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Climate and intraspecific variation in a consumer species drive ecosystem multifunctionality

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Climate change is altering the multifunctionality of ecosystems worldwide and is often associated with changes in biodiversity that can modulate the impacts of climate change on ecosystems through interactive effects. Genetic and phenotypic variation within species are particularly influenced by climatic conditions, and can mediate several ecosystem processes. Here, we tested whether temperature can interact with intraspecific variation to drive ecosystem multifunctionality. Using a common gardening experiment, we test the consequences of intraspecific variation (population identity and trait variation) of a consumer fish species (European minnow *Phoxinus phoxinus*) and temperature on ecosystem multifunctionality, as well as on the biomass of a subsequent fish generation (long-term effects). We found that individuals from different populations affect ecosystem multifunctionality independently of temperature, and that multifunctionality differed between cold and warm mesocosms. Moreover, when investigating sub-components of multifunctionality, we found a positive relationship between individual metabolic rate and multifunctional primary production in warm mesocosms, whereas this relationship was reversed in cold mesocosms. We similarly found evidence that the long-term effect of intraspecific trait variation on the biomass of the next fish generation was temperature-dependent. These findings demonstrate that differences among populations can have strong consequences on ecosystem multifunctionality, and that intraspecific variation must be considered in addition to other components of global change to predict the impacts of global change on ecosystem multifunctionality.

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

Introduction

The multiple components of global change (e.g. fragmentation, climate change, pollution, biological invasion) can often jointly and interactively affect biological processes. For instance, temperature is a major component of climate change that can alter

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key processes such as the primary productivity of ecosystems (Yvon-Durocher et al. 2010, 2015). Climate change is also associated with biodiversity loss that can itself alter the same processes in an opposite or synergetic direction (Parmesan 2006, Bestion et al. 2020). Although some studies have investigated the potential interactive effects between global change components and biodiversity on multiple biological processes (Antiqueira et al. 2018, Giling et al. 2019), there has been surprisingly little evidence that climatic conditions and variation within species can interactively affect multiple biological processes (but see Fryxell and Palkovacs 2017).

Genetic and phenotypic variations within species are important components of biodiversity in natural communities (Siefert et al. 2015, Zhao et al. 2019). Intraspecific variation is strongly impacted by multiple global change components and can lead to population decline and extinction (Clements and Ozgul 2016, Mimura et al. 2016, Baruah et al. 2019, Leigh et al. 2019). Moreover, intraspecific variation has important effects on communities and ecosystem functioning that can be as high as those associated with species diversity (Des Roches et al. 2018, Raffard et al. 2019b). For instance, individuals differing in their genetic and phenotypic features do not interact with their biotic and abiotic environment in the same way, which can alter food web structure and ecosystem properties (Harmon et al. 2009, Bassar et al. 2010, Gibert and DeLong 2017). Moreover, it has been recently suggested that considering both genetic and trait variation can bring complementary insights on the consequences of intraspecific variation on ecosystem functions (Raffard et al. 2021). On the other hand, particular genetic or phenotypic features may allow some individuals to adapt to climate change, whereas other individuals may not (Parmesan 2006, Hoffmann and Sgrò 2011, Rey et al. 2012). Indeed, individuals with a different genetic background and/or displaying different expression of traits (e.g. different metabolic rates) may differ in their ability to adjust to a change in temperature (warm or cold), which would alter the way they use resources and hence how they influence ecosystem multifunctionality. This might subsequently lead to population-specific impacts of climate change on ecosystem properties that are important to quantify. Despite the ubiquity of climate change and loss or changes in intraspecific variation, we still poorly understand how they interact to affect biological processes up toward the ecosystem level.

Ecosystems are maintaining multiple functions simultaneously, and another challenge is to assess the impacts of global change on all these functions, which is usually defined as the 'multifunctionality' of ecosystems (Gamfeldt et al. 2008, Giling et al. 2019). For instance, warming is expected to simultaneously increase ecosystem metabolism, productivity, and nitrogen cycling, leading to impacts on the entire ecosystem, which can be quantified from a multifunctional perspective (Antiqueira et al. 2018). Intraspecific variation has also been shown to alter all these ecological processes, yet separately, through direct and/or indirect (top–down or bottom–up) effects (Crutsinger et al. 2006, Harmon et al. 2009, Bassar et al. 2010). Studying the joint effects of climate and intraspecific variation on ecosystem multifunctionality should provide an integrative perspective and improve our ability to anticipate their combined effects on ecosystem multifunctionality.

Here, we experimentally tested the combined and interactive effects of intraspecific variation and temperature on the multifunctionality of aquatic ecosystems. We specifically ran a common gardening experiment introducing individuals of a consumer fish (European minnow *Phoxinus phoxinus*) from six genetically unique populations displaying differences in phenotypic trait expression (Raffard et al. 2019a) in mesocosms. The temperature was manipulated by setting warm and cold (2°C difference) experimental mesocosms. We here asked 1) whether individuals from different populations and with different traits differed in their impacts on ecosystem multifunctionality and 2) whether these impacts were mediated by the experimental temperature (warm or cold). Finally, because temperature and intraspecific variation can have long-standing (indirect) effects (Matthews et al. 2016, Best et al. 2017), we also tested the long-term effects of these ecosystem changes on the biomass of a subsequent generation of minnows.

Material and methods

Study species

The European minnow *Phoxinus phoxinus* is a small-bodied (maximum length: ~80 mm, mean generation time: ~2 years) cyprinid fish species widely distributed in western Europe. *Phoxinus phoxinus* lives in relatively temperate waters, mainly in streams and rivers but also in mountain lakes (Keith et al. 2011). This ubiquity of minnows (from southern France to Scandinavia) suggests it is a thermal generalist. For instance, in our system (Supporting information), they can tolerate a large annual range of temperatures (approximately from 7 to 25°C, Supporting information), although they are generally associated to the upstream parts of rivers and lakes that are cold environments. It is a generalist species that feeds on small invertebrates, algae, zooplankton and small fish larvae (Keith et al. 2011).

In September 2016, we collected adult minnows by electrofishing in six rivers in southwestern France (Supporting information). We selected populations that were isolated geographically and had distinct environments (Supporting information) to maximize 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, calculated on 30 individuals of each population, Raffard et al. 2019a), indicating a high evolutionary distinctiveness among the populations. The sampled populations also varied for important functional traits (Brown et al. 2004, Woodward et al. 2005, McIntyre et al. 2008), such as body mass and metabolic rate (Raffard et al. 2019a). Furthermore, it has been previously shown that minnow populations in these river systems were characterised by a unique syndrome of functional traits (set of trait variation and covariation) that resulted from a combination of genetic drift and adaptation (either due to plasticity or selection on genetic variants) to both water temperature and predation pressure (Raffard et al. 2019a). 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 kept at a similar density and separately for ~6 months in 1100 l outdoor tanks to soften short-term environmental effects (e.g. prey availability) on phenotypes (e.g. excretion rate). During rearing, the fish were fed until satiety with a mixture of pelletized food and dead chironomids until the start of the experiment.

Common gardening experiment

We conducted a common gardening experiment (i.e. an experiment quantifying the 'effects of organisms on a common type of ecosystem', Matthews et al. 2011), which 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 2 December 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 12 December 2016. Two months later (15 February 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 sediments 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 (Supporting information). 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 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 (Supporting information). This 2°C increase allows maintaining a realistic temperature while limiting potential thermal stresses for the fish.

