and Schmitz 2016). This finding is important
315 because the absence of strong interactive effects reduces biological complexities and
316 may therefore improve our ability to forecast the ecological and evolutionary
317 consequences of environmental and biodiversity changes (Beckage et al. 2011).
318 In conclusion, we demonstrated that the magnitude of the ecological and
319 transgenerational carry-over effects of intraspecific variation were as strong as the
320 effects of temperature variation. This finding strongly supports the growing view that
321 intraspecific variation and resulting transgenerational carry-over effects are not
322 random noise, but are rather biologically substantial. Current environmental changes

are rapid and can directly affect ecosystem functioning (Yvon-Durocher et al. 2015). These changes can also directly modulate the distribution of intraspecific trait variation in landscapes and thereby indirectly affect the dynamics of biological systems (Matthews et al. 2016, Brunner et al. 2017). Importantly, we demonstrate that some specific traits that are often targeted by humans (body size and activity, Biro and Post 2008) can be used to forecast ecosystem modifications under current environmental changes. To sum up, our results reinforce recent reports that changes and shifts in intraspecific variation of wild populations 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 (Mimura et al. 2016).

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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, J.C and F.S interpreted and discussed the results. A.R, S.B and J.C wrote the article, and all authors made corrections.

References

347 Alp, M., J. Cucherousset, M. Buoro, and A. Lecerf. 2016. Phenological response of a
348 key ecosystem function to biological invasion. Ecology Letters 19:519–527.
349 Arbuckle, J. L. 2014. Amos (Version 23.0) [Computer Program]. Chicago: IBM
350 SPSS.
351 Beckage, B., L. J. Gross, and S. Kauffman. 2011. The limits to prediction in
352 ecological systems. Ecosphere 2:125.
353 Best, R. J., J. M. Anaya-Rojas, M. C. Leal, D. W. Schmid, O. Seehausen, and B.
354 Matthews. 2017. Transgenerational selection driven by divergent ecological
355 impacts of hybridizing lineages. Nature Ecology & Evolution 1:1757–1765.
356 Biro, P. A., and J. R. Post. 2008. Rapid depletion of genotypes with fast growth and
357 bold personality traits from harvested fish populations. Proceedings of the National
358 Academy of Sciences 105:2919–2922.
359 Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004.
360 Toward a metabolic theory of ecology. Ecology 85:1771–1789.
361 Brunner, F. S., J. M. Anaya-Rojas, B. Matthews, and C. Eizaguirre. 2017.
362 Experimental evidence that parasites drive eco-evolutionary feedbacks.
363 Proceedings of the National Academy of Sciences 114:3678–3683.
364 Des Roches, S., D. M. Post, N. E. Turley, J. K. Bailey, A. P. Hendry, M. T. Kinnison,
365 J. A. Schweitzer, and E. P. Palkovacs. 2018. The ecological importance of
366 intraspecific variation. Nature Ecology & Evolution 2:57–64.
367 El-Sabaawi, R. W., R. D. Bassar, C. Rakowski, M. C. Marshall, B. L. Bryan, S. N.
368 Thomas, C. Pringle, D. N. Reznick, and A. S. Flecker. 2015. Intraspecific
369 phenotypic differences in fish affect ecosystem processes as much as bottom-up
370 factors. Oikos 124:1181–1191.

371 Grace, J. B. 2006. Structural equation modeling and natural systems. Cambridge
372 University Press. Cambridge, UK.
373 Hendry, A. P. 2016. Eco-evolutionary dynamics. Princeton University Press.
374 Hildrew, A. G., D. Raffaelli, and R. Edmonds-Browns. 2007. Body size: the structure
375 and function of aquatic ecosystems. Cambridge University Press, Cambridge, UK.
376 IPCC. 2014. Climate Change 2014: Synthesis Report. Contribution of Working
377 Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel
378 on Climate Change (eds Core Writing Team, Pachauri, R.K., Meyer, L.A.). IPCC,
379 Geneva, Switzerland.
380 Kawecki, T. J., and D. Ebert. 2004. Conceptual issues in local adaptation. Ecology
381 Letters 7:1225–1241.
382 Langsrud, O. 2003. ANOVA for unbalanced data: Use Type II instead of Type III
383 sums of squares. Statistics and Computing:163–167.
384 Levine, T. R., and C. R. Hullett. 2002. Eta squared, partial eta squared, and
385 misreporting of effect size in communication research. Human Communication
386 Research 28:612–625.
387 Matthews, B., T. Aebischer, K. E. Sullam, B. Lundsgaard-Hansen, and O. Seehausen.
388 2016. Experimental evidence of an eco-evolutionary feedback during adaptive
389 divergence. Current Biology 26:483–489.
390 Matthews, B., A. Narwani, S. Hausch, E. Nonaka, H. Peter, M. Yamamichi, K. E.
391 Sullam, K. C. Bird, M. K. Thomas, T. C. Hanley, and C. B. Turner. 2011. Toward
392 an integration of evolutionary biology and ecosystem science. Ecology Letters
393 14:690–701.
394 Mimura, M., T. Yahara, D. P. Faith, E. Vázquez-Domínguez, R. I. Colautti, H. Araki,
395 F. Javadi, J. Núñez-Farfán, A. S. Mori, S. Zhou, P. M. Hollingsworth, L. E.

