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

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Abstract

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

KEYWORDS
aquatic ecosystems, arthropods, eco-evolutionary dynamics, ecosystem functioning, intraspecific diversity, invasion

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1 | INTRODUCTION

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

Intraspecific trait variation can result from variation in environmental conditions across the range (e.g., abiotic conditions, population or community structure) and/or from the genetic architecture of populations resulting from founder effects, genetic drift or natural selection. When adaptive and/or non-adaptive genetic changes generate rapid evolutionary phenotypic changes, evolutionary dynamics can coincide in space and time with ecological changes, and generate so-called *eco-evolutionary dynamics* (Fussmann et al., 2007; Lowe, Kovach, & Allendorf, 2017). For instance, populations colonizing different environment can rapidly evolve phenotypic divergences by natural selection, which can ultimately lead to differential ecological impacts of these populations on ecosystem properties and functions (i.e., *evo-to-eco dynamics*, Harmon et al., 2009; Matthews, Aebischer, Sullam, Lundsgaard-Hansen, & Seehausen, 2016; Brunner, Anaya-Rojas, Matthews, & Eizaguirre, 2017). Nonetheless, the ecological effects of trait variation can be generated by genetic local differentiation (due to drift or selection), environmentally induced plasticity or a combination of genetic and plastic phenotypic divergences, which makes difficult to evaluate to which extent evolution really matters for ecology (Bassar et al., 2010; Lundsgaard-Hansen, Matthews, & Seehausen, 2014; Pantel, Duvivier, & De Meester, 2015; Schmitz, Beckerman, & O'Brien, 1997). While the evolutionary forces underlying trait variation modulate the strength of these *evo-to-eco dynamics*, a major difficulty is yet to tease apart the ecological impacts associated with genetically driven trait variation to those associated with environmentally driven plastic phenotypic differentiation. Understanding the genetic and plastic contributions to the impact of an organism on ecosystem functioning is yet an essential question for properly predicting the ecological dynamics of ecosystems, in particular under contemporary global change. Indeed, global change is multifaceted and is for instance characterized simultaneously by a large-scale shuffling of genotypes (due to range shifts and/or local adaptation) and changes in key environmental drivers such as temperature regimes that can modulate the phenotypes through developmental plasticity. Moreover, reciprocal dynamics and feedbacks between ecological and evolutionary dynamics can only be attested if adaptive (natural selection) and non-adaptive (genetic drift) processes acting on heritable traits are driving trait variation among populations (Lundsgaard-Hansen et al., 2014). Identifying the genetic and plastic contributions of the ecosystem impact of an organism hence provides a good indication on the potential for eco-evolutionary dynamics to occur.

In this study, we assessed the genetic (G) contribution, the environmental contribution occurring early (E_E) or late (E_L) in the development and the interactive ($G \times E_E$, $G \times E_L$, $E_E \times E_L$, $G \times E_E \times E_L$) contributions to the impact of a range-expanding dragonfly (*Crocothemis erythraea*) on aquatic community and ecosystem properties. To do so, we set a mesocosm experiment manipulating genetic and environmental contributions to trait variation in dragonfly larvae in a full factorial design. Egg clutches from four independent populations along the latitudinal gradient of range expansion (Southern to Northern Europe) were used to manipulate the genetic basis of trait variation in larvae. We further manipulated thermal conditions during the development from egg to larvae with two temperature regimes (24°C and 28°C) to estimate the early-in-life plastic component of trait variation. Thermal conditions were then manipulated in the mesocosms, in which larvae were released, by setting experimental units at two different temperature regimes (14°C and 18°C) to estimate the plastic component of trait variation at a later stage. We then quantified the impacts of larvae on the structure of communities and ecosystem functions after a two-month period, and we teased apart the genetic and environmental contributions of trait variation on these ecological dynamics (Raffard et al., 2018; Des Roches et al., 2018). Genetically based trait variation (i.e., evolution *per se*) should have stronger effects on ecological dynamics than trait variation arising from plasticity since ectotherm life-history traits strongly vary along latitudinal range-expansion gradients (De Block, Slos, Johansson, & Stoks, 2008; Phillips, 2009; Therry, Nilsson-Oertman, Bonte, & Stoks, 2014), and because plastic-induced traits are more labile. We also predicted that the impact of trait variation on ecological dynamics will vary according to the different types of community and ecosystem parameters. In particular, ecological parameters directly impacted by dragonfly larvae (e.g., abundance and composition of prey communities) should be more strongly impacted by trait variation, than parameters related to ecosystem functioning such as the decomposition of organic matter (Raffard et al., 2018).