In March 2017, adult fish were weighed to the nearest 0.01 g and a single fish was randomly introduced to each mesocosm. This individual-based approach prevented the experimental ecosystems from collapsing due to the overdensity of top consumers and allowed precise quantification of the ecological effects of individual trait variation to be measured. After 73 days, each fish was removed and phenotyped, and we measured multiple ecosystem parameters to evaluate differences in ecosystem multifunctionality among treatments.

Phenotypic measurement

We measured three phenotypic traits of each adult fish (body mass, metabolic rate, and activity behaviour) to test for the contribution of each of these traits to ecosystem multifunctionality and long-term effects on juvenile biomass, in addition to the contribution associated to the origin of populations (genetic background). We focused on traits that are likely to mechanistically affect ecosystem properties (Brown et al. 2004, Hildrew et al. 2007, Wolf and Weissing 2012). Body mass, metabolic rate and activity behaviour are indeed important in shaping multiple ecological processes, such as interspecific interactions, prey selectivity, or nutrient excretion (Rudolf and Rasmussen 2013, Toscano et al. 2016, Raffard et al. 2017). This can subsequently alter community structure and ecosystem functioning through modification of biomass productivity, species abundance, community or decomposition rate (Katano 2011, Rudolf and Rasmussen 2013, Raffard et al. 2021). Activity was measured throughout the first step of the experiment. Each morning the experimenters (AR and LDG) noted whether the fish were visible or not in the tank, and we considered a fish as active when it was visible. We then calculated the proportion of time each fish was visible to obtain an activity score. To assess the metabolic rate, we followed the procedure described in Raffard et al. (2019a). Before initiating the measurement, the individuals were starved for two days to ensure the same starvation level among individuals. Then, each fish was individually placed in a metabolic chamber filled with 500 ml of dechlorinated tap water. Measurements of oxygen concentration were taken after 10 min, allowing individuals to acclimate, and continuously every five seconds for 50 min with oxygen probes. Chambers were set in a thermoregulated room at 17°C in the dark to lower the stress level. After one hour, fish were gently released in their home tank. After the common gardening experiment and phenotyping, fish were euthanized in a solution of benzocaine at 25 mg l^{-1}.

Ecosystem parameters

At the end of the experiment (day 73), we measured multiple ecosystem properties to evaluate multifunctionality and to compare the relative effects of population identity and temperature treatment.

1) 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 (µg l^{-1}) in the water column. Two measurements (duplicates) within each mesocosm were taken at the end of the experiment to account for potential measurement error and were averaged for the analyses.

2) Benthic algae stock was assessed as a proxy of the benthic primary productivity using a portable spectrometer (BenthoTorch, bbe moldaenke). The chlorophyll-a concentration (µg cm^{-2}) was measured on two tiles (20 × 20 cm) placed in the mesocosms the day before the start of the experiment. Two measurements (one on each tile) were taken at the end of the experiment, and they were averaged for analyses.
3) The abundance of filamentous algae was quantified at the end of the experiment (after 73 days). Filamentous algae cover (%) was visually estimated by two operators, and the two values were averaged for analyses.
4) Decomposition rate was measured by quantifying the mass loss of black poplar *Populus nigra* (a dominant riparian tree in southern France) abscised leaves (Alp et al. 2016). One day before the start of the experiment, 4 g of air-dried leaves were put in each mesocosm within a coarse mesh (1 × 1 cm) bag. After 73 days, 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 $k = -\dfrac{\ln(X)}{t}$ (Alp et al. 2016), where X is the proportion of litter remaining after phase 1 and t is the elapsed time in days.
5) Specific conductance (µS, reflecting the level of mineralization of water), and turbidity (NTU) were measured once in each tank at the end of the experiment with a multiparameter probe (YSI Pro DSS Water Quality Meter).
6) Zooplankton community was assessed by filtering 5 l of water through a 200 µm sieve. Samples were 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). The abundance of Copepoda or Cladocera was considered as a proxy for their biomass.
7) Macroinvertebrates (> 1 mm, primarily molluscs) were collected from the mesh bags used to measure decomposition rates (at the end of the experiment after 73 days), conserved in a 70% ethanol solution, and identified as Bivalvia or Gastropoda. The abundance of Bivalvia or Gastropoda was considered as a proxy for their biomass.

Ecosystem multifunctionality was estimated using a z-score over all measured metrics (Maestre et al. 2012, Antiqueira et al. 2018). To do so, each ecosystem parameter was scaled to the mean (mean of 0 and variance of 1) and they were then averaged across each mesocosm (Maestre et al. 2012, Antiqueira et al. 2018) to obtain a global score of ecosystem multifunctionality for each mesocosm. High positive scores of multifunctionality indicate high values on most of the individual metrics, which suggests tanks with high primary and secondary productivities and high levels of mineralization. To gain mechanistic insights into how temperature change and intraspecific variation affect ecosystem multifunctionality, we also decomposed multifunctionality into three specific components: multifunctional primary production (pelagic and benthic algae stock, and filamentous algae abundance), multifunctional secondary production (abundance of Copepoda, Cladocera, Bivalvia and Gastropoda) and multifunctional mineralization (decomposition rate, specific conductance and turbidity). Each component was quantified using the z-score approach described above but using only parameters specific to each component.

Long-term effects

Finally, to assess the long-term effects of intraspecific variation, we quantify the biomass of a subsequent generation of minnows (Supporting information). We were specifically interested by 'indirect' long-term effects of intraspecific variation and temperature, i.e. effects due to changes in ecosystem properties that were mediated by intraspecific variation and temperature change. We therefore removed adult minnows from the mesocosms after the 73 days, and juvenile minnows were introduced to each mesocosm to quantify the effects of ecosystem changes due to intraspecific variation (and temperature) on the biomass of these juveniles. Forty-five juveniles were introduced to obtain a density allowing to quantify changes in biomass production due to both individual growth rate and mortality. We used juveniles from a single origin (i.e. fish farm, *Amorvif EURL*) to control for potential effects of the genetic background, to focus on a population that is genetically independent from the populations used in the first step of the experiment, and to ensure the availability of the required number of individuals at a very early stage of development (Supporting information). 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 (Pinder 2001) (Supporting information). They were not manipulated (i.e. weighed and/or measured) before being randomly introduced into the mesocosms to limit potential mortality. The juveniles were removed from the mesocosms 79 days later to assess their biomass. Individuals were counted and weighed to the nearest 0.001 g to assess the final fish biomass.

Statistical analyses

Two adult individuals died before the end of the experiment and these two replicates were not used in subsequent analyses. Moreover, we identified six tanks in which crayfish had been inadvertently introduced; we discarded these six replicates because crayfish are known to have disproportionally strong impacts on ecosystems (Alp et al. 2016). As such, the final analyses were run on 64 replicates (with a minimum of three replicates per treatment).