Neaves, Y. Fukano, G. F. Smith, Y.-I. Sato, H. Tachida, and A. P. Hendry. 2016. Understanding and monitoring the consequences of human impacts on intraspecific variation. Evolutionary Applications 10:121–139.

Nakagawa, S., and I. C. Cuthill. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. Biological Reviews 82:591–605.

Odling-Smee, J., D. H. Erwin, E. P. Palkovacs, M. W. Feldman, and K. N. Laland. 2013. Niche construction theory: a practical guide for ecologists. The Quarterly Review of Biology 88:3–28.

R Core Team. 2013. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Raffard, A., J. Cucherousset, J. G. Prunier, G. Loot, F. Santoul, and S. Blanchet. 2019a. Variability of functional traits and their syndromes in a freshwater fish species (*Phoxinus phoxinus*): The role of adaptive and nonadaptive processes. Ecology and Evolution 9:2833–2846.

Raffard, A., F. Santoul, J. Cucherousset, and S. Blanchet. 2019b. The community and ecosystem consequences of intraspecific diversity: a meta-analysis. Biological Reviews 94:648–661.

Rey, O., E. Danchin, M. Mirouze, C. Loot, and S. Blanchet. 2016. Adaptation to global change: a transposable element–epigenetics perspective. Trends in Ecology & Evolution 31:514–526.

Rosenblatt, A. E., and O. J. Schmitz. 2016. Climate change, nutrition, and bottom-up and top-down food web processes. Trends in Ecology & Evolution.

Royauté, R., and J. N. Pruitt. 2015. Varying predator personalities generates contrasting prey communities in an agroecosystem. Ecology 96:2902–2911.

420 Rudolf, V. H. W., and N. L. Rasmussen. 2013. Ontogenetic functional diversity: Size
421 structure of a keystone predator drives functioning of a complex ecosystem.
422 Ecology 94:1046–1056.
423 Schmid, D. W., M. D. McGee, R. J. Best, O. Seehausen, and B. Matthews. 2019.
424 Rapid divergence of predator functional traits affects prey composition in aquatic
425 communities. The American Naturalist 193:331–345.
426 Schoener, T. W. 2011. The newest synthesis: understanding the interplay of
427 evolutionary and ecological dynamics. Science 331:426–429.
428 Thompson, J. N. 1998. Rapid evolution as an ecological process. Trends in Ecology
429 & Evolution 13:329–332.
430 Turcotte, M. M., D. N. Reznick, and J. Daniel Hare. 2013. Experimental test of an
431 eco-evolutionary dynamic feedback loop between evolution and population density
432 in the green peach aphid. The American Naturalist 181:S46–S57.
433 Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E.
434 Garnier. 2007. Let the concept of trait be functional! Oikos 116:882–892.
435 Wolf, M., and F. J. Weissing. 2012. Animal personalities: consequences for ecology
436 and evolution. Trends in Ecology & Evolution 27:452–461.
437 Yvon-Durocher, G., A. P. Allen, M. Cellamare, M. Dossena, K. J. Gaston, M. Leitao,
438 J. M. Montoya, D. C. Reuman, G. Woodward, and M. Trimmer. 2015. Five years
439 of experimental warming increases the biodiversity and productivity of
440 phytoplankton. PLoS Biol 13:e1002324.
441 Zhao, T., S. Villéger, and J. Cucherousset. 2019. Accounting for intraspecific
442 diversity when examining relationships between non-native species and functional
443 diversity. Oecologia 189:171–183.
444

445 **Figure Captions**

446 **Figure 1.** Experimental design used to test the ecological (phase 1) and
447 transgenerational carry-over (phase 2) effects of intraspecific variation among adult
448 minnows (*Phoxinus phoxinus*) and temperature variation.

449

450 **Figure 2.** (a) Eta squared (η^2) effect size of the intraspecific variation among adults
451 and temperature on ecological (green) and performance (blue) parameters. Error bars
452 represent ± 1 SE. (b) Delta of effect sizes (η^2) of intraspecific variation and
453 temperature on ecological and performance parameters. Positive values indicate a
454 higher effect of intraspecific variation, and negative values indicate a higher effect of
455 temperature.