2 | MATERIALS AND METHODS

2.1 | Study system and collection

Crocothemis erythraea (Brullé, 1832) is a dragonfly species with a predominantly African distribution but with a small historical European breeding range confined to the Mediterranean area (Dijkstra & Lewington, 2006). Triggered by global warming, the species' range expansion towards Northern Europe started in the 1960s, and the northernmost populations are currently found in Northern Germany (Brockhaus, 2015; Ott, 2007). The species breeds in a wide range of stagnant water habitats with a preference for shallow lakes with dense aquatic vegetation (Dijkstra & Lewington, 2006). Odonates

occupy an important intermediate position in aquatic systems as both predator and prey, but are the top predator in shallow fishless water bodies (Corbet, 1999). Odonates are generalist predators, feeding both on benthic invertebrates and on pelagic zooplankton hereby influencing both benthic and pelagic food chains through top-down effects, and ecosystem functions through indirect effects. Odonate larvae show important geographical variation in growth rate, metabolism, feeding activity and body size, which can be shaped by both genetic and environmental factors. Variation in these functional traits have already been shown to have drastic effects on the functioning of aquatic ecosystems, and we hence expect larvae of *C. erythraea* originating from various geographical origins to impact differently the dynamics of communities and ecosystems.

Gravid females of *C. erythraea* were caught in 2015 from four populations distributed across a gradient of 15° of latitude (Figure 1) that coincides with the climate-driven range expansion of the species through Western Europe. Due to logistic constraints, we were unable to collect all populations in the same time period (sampling date per populations: pop A: 4 and 5 August 2015; pop B: 15 August 2015; pop C: 5 and 6 September 2015; and pop D: 5 and 7 August 2015). Egg clutches were extracted by dipping the abdomen of the female in a tube filled with dechlorinated tap water (Hudson & Berrill, 1986). For each population, eggs from five to six different females were collected, resulting in a total of twenty-three collected egg clutches. Eggs were transported to the laboratory in Moulis (France), and eggs (and then hatched F1 larvae) were kept in a wet laboratory at 20°C and a photoperiod of L:D 14:10 h until the start of the temperature treatment. After hatching, F1 larvae were kept in batches of ten in 5-L round containers and fed twice a day ad libitum with freshly hatched *Artemia* nauplii. We considered these four populations displayed unique trait combination that are mostly due to genetic contributions given that they are geographically isolated from each other and that they live in highly divergent environments (L. Therry, F. Finn, K. Koch, T. Brodin, S. Blanchet, & J. Cote, unpublished data). It is noteworthy that traits expressed in F1 can still be affected by non-genetic—yet inherited—processes such as maternal effects (Danchin et al., 2011) and that difference in collection dates might also limit our ability to tease apart pure genetic effects on trait variability. The genetic contribution we consider here may hence be overestimated, as our design does not allow accounting for these potential non-genetic effects (see Section 4).