First, we tested whether populations differed in the measured phenotypic traits (body mass, metabolic rate, and activity) using one-way analysis of variance. Second, we tested whether population identity of fish modulated the effects of temperature on ecosystem multifunctionality, i.e. whether the populations and the experimental temperature have interactive effects on ecosystem multifunctionality. Linear models were used with ecosystem multifunctionality as the response variable, and population identity (six-level factor), temperature treatment (warm versus cold mesocosms), and the two-way interaction term as explanatory variables. Similar models were then used to assess the responses of multifunctional primary production, multifunctional secondary production, multifunctional mineralisation, and juvenile biomass as response variables. Third, we tested for the effects of population identity on multifunctionality and long-term effects after conditioning on the three functional traits. Therefore, models were performed with ecosystem multifunctionality (or juvenile biomass) as the response variable, and population identity, individual body mass, activity, metabolic rate, temperature treatment, and the two-way interaction term between temperature treatment and all other individual characteristics (i.e. populations identity and traits) as explanatory variables. Finally, we tested the effects of intraspecific variation (i.e. population identity and trait variation) on juvenile biomass after conditioning by ecosystem multifunctionality and temperature. To do so, a model was performed with juvenile biomass as the response variable, and ecosystem multifunctionality, population identity, individual body mass, activity, metabolic rate, temperature treatment and the two-way interaction term between temperature treatment and all other individual characteristics (i.e. populations identity, and traits) as explanatory variables. Analyses of variance were performed using the *Anova*’ function from the car R-package (Fox and Weisberg 2019), and the relative importance of each variable (contribution to R^2) was estimated using the *calc.relimp* function in the relaimpo R-package (Grömping 2006). The slope given in the results were obtained using the function *emtrends*’ in the emmeans R-package (Length et al. 2022). The normality of residuals was visually assessed. To assess model performance 1) we verified that collinearity was low using the variance inflation factor (all variables displayed a VIF < 5 indicating low collinearity; Supporting information, Gareth et al. 2013), and 2) we assessed model overfit quantifying the accuracy of model prediction using the correlation between predicted and observed values on 100 bootstraps. Multicollinearity and model accuracy were computed using the *check_collinearity* and *performance_accuracy* functions, respectively, from the performance R-package (Lüdecke et al. 2021). Statistical analyses were performed using R ver. 4.1.0 (www.r-project.org).

Results

We first found that individuals from different populations differed in their body mass and metabolism (one-way ANOVA: $F_{Dfn,Dfd}=10.50_{5,58}$, p-value < 0.001 and $F_{Dfn,Dfd}=3.46_{5,58}$, p-value = 0.008, respectively), but displayed similar activity ($F_{Dfn,Dfd}=1.13_{5,58}$, p-value = 0.353, Fig. 1, Supporting information). Total ecosystem multifunctionality was significantly higher in the warmest mesocosms than in the coldest mesocosms ($F_{Dfn,Dfd}=40.91_{1,52}$, p-value < 0.001, Table 1, Fig. 2a). It was also significantly modulated by population identity (genetic background) of individuals, irrespectively of the experimental temperature (Fig. 2a, Table 1). Specifically, mesocosms hosting fish from particular populations (e.g. Célé and Arize, Fig. 2a) reach a higher multifunctionality than mesocosms hosting fish from other populations (e.g. Lez and Volp), independently of temperature treatment. The inclusion of individual traits in this model resulted in qualitatively similar effects of population identity (Table 2).

Patterns were more complex when investigating each sub-component of ecosystem multifunctionality (Fig. 1). First, the experimental temperature globally altered multifunctionality, with a higher temperature in mesocosms leading to significant increases in primary production ($F_{Dfn,Dfd}=13.62_{1,52}$, p-value < 0.001), secondary production ($F_{Dfn,Dfd}=4.86_{1,52}$, p-value = 0.031) and mineralization multifunctionalities ($F_{Dfn,Dfd}=23.47_{5,52}$, p-value < 0.001, Table 1, Fig. 2b–d). Second, there was solely one significant interaction between populations and temperature on primary production, suggesting that populations may display different patterns ($F_{Dfn,Dfd}=2.82_{5,52}$, p-value = 0.023, Table 1). Finally, when including traits in the models, we found that trait variation modulated sub-components of multifunctionality, but the traits involved in these relationships and the type of effects

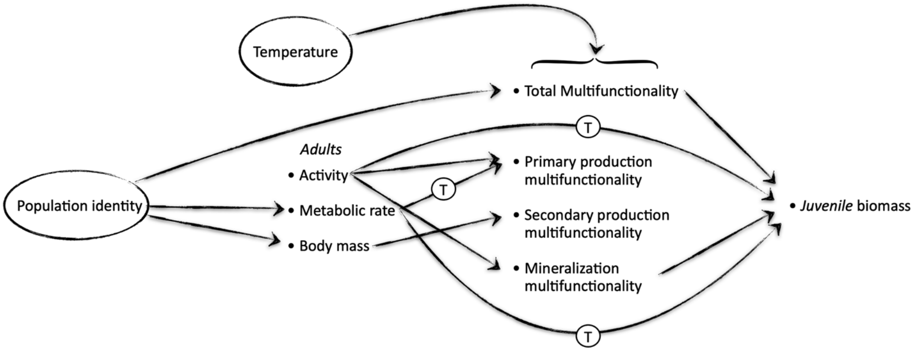

Figure 1. Diagram summarizing the relationships among temperature, population identity, trait variation, ecosystem multifunctionality and juvenile biomass found in this study. The curly bracket indicates that temperature affects each component of ecosystem multifunctionality, and ‘T’ indicates a temperature-dependent relationship.

Table 1. Effect of populations identity and experimental temperature on ecosystem multifunctionality indicators and juvenile biomass. Significant values are displayed in bold. Accuracy represents the correlation between predicted and observed values calculated over 100 bootstraps.

Response	Effect	F-value	df	R^2	p-value
Total multifunctionality (accuracy = 78%)	**Temperature**	**40.91**	**1,52**	**0.37**	**< 0.001**
	Population identity	**2.56**	**5,52**	**0.10**	**0.038**
	Population identity × Temperature	0.49	5,52	0.02	0.780
Primary production multifunctionality (accuracy = 70%)	**Temperature**	**13.62**	**1,52**	**0.14**	**< 0.001**
	Population identity	1.86	5,52	0.09	0.116
	Population identity × Temperature	**2.82**	**5,52**	**0.16**	**0.024**
Secondary production multifunctionality (accuracy = 62%)	**Temperature**	**4.86**	**1,52**	**0.06**	**0.031**
	Population identity	1.48	5,52	0.09	0.211
	Population identity × Temperature	1.63	5,52	0.11	0.168
Mineralization multifunctionality (accuracy = 68%)	**Temperature**	**23.47**	**1,52**	**0.28**	**< 0.001**
	Population identity	0.24	5,52	0.01	0.941
	Population identity × Temperature	1.20	5,52	0.07	0.319
Juvenile biomass (accuracy = 50%)	Temperature	0.02	1,52	< 0.01	0.87
	Population identity	0.41	5,52	0.03	0.83
	Population identity × Temperature	0.68	5,52	0.06	0.63

(additive or interactive) varied (Table 2). Variation in fish activity was positively associated with primary production multifunctionality (standardised slope ± SE = 1.76 ± 1.71, p-value = 0.044, Table 2, Fig. 3b), whereas it was negatively associated with mineralization multifunctionality (Table 2, Fig. 3d). Variation in fish body mass was also additively and positively associated with secondary production multifunctionality, with higher body mass of experimental fish

