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## Genetic, plastic and environmental contributions to the impact of a range-expanding predator on aquatic ecosystems

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### ► To cite this version:

Lieven Therry, Julien Cote, Julien Cucherousset, Fia Finn, Yoann Buoro, et al.. Genetic, plastic and environmental contributions to the impact of a range-expanding predator on aquatic ecosystems. *Journal of Animal Ecology*, 2019, 88 (1), pp.35-46. 10.1111/1365-2656.12938 . hal-02121049

**HAL Id: hal-02121049**

**<https://hal.science/hal-02121049>**

Submitted on 26 Nov 2020

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1 **Genetic, plastic and environmental contributions to the impact of a range-expanding**  
2 **predator on aquatic ecosystems**

3 *Accepted in Journal of Animal Ecology – Therry L., Cote J., Cucherousset J., Finn F.,*  
4 *Yoann B. & S. Blanchet. 2019. Journal of Animal Ecology. 88(1): 35-46. doi :*  
5 *10.1111/1365-2656.12938*

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20

## 21 Abstract

- 22 1. Global change is altering biodiversity locally and globally and subsequently affecting the  
23 dynamics of communities and ecosystems. Biodiversity can be impacted both at the interspecific  
24 (i.e. species composition of communities) and intraspecific (evolutionary modification of  
25 phenotypic traits through selection or plasticity) levels. Changes in intraspecific diversity have  
26 been demonstrated to generate evolutionary feedbacks acting on ecological dynamics.  
27 Quantifying the role of intraspecific trait variation, global change, and their interactions on  
28 ecological dynamics is of utmost importance.
- 29 2. Here, we used the range-expanding dragonfly *Crocothemis erythraea* as a model species to test  
30 the relative effects of intraspecific trait variation in larvae and thermal conditions on the  
31 dynamics of freshwater community and ecosystem functioning. Using experimental mesocosms,  
32 we manipulated intraspecific trait variation arising from genetic (G), early developmental  
33 environment ( $E_E$ ) and late developmental environment ( $E_L$ ) contributions in a full-factorial  
34 design.
- 35 3. We showed that intraspecific trait variation arising from genetic effects have the strongest  
36 consequences on community and ecosystem dynamics relative to trait variation driven by the  
37 thermal environment ( $E_E$  and  $E_L$ ). Importantly, the ecological effects of trait variation due to  
38 genetic effects were partly modulated by thermal conditions ( $G \times E_L$ , and to a lesser extent  $G \times$   
39  $E_E$  interactions), and varied among ecological response variables. For instance, the strongest  $G \times$   
40  $E_L$  effects were observed on primary productivity and zooplankton dynamics. Trait variation  
41 driven by plasticity related to early or late developmental environments has an overall weak  
42 effect on ecological dynamics.
- 43 4. Intraspecific trait variation induced by genetic effects can affect ecological dynamics (evo-to-eco  
44 dynamics) more strongly than variation induced by the developmental environment. However,

45 they likely interact to modulate the structure of communities and the functioning of ecosystems,  
46 highlighting the strong context (environmental)-dependency of evo-to-eco dynamics.

47 **Keywords.** Eco-evolutionary dynamics, invasion, ecosystem functioning, intraspecific diversity,  
48 arthropods, aquatic ecosystems

49

## 50 **Introduction**

51 The phenotypic and genetic characteristics of species vary among populations and across  
52 their distributional range (Hardie & Hutchings, 2010), Chuang & Peterson, 2016). In  
53 particular, in range expanding species, individuals at the expansion front have been reported  
54 to evolve faster life-histories and higher activity levels (Alford, Brown, Schwarzkopf,  
55 Phillips, & Shine, 2009; Phillips, 2009; Therry, Lefevre, Bonte, & Stoks, 2014). As  
56 intraspecific trait variation can strongly shape the structure of prey communities and the  
57 functioning of key ecosystem processes (Raffard, Santoul, Cucherousset, & Blanchet, 2018;  
58 Des Roches et al., 2018), quantifying the ecological consequences of intraspecific trait  
59 variation has recently gained major attention, triggered by the growing field of eco-  
60 evolutionary dynamics (Fussmann, Loreau, & Abrams, 2007; Yoshida, Jones, Ellner,  
61 Fussmann, & Hairston, 2003).

62 Intraspecific trait variation can result from variation in environmental conditions across the  
63 range (e.g. abiotic conditions, population or community structure), and/or from the genetic  
64 architecture of populations resulting from founder effects, genetic drift or natural selection.  
65 When adaptive and/or non-adaptive genetic changes generate rapid evolutionary phenotypic  
66 changes, evolutionary dynamics can coincide in space and time with ecological changes, and  
67 generate so called *eco-evolutionary dynamics* (Fussmann, Loreau & Abrams 2007; Lowe,  
68 Kovach & Allendorf 2017). For instance, populations inhabiting different environment can  
69 rapidly evolve phenotypic divergences by natural selection, which can ultimately to  
70 differential ecological impacts of these populations on ecosystem properties and function (i.e.  
71 *evo-to-eco dynamics*, Harmon et al. 2009; Matthews et al. 2016; Brunner et al. 2017).  
72 Nonetheless, the ecological effects of trait variation can be generated by genetic local  
73 differentiation (due to drift or selection), environmentally-induced plasticity, or by a

74 combination of genetic and plastic phenotypic divergences, which makes difficult to evaluate  
75 to which extent evolution really matters for ecology (Schmitz, Beckerman, & O'Brien, 1997;  
76 Bassar et al., 2010; Lundsgaard-Hansen, Matthews, & Seehausen, 2014; Pantel, Duvivier, &  
77 De Meester, 2015). While the evolutionary forces underlying trait variation modulate the  
78 strength of these *evo-to-eco dynamics*, a major difficulty is yet to tease apart the ecological  
79 impacts associated to genetically-driven trait variation to those associated to  
80 environmentally-driven plastic phenotypic differentiation. Understanding the genetic and  
81 plastic contributions to the impact of an organism on ecosystem functioning is yet an  
82 essential question for properly predicting the ecological dynamics of ecosystems, in particular  
83 under contemporary global change. Indeed, global change is multifaceted, and is for instance  
84 characterized simultaneously by a large-scale shuffling of genotypes (due to range shifts  
85 and/or local adaptation) and changes in key environmental drivers such as temperature  
86 regimes that can modulate the phenotypes through developmental plasticity. Moreover,  
87 reciprocal dynamics and feedbacks between ecological and evolutionary dynamics can only  
88 be attested if adaptive (natural selection) and non-adaptive (genetic drift) processes acting on  
89 heritable traits is driving trait variation among populations (Lundsgaard-Hansen et al., 2014).  
90 Identifying the genetic and plastic contributions of the ecosystem impact of an organism  
91 hence provides a good indication on the potential for eco-evolutionary dynamics to occur.