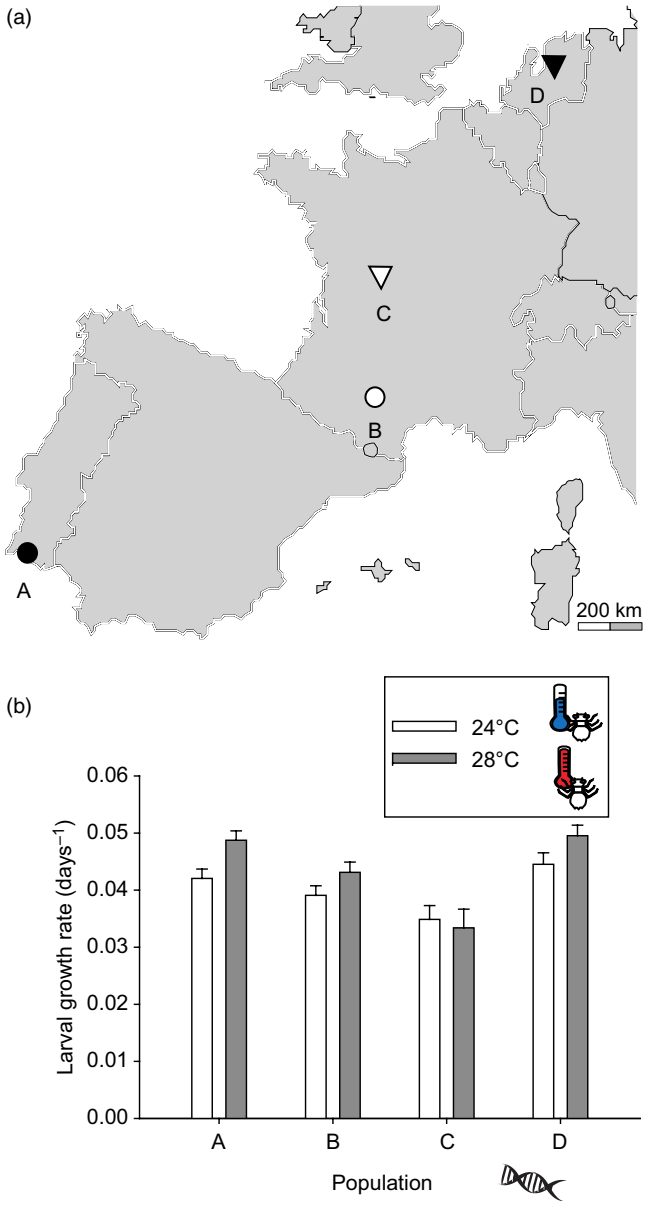


FIGURE 1 Locations of the four *Crocothemis erythraea* populations (A, B, C and D) collected in Western Europe. Populations are ordered according to the latitude (a). Growth rate of *C. erythraea* larvae during 3 weeks at the low and high rearing temperature (i.e., the early developmental environment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

2.2 | Plastic-induced trait variation among larvae

Four weeks after hatching, larvae were individually placed in white opaque vials (diameter: 7.5 cm; height: 10 cm) and assigned for three weeks to one of two temperature treatments in order to induce plastic differences at an early developmental stage (E_E) between dragonfly larvae. This was done in a full factorial design with population of origin and temperature treatment as factors (eight treatments in total). Larvae assigned to the lower temperature treatment were placed in an incubator at 24°C, while larvae assigned to the higher temperature treatment were placed in an incubator at 28°C. 28°C reflects the optimal temperature for growth of *C. erythraea* larvae (Suhling & Suhling, 2013), and this water temperature is reached during summer in the shallow breeding ponds of the studied populations (Supporting Information Appendix S1: Figure S1). Photoperiod at both incubators was L:D 14:10 h, reflecting the photoperiod at summer (August) in Western Europe. During the larval temperature treatment, larvae were fed twice a day ad libitum with freshly hatched *Artemia* nauplii, and this was supplemented with three chironomid larvae every other day during the last two weeks in order to meet the higher food demands of older larvae.