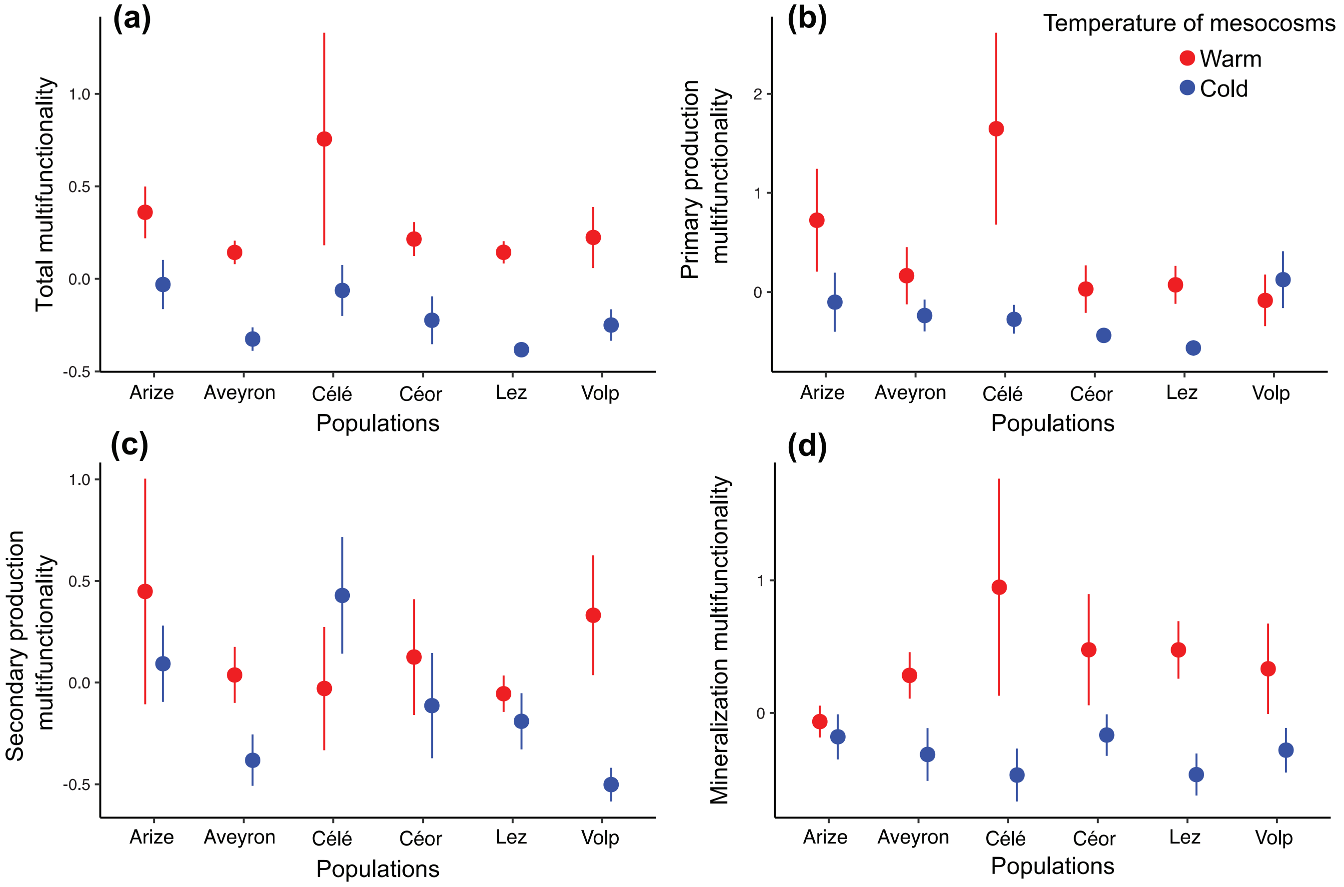

Figure 2. Variation in ecosystem multifunctionality among the six populations of European minnows and between experimental temperature (warm in red and cold in blue). (a) Total multifunctionality, (b) primary production multifunctionality, (c) secondary production multifunctionality, and (d) mineralization multifunctionality. Error bars represent ± 1 SE.

Table 2. Effects of population identity, variation in phenotypic traits and experimental temperature (warm and cold) on ecosystem multifunctionality indicators. Significant values are in bold. Accuracy represents the correlation between predicted and observed values calculated over 100 bootstraps.

Response	Effect	F-value	df	R^2	p-value
Total multifunctionality (accuracy = 82%)	**Temperature**	**36.394**	**1,46**	**0.361**	**< 0.001**
	Population identity	**2.643**	**5,46**	**0.115**	**0.035**
	Body mass	2.923	1,46	0.027	0.094
	Activity	0.040	1,46	0.002	0.842
	Metabolic rate	0.030	1,46	0.002	0.864
	Population identity × Temperature	0.435	5,46	0.023	0.822
	Body mass × Temperature	< 0.001	1,46	< 0.001	0.992
	Activity × Temperature	0.172	1,46	0.001	0.679
	Metabolic rate × Temperature	0.238	1,46	0.003	0.628
Primary production multifunctionality (accuracy = 81%)	**Temperature**	**14.281**	**1,46**	**0.142**	**< 0.001**
	Population identity	2.286	5,46	0.108	0.061
	Body mass	0.011	1,46	0.006	0.915
	Activity	**4.279**	**1,46**	**0.057**	**0.044**
	Metabolic rate	2.008	1,46	0.021	0.163
	Population identity × Temperature	2.022	5,46	0.122	0.093
	Body mass × Temperature	0.279	1,46	0.003	0.599
	Activity × Temperature	0.803	1,46	0.007	0.374
	Metabolic rate × Temperature	**6.197**	**1,46**	**0.068**	**0.016**
Secondary production multifunctionality (accuracy = 75%)	Temperature	3.905	1,46	0.053	0.054
	Population identity	2.035	5,46	0.108	0.091
	Body mass	**4.713**	**1,46**	**0.063**	**0.035**
	Activity	0.105	1,46	0.020	0.747
	Metabolic rate	0.005	1,46	0.002	0.944
	Population identity × Temperature	1.265	5,46	0.094	0.295
	Body mass × Temperature	0.042	1,46	0.003	0.837
	Activity × Temperature	3.458	1,46	0.044	0.069
	Metabolic rate × Temperature	1.034	1,46	0.017	0.314
Mineralization multifunctionality (accuracy = 80%)	**Temperature**	**26.720**	**1,46**	**0.285**	**< 0.001**
	Population identity	0.534	5,46	0.023	0.749
	Body mass	0.594	1,46	0.016	0.444
	Activity	**4.899**	**1,46**	**0.044**	**0.031**
	Metabolic rate	3.129	1,46	0.034	0.083
	Population identity × Temperature	1.226	5,46	0.067	0.312
	Body mass × Temperature	0.641	1,46	0.004	0.427
	Activity × Temperature	0.249	1,46	0.003	0.620
	Metabolic rate × Temperature	0.247	1,46	0.001	0.621

leading to higher secondary productivity in the mesocosms (standardised slope ± SE = 0.26 ± 0.128, p-value = 0.035, Table 2, Fig. 3c). Lastly, a significant interaction term between metabolic rate and temperature on primary production multifunctionality was observed ($F_{Dfn,Dfd} = 6.19_{1,52}$, p-value = 0.016, Table 2). Specifically, primary production multifunctionality was positively related to individual metabolic rate in cold mesocosms (slope = 1.05 ± 1.16), whereas this relationship was negative in the warmest mesocosms (slope = −2.84 ± 1.04; Fig. 3a).