92 In this study, we assessed the genetic (G) contribution, the environmental contribution  
93 occurring early ( $E_E$ ) or late ( $E_L$ ) in the development and the interactive ( $G \times E_E$ ,  $G \times E_L$ ,  $E_E \times E_L$ ,  
94  $G \times E_E \times E_L$ ) contributions to the impact of a range-expanding dragonfly (*Crocothemis*  
95 *erythraea*) on aquatic community and ecosystem properties. To do so, we set a mesocosm  
96 experiment manipulating genetic and environmental contribution to trait variation in  
97 dragonfly larvae in a full factorial design. Egg clutches from four independent populations

98 along the latitudinal gradient of range expansion (southern to northern Europe) were used to  
99 manipulate the genetic basis of trait variation in larvae. We further manipulated thermal  
100 conditions during the development from egg to larvae with two temperature regimes (24°C  
101 and 28°C) to estimate the early-in-life plastic component of trait variation. Thermal  
102 conditions were then manipulated in the mesocosms, in which larvae were released, by  
103 setting experimental units at two different temperature regimes (14°C and 18°C) to estimate  
104 the plastic component of trait variation at a later stage. We then quantified the impacts of  
105 larvae on the structure of communities and ecosystem functions after a two-month period,  
106 and we teased apart the genetic and environmental contributions of trait variation on these  
107 ecological dynamics (Raffard et al., 2018; Des Roches et al., 2018). Genetically-based trait  
108 variation (i.e. evolution *per se*) should have stronger effects on ecological dynamics than trait  
109 variation arising from plasticity since ectotherm life-history traits strongly vary along  
110 latitudinal range-expansion gradients (De Block, Slos, Johansson, & Stoks, 2008; Phillips,  
111 2009; Therry, Nilsson-Oertman, Bonte, & Stoks, 2014), and because plastic-induced traits are  
112 more labile. We also predicted that the impact of trait variation on ecological dynamics will  
113 vary according to the different types of community and ecosystem parameters. In particular,  
114 ecological parameters directly impacted by dragonfly larvae (e.g. abundance and composition  
115 of prey communities) should be more strongly impacted by trait variation, than parameters  
116 related to ecosystem functioning such as the decomposition of organic matter (Raffard et al.,  
117 2018).

118

## 119 **Material and methods**

### 120 *Study system and collection*

121 *Crocothemis erythraea* (Brullé, 1832) is a dragonfly species with a predominantly African  
122 distribution but with a small historical European breeding range confined to the  
123 Mediterranean area (Dijkstra & Lewington, 2006). Triggered by global warming, the species'  
124 range expansion towards Northern Europe started in the 1960's, and the northernmost  
125 populations are currently found in Northern Germany (Brockhaus, 2015; Ott, 2007). The  
126 species breeds in a wide range of stagnant water habitats with a preference for shallow lakes  
127 with dense aquatic vegetation (Dijkstra & Lewington, 2006). Odonates occupy an important  
128 intermediate position in aquatic systems as both predator and prey, but are the top predator in  
129 shallow fishless water bodies (Corbet, 1999). Odonates are generalist predators, feeding both  
130 on benthic invertebrates and pelagic zooplankton hereby influencing both benthic and pelagic  
131 food chains through top-down effects, and ecosystem functions through indirect effects.  
132 Odonate larvae show important geographic variation in growth rate, metabolism, feeding  
133 activity and body size, which can be shaped by both genetic and environmental factors.  
134 Variation in these functional traits have already been shown to have drastic effects on the  
135 functioning of aquatic ecosystems, and we hence expect larvae of *C. erythraea* originating  
136 from various geographical origins to impact differently the dynamics of communities and  
137 ecosystems.

138 Gravid females of *C. erythraea* were caught in 2015 from four populations distributed  
139 across a gradient of 15° of latitude (Fig. 1) that coincides with the climate-driven range  
140 expansion of the species through Western Europe. Due to logistic constraints, we were unable  
141 to collect all populations in the same time period (sampling date per populations: pop A: 4  
142 and 5 August 2015, pop B: 15 August 2015, pop C: 5 and 6 September 2015, pop D: 5 and 7  
143 August 2015). Egg clutches were extracted by dipping the abdomen of the female in a tube  
144 filled with dechlorinated tap water (Hudson & Berrill, 1986). For each population, eggs from



145 5 to 6 different females were collected, resulting in a total of twenty-three collected egg  
146 clutches. Eggs were transported to the laboratory in Moulis (France), and eggs (and then  
147 hatched F1 larvae) were kept in a wet lab at 20°C and a photoperiod of L:D 14:10h until the  
148 start of the temperature treatment. After hatching, F1 larvae were kept in batches of ten in 5L  
149 round containers and fed twice a day ad libitum with freshly hatched *Artemia* nauplii. We  
150 considered that these four populations to display unique trait combination that are mostly due  
151 to genetic contributions given that they are geographically isolated from each other and that  
152 they live in highly divergent environments (Therry et al. submitted). It is noteworthy that  
153 traits expressed in F1 can still be affected by non-genetic -yet inherited- process such as  
154 maternal effects (Danchin et al., 2011), and that difference in collection dates might also limit  
155 our ability to tease apart pure genetic effects on trait variability. The genetic contribution we  
156 consider here may hence be over-estimated, as our design does not allow accounting for these  
157 potential non-genetic effects (see the Discussion).

#### 158 *Plastic-induced trait variation among larvae*

159 Four weeks after hatching, larvae were individually placed in white opaque vials (diameter:  
160 7.5 cm, height: 10 cm) and assigned for three weeks to one of two temperature treatments in  
161 order to induce plastic differences at an early developmental stage ( $E_E$ ) between dragonfly  
162 larvae. This was done in a full-factorial design with population of origin and temperature  
163 treatment as factors (eight treatments in total). Larvae assigned to the lower temperature  
164 treatment were placed in an incubator at 24°C, while larvae assigned to the higher  
165 temperature treatment were placed in an incubator at 28°C. 28°C reflects the optimal  
166 temperature for growth of *C. erythraea* larvae (Suhling & Suhling, 2013), and this water  
167 temperature is reached during summer in the shallow breeding ponds of the studied  
168 populations (Appendix A: Fig. a.1). Photoperiod at both incubators was L:D 14:10h,

169 reflecting the photoperiod at summer (August) in Western Europe. During the larval  
170 temperature treatment, larvae were fed twice a day ad libitum with freshly hatched *Artemia*  
171 nauplii, and this was supplemented with 3 chironomid larvae every other day during the last  
172 two weeks in order to meet the higher food demands of older larvae.