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

2.3 | Mesocosm experiment

Seventy-two black round 100-L mesocosms (Ø 68 cm) were evenly distributed over four compartments of a greenhouse. Each compartment was 40 m^2 and was separated from others by fixed transparent walls. Tanks (18 per compartment) were placed on fixed shelves at 1 m height from the ground. Temperature of each greenhouse compartment was automatically and independently regulated with heating and cooling devices installed in each compartment and programmed from a centralized computer. Two greenhouse compartments were assigned to the low temperature treatment of 14°C and two compartments were assigned to the high temperature treatment of 18°C, with a thermal fluctuation following the daily fluctuation of temperatures. Water temperature followed the same fluctuations and was on average 14.39°C (±0.26 *SD*) and 17.69°C (±0.36 *SD*) for the low temperature and high temperature treatment in average (measured using Hobo® data loggers). There was a low variability in air and water temperature along the experiment. These temperature treatments were used to manipulate the effect of late developmental environment on larvae trait variation (E_L). Growth lights provided a photoperiod of L:D 12:12 h; which reflects the photoperiod during autumn (September) in Western Europe. Two weeks before the introduction of dragonfly larvae, tanks were filled with tap water and supplemented with 20 g of air-dried poplar leaves and 0.5 ml organic fertilizer (Solabiol®) which provided nutrients for phytoplankton growth. Three days later, we added 6 L of phytoplankton/zooplankton aliquots from an established 1,000-L mesocosm that was inoculated from two gravel pit lakes located in the study area (Alp, Cucherousset, Buoro, & Lecerf, 2016). Aquatic benthic invertebrates (snails, chironomids and amphipods, mostly from the following families: Asellidae, Physidae, Tubificidae, Caenidae, Hydra sp., Glossiphoniidae, Lymnaeidae, Chironomidae, Ceratopogonidae, Sphaeriidae and Ecnomidae) originating from another gravel pit lake (lake Lamartine) were added. These gravel pit lake was selected because it is eutrophic and shallow, representing the typical habitat of *C. erythraea*. Fourteen days after filling the mesocosms, the experiment was initiated by adding three dragonfly larvae (i.e., 8.8 larvae/m^2, which is closed to the natural density of a closely related species, *Libellula quadrimaculata*, 6.6 larvae/m^2, Corbet, 1999) from one of the eight "population of origin × temperature of rearing" treatment (except to the control

TABLE 1 The number of replicates for each G × E_E × E_L combination and the number of control mesocosms (without dragonfly larvae) at the G × E_L level

Population of origin (G)	Rearing temperature (E_E)	Date start-up mesocosm	Environmental temperature (E_L)	No. replicates	No. 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 (Central France)	24°C	23-Nov-15	14°C	2	4
C (Central France)	28°C		14°C	2	
C (Central France)	24°C		18°C	2	5
C (Central France)	28°C		18°C	2	
D (Netherlands)	24°C	23-Oct-15	14°C	3	3[a]
D (Netherlands)	28°C		14°C	3	
D (Netherlands)	24°C		18°C	3	4[a]
D (Netherlands)	28°C		18°C	3	

[a]Control mesocosms of populations A and D were shared as these mesocosms are started up at the same time.

tanks where no dragonfly larvae were added). This lead to 16 treatments ($4G \times 2E_E \times 2E_L$) that we replicated four times for populations A and B, and two and three times for populations C and D, respectively, due to a shortage in larvae (see Table 1). Larvae were measured for head width (see above) at the onset and at the end of the mesocosm experiment to test for an effect of E_L on growth rate (calculated as above but with measures averaged at the tank level as larvae were not individualized). Two to five control tanks (without addition of dragonfly larvae) were run at each population × environmental temperature treatment combination (Table 1), to serve as comparison bases and to properly evaluate the strength and direction of the effects of intraspecific trait variation on ecological dynamics. At the time of introduction of dragonfly larvae, three pre-weighted leaf packages (± 4 g air-dried *Populus* leaves) and a white tile (L × W: 20 × 20 cm) were added to each mesocosm to quantify decomposition rate (Alp et al., 2016) and benthic primary production at the end of the experiment, respectively (see further).