Regarding the long-term effects, we found that the (past) activity and metabolic rate of adult fish significantly affected juvenile biomass in interaction with experimental temperature (Table 3, Fig. 1). In cold mesocosms, adult fish with higher metabolic rate led to an ecosystem that increased the final biomass of juveniles (slope ± SE = 4.68 ± 1.35). However, this relationship strongly weakened in warm mesocosms (slope ± SE = 0.24 ± 1.22, Fig. 3e). Conversely, more active adult fish led to an ecosystem that increased the final biomass of juveniles in warm mesocosms (slope ± SE = 9.95 ± 3.62), but not in cold mesocosms (slope ± SE = 0.87 ± 1.71, Fig. 3f). Moreover, when including multifunctionality parameters in the model, we found that total multifunctionality was negatively related to juvenile biomass (slope ± SE = −0.94 ± 0.40, p-value = 0.025, Supporting information). When testing the effects of each subcomponents of multifunctionality, we found that mineralization multifunctionality led to a decrease of biomass (slope ± SE = −0.75 ± 0.23, p-value = 0.002, Supporting information).

Discussion

Although intraspecific variation and climate variability are two important factors mediating ecosystem processes, the interacting effects have rarely been studied. Here, we demonstrated that differences among populations in a consumer species can affect ecosystem multifunctionality, and that these effects were mostly independent from temperature. These

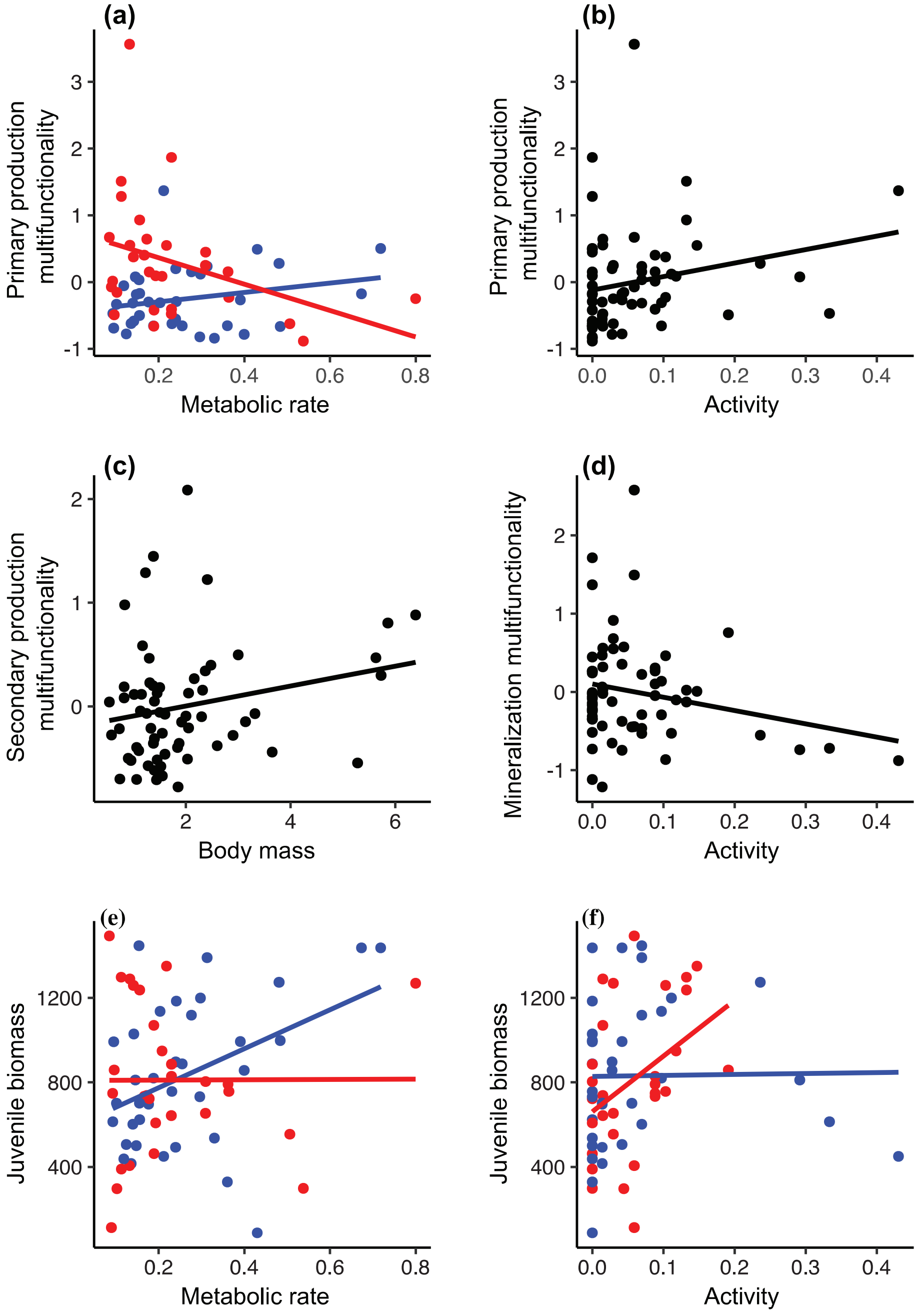

Figure 3. Relationships between (a) primary production multifunctionality and metabolic rate and (b) activity, (c) secondary production multifunctionality and body mass, and (d) mineralization multifunctional and activity. The effects of metabolic rate (e) and activity (f) on juvenile biomass were dependent upon experimental temperature. Blue (cold mesocosms) and red (warm mesocosms) points are displayed when the interaction between traits and the experimental temperature was significant (Table 2, 3).

findings indicate that intraspecific variation can simultaneously alter the rate of multiple ecosystem functions, changing the fate of a whole ecosystem. Ecosystem multifunctionality was also strongly and positively modulated by increased temperature, a finding holding true for all measured ecosystem multifunctionality (Antiqueira et al. 2018). These impacts of temperature and intraspecific variation on ecosystem multifunctionality were mostly independent one from each other, which indicates that changes in temperature and in intraspecific variation may actually have additive – rather than interactive – effects on multifunctionality. Contrastingly, the biomass of the next fish generation (long-term effect) was mostly modulated by interactive effects between trait variation in the previous generation and experimental temperature, and was not systematically increased in warm mesocosms. Our experiment suggests that the combined effects of

Table 3. Long-term effects of population identity, variation in phenotypic traits, and experimental temperature (warm and cold) on the juvenile biomass of a subsequent generation. Significant values are in bold. Accuracy represents the correlation between predicted and observed values calculated over 100 bootstraps.

Response	Effect	F-value	df	R^2	p-value
Juvenile biomass (accuracy = 73%)	Temperature	0.033	1,46	< 0.001	0.856
	Population identity	1.198	5,46	0.052	0.324
	Body mass	0.592	1,46	0.003	0.445
	Activity	2.688	1,46	0.027	0.107
	Metabolic rate	**6.101**	**1,46**	**0.064**	**0.017**
	Population identity × Temperature	1.556	5,46	0.082	0.191
	Body mass × Temperature	0.008	1,46	0.002	0.925
	Activity × Temperature	**5.145**	**1,46**	**0.067**	**0.028**
	Metabolic rate × Temperature	**5.962**	**1,46**	**0.069**	**0.018**

global change components (i.e. changes in temperature) and its consequences (i.e. changes in intraspecific variation) can be either additive or interactive depending on the temporal and biological scales being investigated.