173 To quantify the effects of the population of origin (i.e. genetic contribution) and the early-  
174 in-life temperature treatment (i.e. early developmental environment effect) on larval growth  
175 rate, a key integrative trait, head width of each larvae was measured the first time at the start  
176 of the temperature treatment and a second time three weeks later. Head width was quantified  
177 by taking pictures of the larval head and of a scale with a camera (Nikon® coolpix 4500)  
178 connected with a binocular, hereafter head width was measured using ImageJ® (v.445).  
179 Growth rate was calculated as  $[(\ln(\text{head width end experiment}) - \ln(\text{head width start}$   
180  $\text{experiment})) / \text{number of days of the experiment}]$ , as growth trajectories of insects follow an  
181 exponential function. Larvae were kept in the incubators at the allocated temperature for an  
182 additional two weeks period, before larvae were introduced in the experimental mesocosms.

### 183 *Mesocosm experiment*

184 Seventy-two black round 100L mesocosms (Ø 68cm) were evenly distributed over 4  
185 compartments of a greenhouse. Each compartment was 40 m<sup>2</sup> and was separated from others  
186 by fixed transparent walls. Tanks (18 per compartment) were placed on fixed shelves at 1-  
187 meter height from the ground. Temperature of each greenhouse compartment was  
188 automatically and independently regulated with heating and cooling devices installed in each  
189 compartment and programmed from a centralized computer. Two greenhouse compartments  
190 were assigned to the low temperature treatment of 14°C and two compartments were assigned  
191 to the high temperature treatment of 18°C, with a thermal fluctuation following the daily  
192 fluctuation of temperatures. Water temperature followed the same fluctuations and was on

193 average 14.39°C ( $\pm 0.26$  SD) and 17.69°C ( $\pm 0.36$  SD) for the low temperature and high  
194 temperature treatment in average (measured using Hobo® data loggers). There was a low  
195 variability in air and water temperature along the experiment. These temperature treatments  
196 were used to manipulate the effect of late developmental environment on larvae trait variation  
197 ( $E_L$ ). Growth lights provided a photoperiod of L:D 12:12h; which reflects the photoperiod  
198 during autumn (September) in Western Europe. Two weeks before the introduction of  
199 dragonfly larvae, tanks were filled with tap water and supplemented with 20 g of air dried  
200 poplar leaves and 0.5 ml organic fertilizer (Solabiol®) which provided nutrients for  
201 phytoplankton growth. Three days later, 6 litres of phytoplankton/zooplankton aliquots from  
202 an established 1000 liter mesocosm that were inoculated from two gravel pit lakes located in  
203 the study area (Alp, Cucherousset, Buoro, & Lecerf, 2016). Aquatic benthic invertebrates  
204 (snails, chironomids and amphipods, mostly from the following families: Asellidae, Physidae,  
205 Tubificidae, Caenidae, Hydra sp., Glossiphoniidae, Lymnaeidae, Chironominidae,  
206 Ceratopogonidae, Sphaeridae and Ecnomidae) originating from another gravel pit lake (lake  
207 Lamartine) were added. These gravel pit lakes were selected because they are eutrophic and  
208 shallow, representing the typical habitat of *C. erythraea*. Fourteen days after filling the  
209 mesocosms, the experiment was initiated by adding three dragonfly larvae (i.e. 8.8 larvae.m<sup>-2</sup>,  
210 which is closed to the natural density of a closely-related species, *Libellula quadrimaculata*,  
211 6.6 larvae.m<sup>-2</sup>, Corbet 1999) from one of the eight “population of origin x temperature of  
212 rearing” treatment (except to the control tanks where no dragonfly larvae were added). This  
213 lead to 16 treatments (4G x 2E<sub>E</sub> x 2E<sub>L</sub>) that we replicated four times for population A and B,  
214 and two and three times for populations C and D respectively due to a shortage in larvae (see  
215 Table 1). Larvae were measured for head width (see above) at the onset and at the end of the  
216 mesocosm experiment to test for an effect of  $E_L$  on growth rate (calculated as above but with  
217 measures averaged at the tank level as larvae were not individualized). Two to five control

218 tanks (without addition of dragonfly larvae) were ran at each population × environmental  
219 temperature treatment combination (Table 1), to serve as comparison bases and to properly  
220 evaluate the strength and direction of the effects of intraspecific trait variation on ecological  
221 dynamics. At the time of introduction of dragonfly larvae, three pre-weighted leaf packages  
222 ( $\pm$  4g air-dried *Populus* leaves) and a white tile (L × W: 20 × 20 cm) were added to each  
223 mesocosm to quantify decomposition rate (Alp et al., 2016) and benthic primary production  
224 at the end of the experiment, respectively (see further).

225 The experiment lasted 60 days after dragonfly larvae introduction and fifteen community and  
226 ecosystem parameters were quantified in each mesocosm at the end of the experiment. The  
227 parameters were Daphniidae abundance, Cyclopidae abundance, shannon's diversity index  
228 (H) of the zooplankton community, shannon's equitability (EH) of the zooplankton  
229 community, Aselidae abundance, Physidae abundances, H shannon diversity of benthic  
230 macro-invertebrate community, E shannon evenness of benthic macro-invertebrate  
231 community, pelagic primary production (measured as in the water column), benthic primary  
232 production (measured as chlorophyll-a concentration on tiles), gross primary production  
233 (GPP), decomposition rate, total nitrogen and total phosphorous concentration of the water  
234 and pH.

235 Pelagic primary production (chlorophyll-a concentration,  $\mu\text{g/l}$ ) was measured using a  
236 portable spectrophotometer (AlgaeTorch, bbe ®) in the water column of the mesocosm.  
237 Benthic primary production (chlorophyll-a concentration on tiles,  $\mu\text{g/cm}^2$ ) and was measured  
238 using a portable spectrophotometer (BenthoTorch, bbe ®) at three different location on each  
239 tile. Dissolved oxygen (DO) concentration was measured using an oxygen probe (Jenway®)  
240 at three successive time slots during a 24h timeframe: dawn, dusk and dawn at the following  
241 day. GPP was calculated as the sum of net primary production ( $\text{NPP} = \text{DO}_{\text{dusk } 1} - \text{DO}_{\text{dawn } 1}$ )

242 and ecosystem respiration [ $ER = DO_{dusk1} - DO_{dawn2}$ ]. The mesocosms' pH was measured  
243 using a pH probe (Jenway®). Water samples were collected using a 100 mL syringe, filtered  
244 using a 0.45  $\mu\text{m}$  mesh filter, and then stored at  $-18^{\circ}\text{C}$  until quantification of total nitrogen and  
245 total phosphorous concentrations using a high-performance ionic chromatograph (Dionex  
246 DX-120). Zooplankton was sampled by filtering 30L of water using a zooplankton net (mesh  
247 size: 200  $\mu\text{m}$ ). Zooplankton was then stored in 100 ml flasks filled with 80% ethanol for  
248 further quantification and sorting up to the family level using a binocular (Nikon®).  
249 Shannon's diversity index (H) and shannon's equitability (EH) index were calculated from  
250 the zooplankton counts at the family level. Additionally, the counts of the most abundant  
251 families (Daphniidae and Cyclopoidae) were extracted as additional variables accounting for  
252 the abundance of these two families. The sediment of the mesocosm was sieved over a  
253 zooplankton net (200  $\mu\text{m}$ ) to collect the benthic macro-invertebrates, which were stored on  
254 80% ethanol in 250 ml flasks. In a first step, macro-invertebrates larger than 2 mm were  
255 counted and sorted up to the family level using a binocular (Nikon ®) and according to the  
256 European determination key (Tachet, Richoux, Bournaud, & Usseglio-Polatera, 2010). In a  
257 second step, the content of the flask was homogenously distributed in a white tray (L  $\times$  W: 49  
258  $\times$  33.5 cm), and all macro-invertebrates from one quarter of the tray were determined and  
259 counted. The estimate of total macro-invertebrate abundance was obtained summing the  
260 counts of the larger invertebrates to four times the count of the smaller invertebrates.  
261 Shannon's diversity index (H) and shannon's equitability (EH) index were calculated from  
262 the macro-invertebrate counts. Additionally the counts of the most abundant families  
263 (Asellidae and Physidae) were extracted as additional variables synthetizing the abundance of  
264 these two families.