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

Pelagic primary production (chlorophyll-a concentration, µg/L) was measured using a portable spectrophotometer (AlgaeTorch, bbe ®) in the water column of the mesocosm. Benthic primary production (chlorophyll-a concentration on tiles, µg/cm²) was measured using a portable spectrophotometer (BenthoTorch, bbe®) at three different location on each tile. Dissolved oxygen (DO) concentration was measured using an oxygen probe (Jenway®) at three successive time slots during a 24-h timeframe: dawn, dusk and dawn at the following day. GPP was calculated as the sum of net primary production ($NPP = DO_{dusk\ 1} - DO_{dawn\ 1}$) and ecosystem respiration ($ER = DO_{dusk1} - DO_{dawn2}$). The mesocosms' pH was measured using a pH probe (Jenway®). Water samples were collected using a 100-ml syringe, filtered using a 0.45-µm mesh filter and then stored at −18°C until quantification of total nitrogen and total phosphorous concentrations using a high-performance ionic chromatograph (Dionex DX-120). Zooplankton was sampled by filtering 30 L of water using a zooplankton net (mesh size: 200 µm). Zooplankton was then stored in 100-ml flasks filled with 80% ethanol for further quantification and sorting up to the family level using a binocular (Nikon®). Shannon's diversity index (H) and Shannon's equitability (EH) index were calculated from the zooplankton counts at the family level. Additionally, the counts of the most abundant families (Daphniidae and Cyclopoidae) were extracted as additional variables accounting for the abundance of these two families. The sediment of the mesocosm was sieved over a zooplankton net (200 µm) to collect the benthic macro-invertebrates, which were stored on 80% ethanol in 250-ml flasks. In a first step, macro-invertebrates larger than 2 mm were counted and sorted up to the family level using a binocular (Nikon®) and according to the European determination key (Tachet, Richoux, Bournaud, & Usseglio-Polatera, 2010). In a second step, the content of the flask was homogenously distributed in a white tray (L × W: 49 × 33.5 cm), and all macro-invertebrates from one quarter of the tray were determined and counted. The estimate of total macro-invertebrate abundance was obtained summing the counts of the larger invertebrates to four times the count of the smaller invertebrates. Shannon's diversity index (H) and Shannon's equitability (EH) index were calculated from the macro-invertebrate counts. Additionally, the counts of the most abundant families (Asellidae and Physidae) were extracted as additional variables synthetizing the abundance of these two families.

2.4 | Statistical analyses

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

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

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

LMMs included the greenhouse compartment nested in the environmental treatment as random intercept, and the mean head width of larvae at the onset of the mesocosm experiment and the number of surviving larvae at the end of the mesocosm experiment as covariates. We added these two covariates to remove any confounding effects from the genetic contributions and to test whether heritable traits such as body size may contribute to ecological dynamics. Models without these covariates give similar results (Table a.2 and a.3). Note that one tank was removed from the final dataset since we detected the accidental presence of a crayfish, which may have strongly affected the general dynamics of the ecosystem. Second, we quantified the size of the effect of each contributor on ecological dynamics by calculating eta-squared (η^2) effect sizes of the genetic, early environment, late environment and interactive contributions of the effect induced by dragonfly larvae on community and ecosystem dynamics as the ratio of the sum of squares of the effect of the factor of interest on the total sum of squares using type III analysis of variance. Third, we synthesized quantitative information by performing a meta-analysis on the calculated eta-squared effect sizes (see Neyeloff, Fuchs, & Moreira, 2012). This meta-analysis was used to test whether effect sizes of each contributor varied between ecological parameters. To do so, we combined (for each contributor and interaction terms independently) the effect sizes calculated for each ecological parameter and we calculated the Q test for heterogeneity in effect sizes (Rosenberg, Adams, & Gurevitch, 2000), and its significance was tested using chi-square statistics (a significant Q value for a given contributor indicating that effect sizes of this contributor vary among ecological parameters). The meta-analysis was also used to test what drives variation in effect sizes among ecological parameters. To do so, we ran a fixed-effect meta-regression with effect sizes (from all ecological parameters and all contributors as the dependent variable). Fixed effects included the type of contributor (G, E_E, E_L, G × E_E, G × E_L, E_E × E_L or G × E_E × E_L) and two classifications for the ecological parameters: (a) according to the position in the aquatic system (two factors: pelagic vs. benthic) and (b) according to the functional group (four factors: primary production, zooplankton, benthic invertebrates or nutrient cycling). We also included all interaction terms as additional fixed effects. This meta-regression allowed testing whether effect sizes significantly varied among types of contributors and the class of ecological parameters being considered.