Most previous studies investigated the links between intraspecific variation and ecosystem dynamics by considering each ecosystem function independently from each other (Harmon et al. 2009, Matthews et al. 2016). Here, we further demonstrated that individuals from different populations significantly lead to variable ecosystem multifunctionality. Interestingly, we found that different components of intraspecific variation alter different component of multifunctionality. For example, population identity (the genetic background of populations) affects the global ecosystem multifunctionality independently of phenotypic traits. On the other hand, the effects of population identity on subcomponents of multifunctionality were mainly mediated by population-dependent trait expression (Fig. 1). Individual traits (activity, body mass) indeed affect sub-components of ecosystem multifunctionality, such as the secondary productivity and the mineralization of the ecosystem. This is probably because population identity is an integrative variable encompassing global functional variation among individuals (i.e. populations of minnows differ in multiple functional traits; Raffard et al. 2019a, 2020), hence affecting the overall ecosystem multifunctionality. Alternatively, phenotypic traits taken individually are most likely related to specific functions of the ecosystem. Inclusive studies accounting for both genetic (or population identity) and trait differences among individuals are hence a powerful approach to bring complementary insights into the role of intraspecific variation in ecosystems (Raffard et al. 2021).

Our findings show that trait–function relationships were difficult to predict since multiple traits differed in their ecological effects. We specifically found that body mass and metabolic rate significantly altered the secondary production and primary production of the ecosystem respectively. Interestingly, small fish decreased the abundance of Copepoda species (and also Cladocera to a lesser extent), suggesting that body mass variation among individuals might alter prey selectivity, which ultimately alters multifunctionality (Supporting information). These functional traits are more generally affecting the energetic needs and assimilation of individuals (Brown et al. 2004, Hildrew et al. 2007), leading to trophic differences among individuals that can contribute to subsequent ecosystem differentiation. Our results also suggest that temperature change mediates the relationship between metabolic rate and primary production multifunctionality. It is interesting to notice that in warm environments individuals with a higher metabolic rate led to a decrease in primary production multifunctionality. Those individuals may potentially shift their diet to include more plant debris or periphyton, to meet their nutrient and energetic demand (Boersma et al. 2016, Rosenblatt and Schmitz 2016), ultimately decreasing ecosystem multifunctionality. We further identified traits, such as activity, that were previously found to increase niche partitioning within population and individual performance, which ultimately affect communities and ecosystems (Wolf and Weissing 2012). For instance, our findings suggest that the effects of the activity of individuals on multifunctional primary production likely arise from a positive effect on the quantity of filamentous algae (Supporting information). We can speculate that less active individuals probably include more algae in their diet than active individual decreasing the quantity of filamentous algae (Frost 1943, Collin and Fumagalli 2011). The level of trait variation between individuals in our study is within the order of that of previous eco-evolutionary studies, and is much lower than variation due to ontogenetic changes (Harmon et al. 2009, Des Roches et al. 2013, Rudolf and Rasmussen 2013, Rudman et al. 2015). Hence, the ecosystem consequences of individual trait variation that we report here can be ubiquitous across organisms. Our study therefore confirms that individuals are not functionally equal (Schmid et al. 2019). Although these specific traits can be used in modelling frameworks to predict changes in ecosystem properties, our study reveals that a single trait cannot be used to predict all ecosystem properties. Moreover, it is necessary that future works focus on the effects of trait variation in natural systems with more environmental noise to fully generalise the importance of intraspecific variation.

Numerous studies have shown the key role of climate change for ecosystems (Yvon-Durocher et al. 2010, 2015, Antiqueira et al. 2018). While a warming of 2°C is likely during the next century, we here confirm that this change can lead to very different environments by strongly (delta of z-score up to 0.74, representing an increase of 20% in multifunction) affecting the rate of multiple ecosystem functions simultaneously. Temperature regulates the rate of multiple biological processes such as nutrient turnover, microbial activity, rates of physiological functions of consumers, and growth rate, which makes it likely to increase the biomass of primary and secondary producers, as well as the decomposition of organic matter (Brown et al. 2004, Woodward et al. 2010, Rosenblatt and Schmitz 2016). Interestingly, our experiment suggests that the effects of temperature were mostly independent from those of intraspecific variation. This is surprising because we used individuals from wild populations living in highly diverse environments (Raffard et al. 2019a). Therefore, we primarily expected that the physiological and behavioural responses of individuals to thermal conditions would have depended upon their origin, and hence that ecosystem multifunctionality would be modulated by the interaction between climatic condition and intraspecific variation. This finding highlights that temperature changes and intraspecific variation can act additively on ecosystem multifunctionality, which may ease future predictions, although this might depend upon the magnitude of temperature change.

Contrary to our observation on ecosystem multifunctionality, we found that intraspecific trait variation actually interacts with temperature to drive the juvenile biomass (productivity) of the next generation. Indeed, we found that the ecosystem imprints of intraspecific trait variation we measured during the first step of the experiment were long standing enough to affect the biomass of a next generation, and were conditioned upon temperature. Although these effects were relatively weak ($R^2 < 7\%$), they are important as they correspond to long-lasting indirect effects of trait variation among adult minnows on the performance of juveniles, which were mediated by the direct consequences of adult minnows on ecosystem multifunctionality. Interestingly, since these effects were temperature-dependent, they suggest that the role of 'environmental inheritance' (such as abiotic condition or prey abundance), is likely to be temporally persistent and conditioned upon temperature to affect the biomass of juveniles (Matthews et al. 2016). Here, an increase in ecosystem multifunctionality leads to a decrease in biomass, suggesting that it may alter juvenile performance. Especially, higher mineralization decreases juvenile biomass, suggesting that they might be sensitive to specific abiotic conditions. Yet, the effects of traits persisted when ecosystem parameters were included as additional covariates to the models (Supporting information), indicating that unmeasured predictors can be underlying the observed variation in juveniles. A further step would be to test these long-term effects using offsprings from the same starting population. Such an approach would allow testing the local adaptation of juveniles to the ecosystem effects of their parents. Few studies with this specific design suggested that – while transgenerational effects were shown – juveniles did not necessarily exert higher survival in mesocosms where their parents were present (Best et al. 2017). Ecosystem differentiation arising from interindividual variability might then lead to intricate transgenerational effects. Overall, these results are important because the presence or absence of strong interactive effects may modify the biological complexities and highlight the needs of further studies quantifying the long-term consequences of climate and biodiversity changes (Beckage et al. 2011, Fryxell and Palkovacs 2017).

In conclusion, we demonstrated that differences among populations can affect ecosystem multifunctionality. This finding, combined with previous studies comparing the effects of intraspecific variation to those induced by biotic factors (e.g. parasite presence and density; Best et al. 2017, Brunner et al. 2017), strongly supports the growing view that intraspecific variation can be important for the dynamics of a whole ecosystem. 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 variation in landscapes and thereby indirectly affect the dynamics of biological systems (Matthews et al. 2016, Brunner et al. 2017). Importantly, we demonstrated that some specific traits that are often modified by humans (body size and activity; Biro and Post 2008) can be used to forecast particular ecosystem modifications under current climate change. Therefore, our results reinforce recent reports that changes and shifts in intraspecific variation of wild populations (due for instance to harvest or pollution; Brodin et al. 2013, Palkovacs et al. 2018) must be considered to predict the impacts of global change on ecosystem multifunctionality. This facet of biodiversity contributes to maintain a diversity of ecosystem functionality and community structure under global change, and is important to account for in ecological surveys, biodiversity–ecosystem functioning relationships studies or management strategies.