265 *Statistical analyses*

266 We first studied the growth rate of larvae before the mesocosm experiment and during the  
267 mesocosm experiment mesocosm using linear model with the previously mentioned traits as  
268 dependent variables and the population of origin and thermal conditions (early environment  
269 for variables before the mesocosm experiment and early and late environments for body  
270 growth during the mesocosm experiment) as independent variables. Tukey tests were used for  
271 specific post-hoc comparisons. Similar models were computed to test for body size  
272 differences at the onset and at the end of the mesocosm experiment.

273 As we are interested in the effects of trait variation of dragonfly larvae on community and  
274 ecosystem dynamics, we compared mesocosms (within each compartment) with and without  
275 (control) larvae by calculating -for each parameter independently- the residuals from a  
276 regression between the value of a given parameter in mesocosms with larvae and the  
277 associated value obtained from the control mesocosms. In particular, this allowed teasing  
278 apart the ecological effects of trait variation arising from late developmental environment  
279 ( $E_L$ ) from those directly related to change in ecosystem temperature (i.e. direct climatic  
280 effects). The associated value of the parameter in control mesocosms was obtained by  
281 averaging the values of the parameter from the control tanks that were located in the same  
282 greenhouse compartment and set-up at the same date as the experimental mesocosm. At  
283 14°C, we had only one control mesocosm for one of the two compartments for populations A,  
284 B and D. The residual values were used for all subsequent statistical analyses.

285 We first tested the significance of the contribution of genetics (G: populations A, B, C or  
286 D), early developmental environment ( $E_E$ : larvae reared at low vs. high temperature), late  
287 developmental environment ( $E_L$ : mesocosms at low vs. high temperature) and their  
288 interactions to the variation in community and ecosystem dynamics using linear mixed  
289 models (LMMs, one LMM per parameter). All LMMs included the greenhouse compartment

290 nested in the environmental treatment as random intercept, and the mean head width of larvae  
291 at the onset of the mesocosm experiment and the number of surviving larvae at the end of the  
292 mesocosm experiment as covariates. We added these two covariates to remove any  
293 confounding effects from the genetic contributions and to test whether any heritable traits such  
294 as body size may contribute to ecological dynamics. Models without these covariates give  
295 similar results (table a.2 and a.3). Note that one tank was removed from the final dataset since  
296 we detected the accidental presence of a crayfish, which may have strongly affected the  
297 general dynamics of the ecosystem. Second, we quantified the size of the effect of each  
298 contributor on ecological dynamics by calculating eta squared ( $\eta^2$ ) effect sizes of the genetic,  
299 early environment, late environment and interactive contributions of the effect induced by  
300 dragonfly larvae on community and ecosystem dynamics as the ratio of the sum of squares of  
301 the effect of the factor of interest on the total sum of squares using type III-analysis of  
302 variance. Third, we synthesized quantitative information by performing a meta-analysis on  
303 the calculated eta squared effect sizes (see Neyeloff, Fuchs, & Moreira, 2012). This meta-  
304 analysis was used to test whether effect sizes of each contributor varied between ecological  
305 parameters. To do so we combined (for each contributor and interaction terms independently)  
306 the effect sizes calculated for each ecological parameter and we calculated the Q-test for  
307 heterogeneity in effect sizes (Rosenberg, Adams, & Gurevitch, 2000), and its significance  
308 was tested using chi-square statistics (a significant Q value for a given contributor indicating  
309 that effect sizes of this contributor vary among ecological parameters). The meta-analysis  
310 was also used to test what drives variation in effect sizes among ecological parameters. To do  
311 so we ran a fixed effect meta-regression with effect sizes (from all ecological parameters and  
312 all contributors as the dependent variable). Fixed effects included the type of contributor (G,  
313  $E_E$ ,  $E_L$ ,  $G \times E_E$ ,  $G \times E_L$ ,  $E_E \times E_L$  or  $G \times E_E \times E_L$ ), and two classifications for the ecological  
314 parameters: 1) according to the position in the aquatic system (two factors; pelagic vs

315 benthic) and 2) according to the functional group (four factors; primary production,  
316 zooplankton, benthic invertebrates or nutrient-cycling). We also included all interaction terms  
317 as additional fixed effects. This meta-regression allowed testing whether effect sizes  
318 significantly varied among types of contributors and the class of ecological parameters being  
319 considered.

320 All statistical analyses were done using the proc Mixed of SAS v9.0 and a Satterthwaite  
321 approximation to estimate degree of freedom.

322

## 323 **Results**

### 324 *Genetic and environmental effects on larval growth rate*

325 Growth rate of larvae before the mesocosm experiment greatly differed among populations  
326 ( $F_{3,135} = 11.38$ ,  $p < 0.001$ ), suggesting a strong contribution of G on larval growth rate.  
327 Larvae originating from the C population grew significantly less than larvae from all other  
328 populations (Tukey test,  $p < 0.05$  for all comparisons), and population B grew significantly  
329 less than the northern population (pop D, Tukey test,  $p < 0.05$ ). Populations A and D had the  
330 same growth rate (Tukey test,  $p > 0.05$ ). Overall, populations originating from the central  
331 area hence tended to grow less than populations from the most extreme latitudinal locations  
332 (Fig. 1b). Furthermore, growth rate was higher at the highest rearing temperature ( $F_{1,135} =$   
333  $5.71$ ,  $p = 0.018$ ), and there was no significant interaction between rearing temperature and the  
334 populations of origin (i.e. genetic background,  $F_{3,135} = 1.04$ ,  $p = 0.377$ , Fig. 1b).

335 During the mesocosm experiment, larvae growth rate did not vary among populations ( $F_{3,34.32}$   
336  $= 0.97$ ,  $p = 0.420$ ) and among climatic conditions in the mesocosm ( $F_{1,1.94} = 0.97$ ,  $p = 0.412$ ).