456

457 **Figure 3.** Cumulated absolute β path coefficients extracted from the simplified path-
458 analysis described the direct and indirect relationships between intraspecific trait
459 variation among adult minnows, temperature, ecological parameters (a) and
460 performance parameters (b) and (c). The effects of intraspecific trait variation on
461 performance of juveniles can only be indirect because the adult fish were removed
462 before phase 2 of the experiment. The horizontal bar in (c) represents the indirect
463 effects of temperature on performance parameters. The abbreviation 'SGR' stands for
464 specific growth rate of adult minnows, and "#" for organism abundance.

465

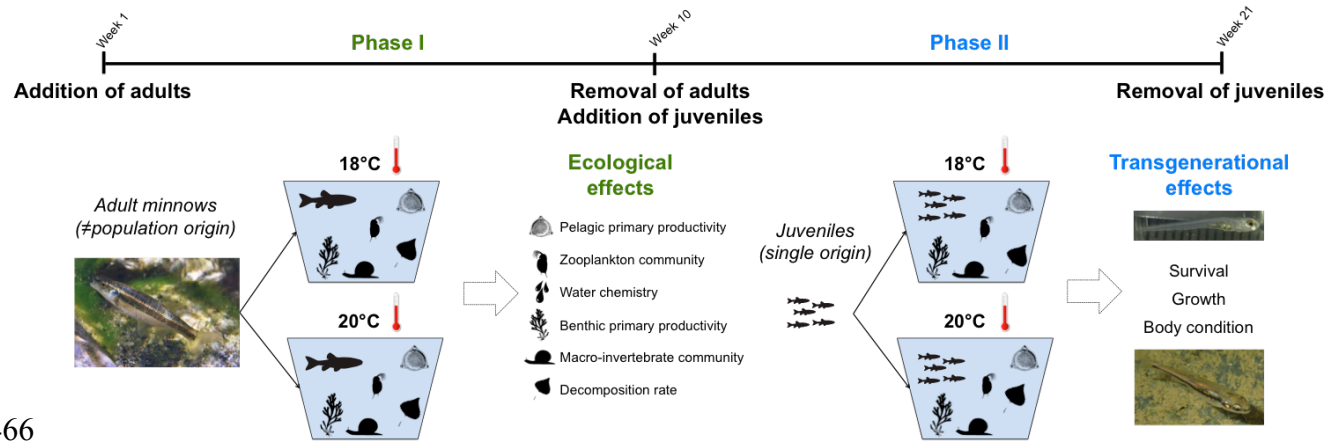
Week 1
Phase I
Week 10
Phase II
Week 21
Addition of adults
Removal of adults
Addition of juveniles
Removal of juveniles
Adult minnows
(≠population origin)
18°C
20°C
Ecological
effects
Pelagic primary productivity
Zooplankton community
Water chemistry
Benthic primary productivity
Macro-invertebrate community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

Figure 1.

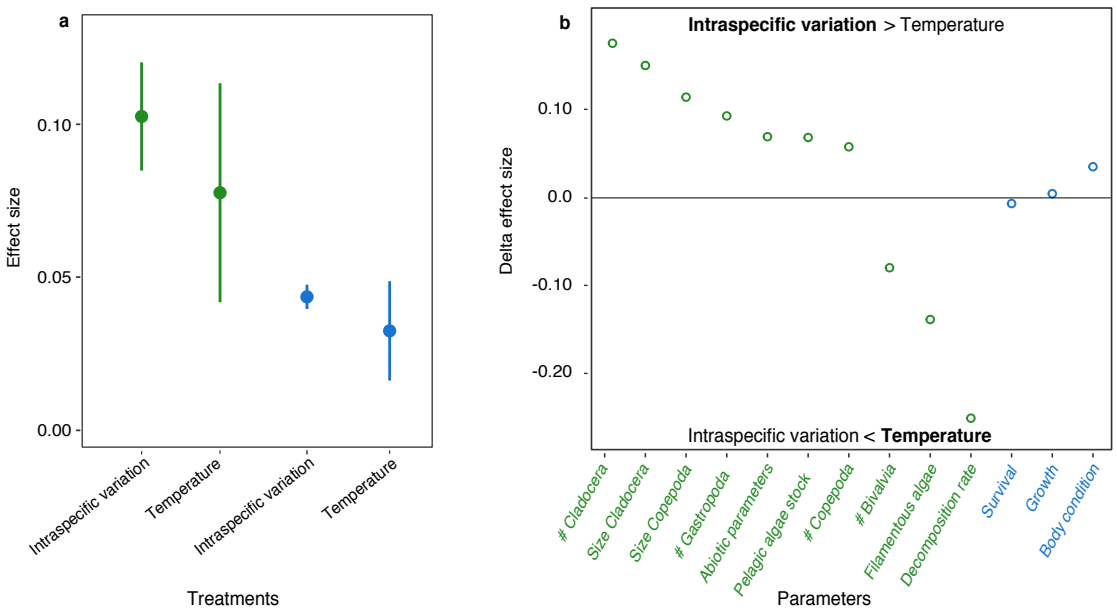
a
Effect size
0.10
0.05
0.00
Intraspecific variation
Temperature
Intraspecific variation
Temperature
Treatments
b
Intraspecific variation > Temperature
Delta effect size
0.10
0.0
-0.10
-0.20
Intraspecific variation < Temperature
Cladocera
Size Cladocera
Size Copepoda
Gastropoda
Abiotic parameters
Pelagic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