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Author contributions

Allan Raffard: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Methodology (equal); Writing – original draft (lead). **Julien Cucherousset**: Conceptualization (supporting); Methodology (equal); Supervision (equal); Writing – review and editing (equal). **Frederic Santoul**: Funding acquisition (equal); Supervision (supporting); Writing – review and editing (supporting). **Lucie Di Gesu**: Data curation (equal); Methodology (equal);

Writing – review and editing (supporting). **Simon Blanchet**: Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Funding acquisition (equal); Methodology (equal); Supervision (lead); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Figshare Digital Repository: https://doi.org/10.6084/m9.figshare.19168385.v1 (Raffard et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Alp, M., Cucherousset, J., Buoro, M. and Lecerf, A. 2016. Phenological response of a key ecosystem function to biological invasion. – Ecol. Lett. 19: 519–527.

Antiqueira, P. A. P., Petchey, O. L. and Romero, G. Q. 2018. Warming and top predator loss drive ecosystem multifunctionality. – Ecol. Lett. 21: 72–82.

Baruah, G., Clements, C. F., Guillaume, F. and Ozgul, A. 2019. When do shifts in trait dynamics precede population declines? – Am. Nat. 193: 633–644.

Bassar, R. D., Marshall, M. C., Lopez-Sepulcre, A., Zandona, E., Auer, S. K., Travis, J., Pringle, C. M., Flecker, A. S., Thomas, S. A., Fraser, D. F. and Reznick, D. N. 2010. Local adaptation in Trinidadian guppies alters ecosystem processes. – Proc. Natl Acad. Sci. USA 107: 3616–3621.

Beckage, B., Gross, L. J. and Kauffman, S. 2011. The limits to prediction in ecological systems. – Ecosphere 2: 125.

Best, R. J., Anaya-Rojas, J. M., Leal, M. C., Schmid, D. W., Seehausen, O. and Matthews, B. 2017. Transgenerational selection driven by divergent ecological impacts of hybridizing lineages. – Nat. Ecol. Evol. 1: 1757–1765.

Bestion, E., Barton, S., García, F. C., Warfield, R. and Yvon-Durocher, G. 2020. Abrupt declines in marine phytoplankton production driven by warming and biodiversity loss in a microcosm experiment. – Ecol. Lett. 23: 457–466.

Biro, P. A. and Post, J. R. 2008. Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. – Proc. Natl Acad. Sci. USA 105: 2919–2922.

Boersma, M., Mathew, K. A., Niehoff, B., Schoo, K. L., Franco-Santos, R. M. and Meunier, C. L. 2016. Temperature driven changes in the diet preference of omnivorous copepods: no more meat when it's hot? – Ecol. Lett. 19: 45–53.

Brodin, T., Fick, J., Jonsson, M. and Klaminder, J. 2013. Dilute concentrations of a psychiatric drug alter behavior of fish from natural populations. – Science 339: 814–815.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. and West, G. B. 2004. Toward a metabolic theory of ecology. – Ecology 85: 1771–1789.

Brunner, F. S., Anaya-Rojas, J. M., Matthews, B. and Eizaguirre, C. 2017. Experimental evidence that parasites drive eco-evolutionary feedbacks. – Proc. Natl Acad. Sci. USA 114: 3678–3683.

Clements, C. F. and Ozgul, A. 2016. Including trait-based early warning signals helps predict population collapse. – Nat. Commun. 7: 10984.

Collin, H. and Fumagalli, L. 2011. Evidence for morphological and adaptive genetic divergence between lake and stream habitats in European minnows (*Phoxinus phoxinus*, Cyprinidae). – Mol. Ecol. 20: 4490–4502.

Crutsinger, G. M., Collins, M. D., Fordyce, J. A., Gompert, Z., Nice, C. C. and Sanders, N. J. 2006. Plant genotypic diversity predicts community structure and governs an ecosystem process. – Science 313: 966–968.

Des Roches, S., Post, D. M., Turley, N. E., Bailey, J. K., Hendry, A. P., Kinnison, M. T., Schweitzer, J. A. and Palkovacs, E. P. 2018. The ecological importance of intraspecific variation. – Nat. Ecol. Evol. 2: 57–64.

Des Roches, S., Shurin, J. B., Schluter, D. and Harmon, L. J. 2013. Ecological and evolutionary effects of stickleback on community structure. – PLoS One 8: e59644.

Fox, J. and Weisberg, S. 2019. An R companion to applied regression, 3rd edn. – Sage.

Frost, W. E. 1943. The natural history of the minnow, *Phoxinus phoxinus*. – J. Anim. Ecol. 12: 139.

Fryxell, D. C. and Palkovacs, E. P. 2017. Warming strengthens the ecological role of intraspecific variation in a predator. – Copeia 105: 523–532.

Gamfeldt, L., Hillebrand, H. and Jonsson, P. R. 2008. Multiple functions increase the importance of biodiversity for overall ecosystem functioning. – Ecology 89: 1223–1231.

Gareth, J., Witten, D., Hastie, T. and Tibshirani, R. 2013. An introduction to statistical learning. – Springer.

Gibert, J. P. and DeLong, J. P. 2017. Phenotypic variation explains food web structural patterns. – Proc. Natl Acad. Sci. USA 114: 11187–11192.

Giling, D. P., Beaumelle, L., Phillips, H., R. P., Cesarz, S., Eisenhauer, N., Ferlian, O., Gottschall, F., Guerra, C., Hines, J., Sendek, A., Siebert, J., Thakur, M. P. and Barnes, A. D. 2019. A niche for ecosystem multifunctionality in global change research. – Global Change Biol. 25: 763–774.

Grömping, U. 2006. Relative importance for linear regression in R: the package relaimpo. – J. Stat. Softw. 17: 1–17.

Harmon, L. J., Matthews, B., Des Roches, S., Chase, J. M., Shurin, J. B. and Schluter, D. 2009. Evolutionary diversification in stickleback affects ecosystem functioning. – Nature 458: 1167–1170.

Hildrew, A. G., Raffaelli, D. and Edmonds-Browns, R. 2007. Body size: the structure and function of aquatic ecosystems. – Cambridge Univ. Press.

Hoffmann, A. A. and Sgrò, C. M. 2011. Climate change and evolutionary adaptation. – Nature 470: 479–485.

Katano, O. 2011. Effects of individual differences in foraging of pale chub on algal biomass through trophic cascades. – Environ. Biol. Fish. 92: 101–112.

Keith, P., Persat, H., Feunteun, E. and Allardi, J. 2011. Les poissons d'eau douce de France. – Muséum National d'Histoire Naturelle and Publications Biotope.

Leigh, D. M., Hendry, A. P., Vázquez-Domínguez, E. and Friesen, V. L. 2019. Estimated six per cent loss of genetic variation in wild populations since the industrial revolution. – Evol. Appl. 12: 1505–1512.

Length, R. V., Buerkner, P., Giné-Vazquez, I., Herve, M., Jung, M., Love, J., Miguez, F., Riebl, H. and Singmann, H. 2022. emmeans: estimated marginal means, aka least-squares means. – R-package ver. 1.7.3. https://CRAN.R-project.org/package=emmeans

Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P. and Makowski, D. 2021. performance: an R package for assessment, comparison and testing of statistical models. – J. Open Source Softw. 6: 3139.