337 The interaction between mesocosm temperature and the population of origin was also not



338 significant ( $F_{3,34.44} = 0.72$ ,  $p = 0.545$ ). Nonetheless, at the onset of the mesocosm experiment,  
339 the head width of larvae tended to be higher for populations A and D than for populations B  
340 and C ( $F_{3,43.12} = 2.49$ ,  $p = 0.072$ ), whereas this was not the case at the end of the mesocosm  
341 experiment ( $F_{3,38.41} = 0.82$ ,  $p = 0.489$ ). This suggests that populations B and C partly  
342 compensate the body size difference during the mesocosm experiment. After 60 days,  
343 survival rate in the mesocosm experiment was 73.3% ( $\pm 0.04\%$ , SE), and did not vary among  
344 treatments (GLM, all p-values  $> 0.05$ ).

345 *Genetic (G) and environmental ( $E_E$  and  $E_L$ ) contributions to ecological dynamics*

346 Genetic (G), environmental ( $E_E$  and  $E_L$ ) and interactive ( $G \times E_E$ ,  $G \times E_L$ ,  $E_E \times E_L$  and  $G \times E_E \times$   
347  $E_L$ ) contributions to the impact of dragonfly larvae on community and ecosystem dynamics  
348 were found for all ecological parameters, although not consistently (Fig. 2, Appendix A:  
349 Table a.1). In particular, effect sizes of genetic contributions were significantly  
350 heterogeneous across ecological parameters ( $Q_G = 24.132$ ,  $p = 0.044$ ). A significant genetic  
351 effect (G) of dragonfly larvae on ecological dynamics was found for six out of the fifteen  
352 ecological parameters. Early environmental ( $E_E$ ) and late environmental ( $E_L$ ) effects were  
353 found at lower occurrence, with three out of fifteen ecological parameters being significantly  
354 affected by  $E_E$  and  $E_L$  respectively. Interestingly, late environmental contributions to  
355 variation in ecological dynamics were strongly dependent upon the population (six out of  
356 fifteen significant  $G \times E_L$  interactions, Appendix A: Table a.1), which was not the case for  
357 early environment (one out of fifteen significant  $G \times E_E$  interactions, Appendix A: Table a.1).

358 Meta-regressions revealed that the overall contributions (across all ecological parameters)  
359 of G,  $E_E$ ,  $E_L$  and their interactions significantly differed among these types of contributors  
360 (Table 2, Fig. 3), with the strongest overall contributions being detected for the G, the  $G \times E_L$   
361 and, to a lesser extent,  $G \times E_E$  and  $G \times E_E \times E_L$  interactions. In contrast, the lowest overall

362 contributions were detected for  $E_E$ ,  $E_L$  and  $E_E \times E_L$  for which the 95% confidence intervals  
363 (CIs) included 0. Nonetheless, these differences among types of contributors differed  
364 between the position of the ecological parameters in the ecosystems (pelagic vs. benthic) and  
365 the functional group being measured (primary productivity, zooplankton, benthic macro-  
366 invertebrates and nutrient cycling), as shown by significant interaction terms (Table 2). For  
367 instance,  $E_L$  contributions tended to be higher for benthic ecological parameters than for  
368 pelagic ecological parameters (Fig 3). Further, the contributions of both  $G \times E_E$  and  $G \times E_L$   
369 were stronger for parameters related to primary production and zooplankton dynamics than  
370 for parameters related to the dynamics of benthic invertebrates and nutrient-cycling.

## 371 **Discussion**

372 Phenotypic and genetic differentiation between populations can take place when populations  
373 are exposed to contrasting selection pressures, and/or when genetic drift is strong enough to  
374 generate significant differentiation (Chuang & Peterson, 2016; Hoffmann & Sgrò, 2011;  
375 Lowe et al., 2017). A growing number of studies documented that intraspecific trait variation  
376 arising from evolutionary processes (selection and/or drift) can affect the dynamics of  
377 communities and ecosystems, leading to *evo-to-eco* feedbacks (El-Sabaawi et al., 2015;  
378 Harmon et al., 2009; Lundsgaard-Hansen et al., 2014; Matthews et al., 2011; Matthews et al.,  
379 2009; Pantel et al., 2015; Rudman et al., 2015; Lowe et al. 2017). In this study, we  
380 disentangled the genetic and environmental contributions of intraspecific trait variation in a  
381 range expanding predator to the dynamics of communities and the functioning of ecosystem.  
382 We demonstrated that community and ecosystem dynamics were more influenced by  
383 populations of origin than by developmental thermal conditions experienced early and late in  
384 life, suggesting a stronger genetic contribution to the overall ecological dynamics than plastic  
385 contributions. Nonetheless, the genetic contributions were partially modulated by late (and to

386 a lesser extent early) thermal environments and varied among the functional groups and  
387 different compartments of the ecosystem. This study allowed to better estimate the relative  
388 contribution of intraspecific trait variation either due to genetic or environmental factors to  
389 the ecological impact of a predator, and therefore of the eco-evolutionary dynamics.

390 Abiotic and biotic environmental gradients can generate strong adaptive phenotypic  
391 differentiation among populations within a species distribution range. In range-expanding  
392 species, colonization and invasion processes often strengthen phenotypic clines along spatial  
393 gradients as found with behaviours and pace-of-life (Chuang & Peterson, 2016; Phillips,  
394 2009; Therry et al., 2014). Additionally, range-expanding species are characterized by series  
395 of founder effects that can also generate rapid phenotypic differentiation (due to drift) among  
396 colonizing populations. In this later case, spatial patterns of phenotypic differentiation should  
397 be independent from environmental clines. However, genetic and environmental  
398 differentiations are often confounded in range-expanding species. For example, *C. erythraea*  
399 expanded its range from South to North and therefore populations at the expanding edge are  
400 at higher latitude and encounter –amongst others- colder conditions. In this study, we  
401 collected egg clutches to limit environmental influences as much as possible, and we  
402 manipulated developmental thermal conditions at different important life stages. This  
403 protocol allows estimating the relative contribution of heritable and environmental  
404 determinants of trait variation in this range expanding species. It must be acknowledged that  
405 –because of field constraints- eggs from one of the populations were collected one month  
406 after the others, which may limit clear-cut conclusions related to the pure effect of range  
407 expansion on trait diversity. However, either with or without this specific population, we  
408 found large population differentiation in the growth rate of *C. erythraea* larvae reared in  
409 standardized conditions from eggs, and additional differences in growth rate induced by  
410 temperature at early stages of development. These effects suggest both heritable and plastic

411 determinants of growth rate. Given that eggs have been fecundated in the wild, our design  
412 cannot rule out the possibility that both non-genetic (yet heritable such as maternal effect or  
413 epigenetic marks) and genetic processes explained phenotypic differentiation observed  
414 between populations. While we did not quantify them, differences in growth rate likely  
415 encompass differences among populations in many other response traits (e.g. behaviour and  
416 metabolism, Chuang & Peterson, 2016; Stoks, Swillen, & De Block, 2012) and effect traits  
417 (e.g. nutrient excretion, consumption rate Raffard et al., 2017; Tilman, 2001; Vanni, 2002),  
418 which is actually sustained by a companion study showing that patterns of trait covariation  
419 strongly varied in this species along the expansion gradient (Therry et al. submitted).  
420 Covariation between effect and response traits (the functional syndrome) might actually  
421 contribute to differential ecological impacts across a species range (Raffard et al., 2017).  
422 Surprisingly, growth rate did not vary linearly with latitudes as it was expected (Kivelä et al.  
423 2011, Therry et al. 2014b). This suggests that variation among populations does not result  
424 (only) from climatic conditions or from population colonization history, but probably from  
425 other environmental differences and/or from founder effects inducing population divergence  
426 in heritable traits.