Figure 2.

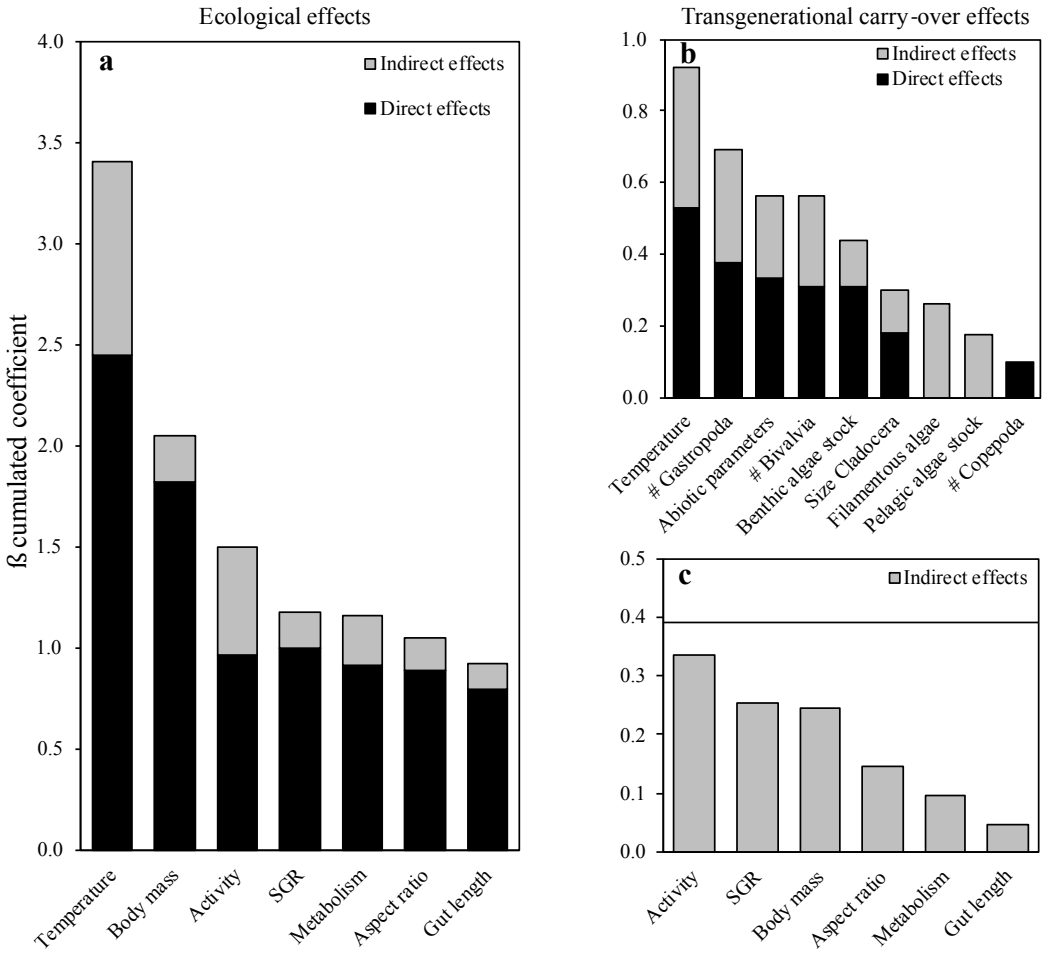
Ecological effects
a
Indirect effects
Direct effects
ß cumulated coefficient
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Temperature
Body mass
Activity
SGR
Metabolism
Aspect ratio
Gut length
Transgenerational carry-over effects
b
Indirect effects
Direct effects
1.0
0.8
0.6
0.4
0.2
0.0
Temperature
Gastropoda
Abiotic parameters
Bivalvia
Benthic algae stock
Size Cladocera
Filamentous algae
Pelagic algae stock
Copepoda
c
Indirect effects
0.5
0.4
0.3
0.2
0.1
0.0
Activity
SGR
Body mass
Aspect ratio
Metabolism
Gut length

Figure 3.