Maestre, F. T., Quero, J. L., Gotelli, N. J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., García-Gómez, M., Bowker, M. A., Soliveres, S., Escolar, C., García-Palacios, P., Berdugo, M., Valencia, E., Gozalo, B., Gallardo, A., Aguilera, L., Arredondo, T., Blones, J., Boeken, B., Bran, D., Conceição, A. A., Cabrera, O., Chaieb, M., Derak, M., Eldridge, D. J., Espinosa, C. I., Florentino, A., Gaitán, J., Gatica, M. G., Ghiloufi, W., Gómez-González, S., Gutiérrez, J. R., Hernández, R. M., Huang, X., Huber-Sannwald, E., Jankju, M., Miriti, M., Monerris, J., Mau, R. L., Morici, E., Naseri, K., Ospina, A., Polo, V., Prina, A., Pucheta, E., Ramírez-Collantes, D. A., Romão, R., Tighe, M., Torres-Díaz, C., Val, J., Veiga, J. P., Wang, D. and Zaady, E. 2012. Plant species richness and ecosystem multifunctionality in global drylands. – Science 335: 214–218.

Matthews, B., Narwani, A., Hausch, S., Nonaka, E., Peter, H., Yamamichi, M., Sullam, K. E., Bird, K. C., Thomas, M. K., Hanley, T. C. and Turner, C. B. 2011. Toward an integration of evolutionary biology and ecosystem science. – Ecol. Lett. 14: 690–701.

Matthews, B., Aebischer, T., Sullam, K. E., Lundsgaard-Hansen, B. and Seehausen, O. 2016. Experimental evidence of an eco-evolutionary feedback during adaptive divergence. – Curr. Biol. 26: 483–489.

McIntyre, P. B., Flecker, A. S., Vanni, M. J., Hood, J. M., Taylor, B. W. and Thomas, S. A. 2008. Fish distributions and nutrient cycling in streams: can fish create biogeochemical hotspots. – Ecology 89: 2335–2346.

Mimura, M., Yahara, T., Faith, D. P., Vázquez-Domínguez, E., Colautti, R. I., Araki, H., Javadi, F., Núñez-Farfán, J., Mori, A. S., Zhou, S., Hollingsworth, P. M., Neaves, L. E., Fukano, Y., Smith, G. F., Sato, Y.-I., Tachida, H. and Hendry, A. P. 2016. Understanding and monitoring the consequences of human impacts on intraspecific variation. – Evol. Appl. 10: 121–139.

Palkovacs, E. P., Moritsch, M. M., Contolini, G. M. and Pelletier, F. 2018. Ecology of harvest-driven trait changes and implications for ecosystem management. – Front. Ecol. Environ. 16: 20–28.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. – Annu. Rev. Ecol. Evol. Syst. 37: 637–669.

Pinder, A. C. 2001. Keys to larval and juvenile stages of coarse fishes from fresh waters in the British isles. – Freshwater Biological Association.

Raffard, A., Cucherousset, J., Montoya, J. M., Richard, M., Acoca-Pidolle, S., Poésy, C., Garreau, A., Santoul, F. and Blanchet, S. 2021. Intraspecific diversity loss in a predator species alters prey community structure and ecosystem functions. – PLoS Biol. 19: e3001145.

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

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

Raffard, A., Cucherousset, J., Santoul, F., Di Gesu, L. and Blanchet, S. 2023. Data from: Climate and intraspecific variation in a consumer species drive ecosystem multifunctionality. – Figshare Digital Repository, https://doi.org/10.6084/m9.figshare.19168385.v1.

Raffard, A., Lecerf, A., Cote, J., Buoro, M., Lassus, R. and Cucherousset, J. 2017. The functional syndrome: linking individual trait variability to ecosystem functioning. – Proc. R. Soc. B 284: 20171893.

Raffard, A., Santoul, F., Blanchet, S. and Cucherousset, J. 2020. Linking intraspecific variability in trophic and functional niches along an environmental gradient. – Freshwater Biol. 65: 1401–1411.

Rey, O., A. Estoup, M. Vonshak, A. Loiseau, S. Blanchet, L. Calcaterra, L. Chifflet, J.-P. Rossi, G. J. Kergoat, J. Foucaud, J. Orivel, M. Leponce, T. Schultz, and B. Facon. 2012. Where do adaptive shifts occur during invasion? A multidisciplinary approach to unravelling cold adaptation in a tropical ant species invading the Mediterranean area. – Ecol. Lett. 15: 1266–1275.

Rosenblatt, A. E. and Schmitz, O. J. 2016. Climate change, nutrition and bottom–up and top–down food web processes. – Trends Ecol. Evol. 31: 965–975.

Rudman, S. M., Rodriguez-Cabal, M. A., Stier, A., Sato, T., Heavyside, J., El-Sabaawi, R. W. and Crutsinger, G. M. 2015. Adaptive genetic variation mediates bottom–up and top–down control in an aquatic ecosystem. – Proc. R. Soc. B 282: 125–132.

Rudolf, V. H. W. and Rasmussen, N. L. 2013. Ontogenetic functional diversity: size structure of a keystone predator drives functioning of a complex ecosystem. – Ecology 94: 1046–1056.

Schmid, D. W., McGee, M. D., Best, R. J., Seehausen, O. and Matthews, B. 2019. Rapid divergence of predator functional traits affects prey composition in aquatic communities. – Am. Nat. 193: 331–345.

Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., Aarssen, L. W., Baraloto, C., Carlucci, M. B., Cianciaruso, M. V., Dantas, V. de L., de Bello, F., Duarte, L. D. S., Fonseca, C. R., Freschet, G. T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., Jung, V., Kamiyama, C., Katabuchi, M., Kembel, S. W., Kichenin, E., Kraft, N. J. B., Lagerström, A., Bagousse-Pinguet, Y. L., Li, Y., Mason, N., Messier, J., Nakashizuka, T., Overton, J. C., Peltzer, D. A., Pérez-Ramos, I. M., Pillar, V. D., Prentice, H. C., Richardson, S., Sasaki, T., Schamp, B. S., Schöb, C., Shipley, B., Sundqvist, M., Sykes, M. T., Vandewalle, M. and Wardle, D. A. 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. – Ecol. Lett. 18: 1406–1419.

Toscano, B. J., Gownaris, N. J., Heerhartz, S. M. and Monaco, C. J. 2016. Personality, foraging behavior and specialization: integrating behavioral and food web ecology at the individual level. – Oecologia 182: 55–69.

Wolf, M. and Weissing, F. J. 2012. Animal personalities: consequences for ecology and evolution. – Trends Ecol. Evol. 27: 452–461.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J., Olesen, J., Valido, A. and Warren, P. 2005. Body size in ecological networks. – Trends Ecol. Evol. 20: 402–409.

Woodward, G., Perkins, D. M. and Brown, L. E. 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. – Phil. Trans. R. Soc. B 365: 2093–2106.

Yvon-Durocher, G., Allen, A. P., Cellamare, M., Dossena, M., Gaston, K. J., Leitao, M., Montoya, J. M., Reuman, D. C., Woodward, G. and Trimmer, M. 2015. Five years of experimental warming increases the biodiversity and productivity of phytoplankton. – PLoS Biol. 13: e1002324.

Yvon-Durocher, G., Jones, J. I., Trimmer, M., Woodward, G. and Montoya, J. M. 2010. Warming alters the metabolic balance of ecosystems. – Phil. Trans. R. Soc. B 365: 2117–2126.

Zhao, T., Villéger, S. and Cucherousset, J. 2019. Accounting for intraspecific diversity when examining relationships between non-native species and functional diversity. – Oecologia 189: 171–183.