427 Overall, genetic (adaptive and/or non-adaptive) effects towered over temperature-driven  
428 plastic effects on community and ecosystem dynamics, as found for the effects of white fish's  
429 ecotypes on aquatic ecosystems (Lundsgaard-Hansen et al., 2014). As stated above, we  
430 cannot exclude that non-genetic heritable processes are also part of these *evo-to-eco* links.  
431 Future studies should aim at tackling the respective role of genetic and non-genetic heritable  
432 processes on *evo-to-eco* links, notably given that eco-evolutionary feedbacks might vary in  
433 their dynamics depending of the underlying processes driving trait variation. The observed  
434 *evo-to-eco* links were related to a broad range of ecosystem variables, ranging from the  
435 zooplanktic and benthic prey species to primary production and nutrient cycling.

436 Nonetheless, ecological effects sizes of trait variation arising from genetic contributions and  
437 (to a lesser extent) from the interaction between genetic contributions and late developmental  
438 conditions ( $G \times E_L$ ) were not homogeneous among ecological parameters. For example,  $G \times$   
439  $E_L$  had stronger effects on zooplanktic species and on primary production, than on benthic  
440 prey species and nutrient cycling. This variability of effects makes difficult to predict  
441 precisely differences in ecosystem functioning across the species range. However, it appears  
442 that all ecological parameters are more strongly influenced by genetic background, directly or  
443 environmentally-mediated, than by the sole effect of developmental thermal conditions. In  
444 aquatic ecosystems, predators often have strong top-down impacts by directly controlling  
445 prey species and indirectly primary production and nutrient cycling (Bestion, Cucherousset,  
446 Teyssier, & Cote, 2015; Shurin et al., 2002). This may explain why (heritable) trait variation  
447 in predators such as *C. erythrea* has substantial consequences on several ecosystem  
448 parameters (see also El-Sabaawi et al., 2015; Harmon et al., 2009; Raffard et al., 2018).

449 It further shows that the temperature-mediated plastic contributions to ecological  
450 dynamics were largely dependent on the genetic contribution as indicated by  $G \times E_E$  and  $G \times$   
451  $E_L$  interactions. These interactions could have been caused by adaptive plastic evolution.  
452 Accordingly, reaction norms have been shown to differ between populations subjected to  
453 different selection pressures (Ghalambor, McKay, Carroll, & Reznick, 2007), and to evolve  
454 during species range expansion (Aubret & Shine, 2009; Ducatez, Crossland, & Shine, 2016).  
455 However, while population latitudes should reflect larvae thermal adaptation, it does not  
456 explain well the  $G \times E$  interactions in our case. On the contrary, the southern and northern  
457 populations display more similar reactions to late and early developmental temperatures than  
458 the two intermediate populations. These differences among populations match the differences  
459 in growth rate and body size before the mesocosm experiment. The similar dependency to  
460 thermal conditions could have therefore resulted from the differences in growth rate, body

461 size or growth compensation during the experiment. The comparison between effects sizes  
462 controlled or not by body size however does not provide strong support for this hypothesis.  
463 Additionally, linear models computed for each response variable (Appendix: Table a.1) did  
464 not highlight strong and significant effects of body size of larvae on community and  
465 ecosystem dynamics. This suggests that other phenotypic traits may differ among populations  
466 and explain both differences in growth rate and in the impacts on ecosystem functioning. In  
467 this study, we failed at uncovering the proper phenotypic trait involved in these *evo-to-eco*  
468 links, probably because the ecological effects of intraspecific trait variation might rather arise  
469 from a suite of correlated traits varying among these populations (Therry et al submitted).  
470 Future studies should focus on whether a single trait or a suite of traits can predict the  
471 observed *evo-to-eco* links, as this will be the key for providing quantitative predictions on the  
472 ecological consequences of evolution at the intraspecific level.

473 Finally the contributions of early and late thermal environment, alone or in interaction, to  
474 the impacts of dragonfly larvae on ecosystems were particularly low, while we could have  
475 expected that the temperature an organism experienced during early stages of development  
476 can shape its thermal performance in later stages (Schulte, Healy, & Fanguie, 2011), and  
477 hence its impact on ecosystems. The finding that plasticity has an overall weak effect on  
478 ecological dynamics contrasted with previous findings (e.g. Lundsgaard-Hansen et al., 2014),  
479 hence indicating that the respective roles of genetic and plastic contributions to ecological  
480 dynamics are probably context and/or species dependent. The benthic variables tended  
481 however to be more impacted by the environmental conditions encountered late in the life of  
482 the dragonfly larvae than the pelagic variables. Temperature may differently impact species  
483 across trophic levels and ecological compartments, and via these mechanisms alter prey-  
484 predator dynamics (Grigaltchik, Ward, & Seebacher, 2012). Sensitivity to climatic conditions

485 may indeed depend on position within food webs (Thackeray et al., 2016). Across a food  
486 web, species vary for example for their thermal performance curves, for micro-climatic  
487 conditions in habitats and for the strength of bottom-up effects and top-down they endure. A  
488 different response of pelagic and benthic organisms to temperature (e.g. activity budget) may  
489 explain the observed higher impact of the environmental contribution of the dragonfly larvae  
490 to the benthic variables compared to the pelagic variables. A major future objective will be to  
491 elucidate what makes the balance shifting from genetic to plastic (and vice versa)  
492 contributions to ecological dynamics, so as to improve our predictive capabilities.

493

#### 494 **Conclusion**

495 Our study demonstrates that heritable differences in dragonfly larvae, alone or in  
496 interaction with thermal conditions, drive the impacts of this range expanding species on the  
497 ecosystem. This study adds to the growing literature documenting that heritable intraspecific  
498 variation shapes ecosystem functioning (Raffard et al. 2018). The impact of dragonfly larvae  
499 on the ecosystem was dominated by the heritable characteristics, showing that *evo-to-eco*  
500 dynamics are at play in this species. This study motivates for a better integration of  
501 evolutionary biology and ecosystem science in the scope of current environmental change,  
502 which opens to species new habitats with different thermal conditions. Further researches  
503 should investigate how altered ecosystems will influence selection pressures on subsequent  
504 generations after a species colonization, and hence generate *evo-to-eco-to-evo* feedbacks  
505 (Matthews, Aebischer, Sullam, Lundsgaard-Hansen, & Seehausen, 2016)

#### 506 **Acknowledgment**

507 We kindly thank Yohan Morizet, Iago Sanmartín-Villar and Jens d’Haeseleer for guiding us  
508 to populations and for collecting egg clutches. A Rocha provided access to the Portuguese  
509 study population. Nicolas Canto, Allan Raffard and Kéoni Saint-Pé helped out during  
510 bottlenecks of the mesocosm experiment. We thanks two anonymous referees for their  
511 constructive comments. This study is part of the project PROBIS (Biodiversa) and financially  
512 supported by ONEMA, DFG and SEPA. JCo is supported by an ANR-12-JSV7-0004-01.  
513 JCo, JCu and SB are part of the Laboratoire d’Excellence (LABEX) entitled TULIP (ANR-  
514 10-LABX-41).

515

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643

644 **Tables**

645 Table 1. The number of replicates for each  $G \times E_E \times E_L$  combination and the number of control  
 646 mesocosms (without dragonfly larvae) at the  $G \times E_L$  level.

Population of origin (G)	Rearing temperature ( $E_E$ )	Date start- up mesocosm	Environmental temperature ( $E_L$ )	# replicates	# control mesocosms
A (Portugal)	24°C	23-Oct-15	14°C	4	3
A (Portugal)	28°C		14°C	4	
A (Portugal)	24°C		18°C	4	4
A (Portugal)	28°C		18°C	4	
B (Southern France)	24°C	31-Oct-15	14°C	4	2
B (Southern France)	28°C		14°C	3	
B (Southern France)	24°C		18°C	4	3
B (Southern France)	28°C		18°C	3	
C (Center France)	24°C	23-Nov-15	14°C	2	4
C (Center France)	28°C		14°C	2	
C (Center France)	24°C		18°C	2	5
C (Center France)	28°C		18°C	2	
D (Netherlands)	24°C	23-Oct-15	14°C	3	3*
D (Netherlands)	28°C		14°C	3	
D (Netherlands)	24°C		18°C	3	4*
D (Netherlands)	28°C		18°C	3	

\* control mesocosms of population A and D were shared as these mesocosms are started-up at the same time

647

648

649 Table 2. Meta-regression assessing the effect of effect type (G,  $E_E$ ,  $E_L$ ,  $G \times E_E$ ,  $G \times E_L$ ,  $E_E \times E_L$   
 650 or  $G \times E_E \times E_L$ ), positional group (pelagic vs benthic) and functional group (primary  
 651 production, zooplankton, benthic invertebrates or nutrient cycling) on eta squared effect sizes  
 652 of the impact of *Crocothemis erythraea* larvae on community and ecosystem properties.

Factor	df	F	p
Effect_type	6, 63	9.19	<.001
Group_position	1, 63	0.03	0.864
Group_functional	3, 63	0.75	0.526
Effect_type $\times$ Group_position	6, 63	2.42	<b>0.036</b>
Effect_type $\times$ Group_functional	18, 63	2.63	<b>0.002</b>
Group_position $\times$ Group_functional	1, 63	0.13	0.712
Effect_type $\times$ Group_position $\times$ Group_functional	6, 63	0.81	0.548

653

### 654 **Figure legends**

655 Figure 1. Locations of the four *Crocothemis erythraea* populations (A, B, C and D) collected  
 656 in West-Europe. Populations are ordered according to the latitude (a). Growth rate of *C.*  
 657 *erythraea* larvae during 3 weeks at the low and high rearing temperature (i.e. the early  
 658 developmental environment  $E_E$ ) of larvae originating from populations A, B, C and D (i.e. the  
 659 genetic contribution G) (b).

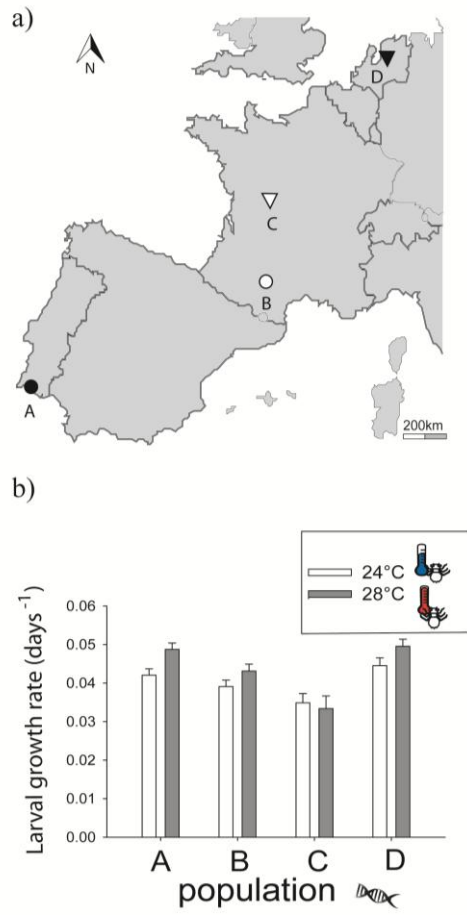
660 Figure 2. Mean ( $\pm$  1SE) residuals of the regression between the values for experimental and  
 661 control mesocosms for pelagic chlorophyll concentration, benthic chlorophyll concentration  
 662 and gross primary production (GPP) (a), for the number of Daphniidae, number of  
 663 Cyclopidae, H shannon diversity of the zooplankton and E shannon evenness of the  
 664 zooplankton (b), for the number of Asellidae, number of Physidae, H shannon diversity of the  
 665 benthic invertebrates, E shannon diversity of the benthic invertebrates, (c) total nitrogen  
 666 concentration, total phosphorous concentration, pH, and decomposition rate (d); for each  
 667 *Crocothemis erythraea* population (G) at each of the early developmental environment ( $E_E$ )  $\times$   
 668 late developmental environment ( $E_L$ ) combinations. Mean value and 95% CI for each  $E_E \times E_L$   
 669 combination is represented by a black horizontal line and a grey shaded area respectively.  
 670 The dotted grey line indicates that introducing larvae in the mesocosms has no effects  
 671 compared to the control for a given response variable. Dots above the lines indicate that  
 672 introducing larvae increases the value of a given response variable compared to the control  
 673 tanks, and inversely for dots below that line.

674 Figure 3. Eta squared effect sizes for the genetic (G), early developmental environment ( $E_E$ ),  
 675 late developmental environment ( $E_L$ ) and interactive ( $G \times E_E$ ,  $G \times E_L$ ,  $E_E \times E_L$ ) contributions  
 676 to the effect induced by *Crocothemis erythraea* larvae on the community and ecosystem  
 677 properties measured in the mesocosms. For each effect type the combined effect size with 95  
 678 % CI is given, together with the 95 % CI's of the effect sizes split up according to the  
 679 positional group (pelagic vs benthic) and according to the functional group (primary

680 production, zooplankton, benthic macro-invertebrates or nutrient cycling) of the variables  
681 quantified in the mesocosms.

682

683 FIGURES

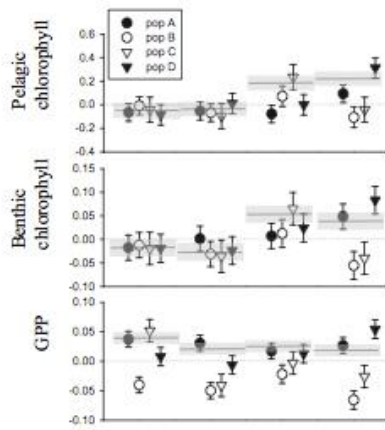


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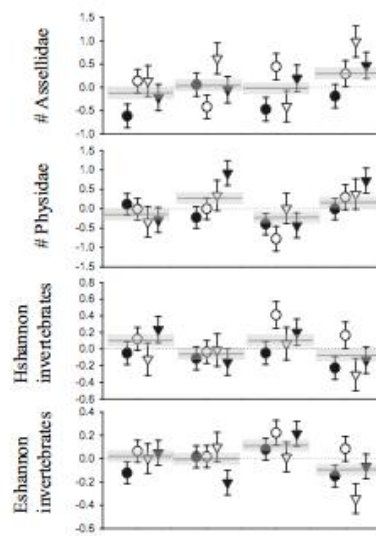
685 Figure 1.

686

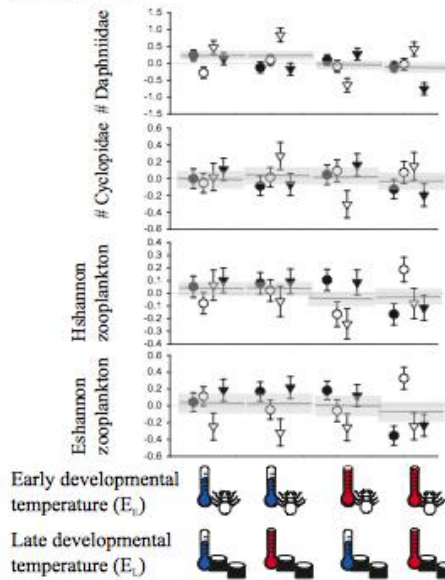
a) Primary production



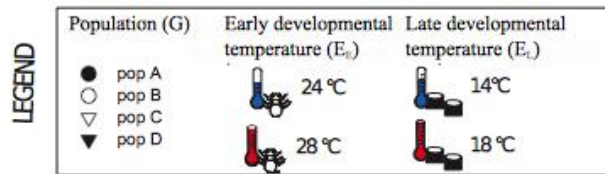
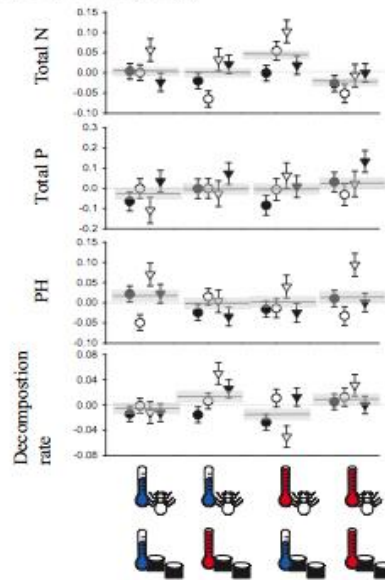
c) Benthic macro-invertebrates



b) zooplankton



d) Nutrient cycling



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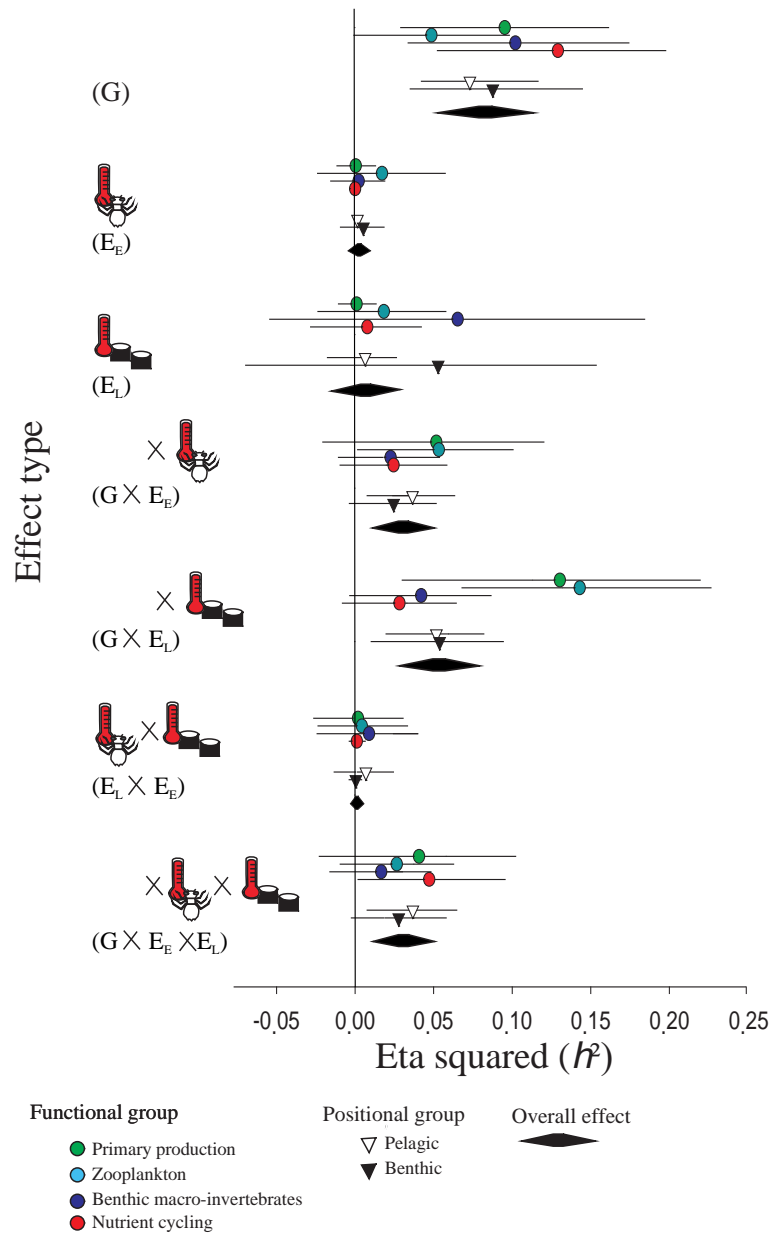
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691 Figure 2.

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695 Figure 3.

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