All statistical analyses were done using the PROC MIXED of SAS v9.0 and a Satterthwaite approximation to estimate degree of freedom. Dataset is available online (Therry et al., 2018)

3 | RESULTS

3.1 | Genetic and environmental effects on larval growth rate

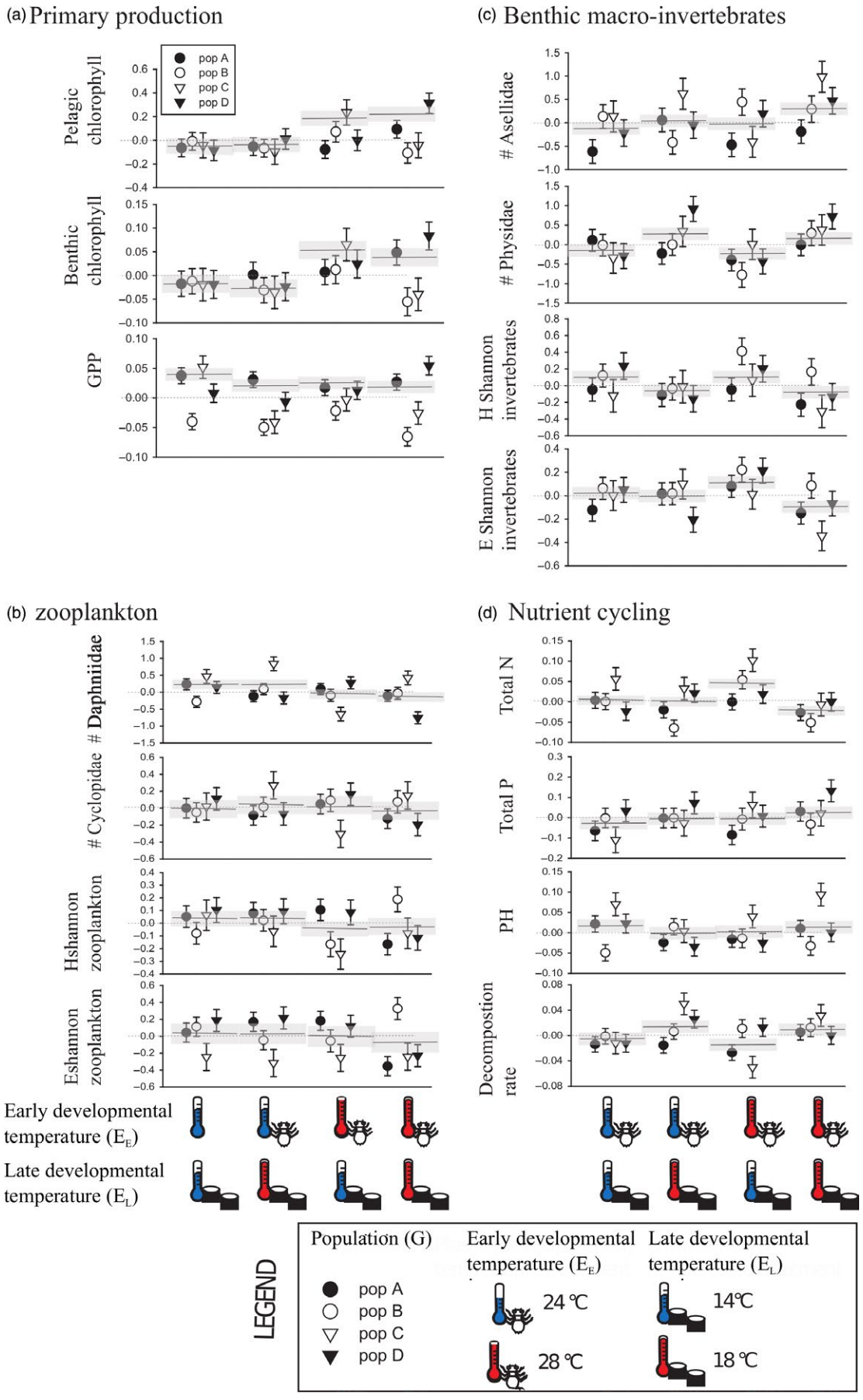
Growth rate of larvae before the mesocosm experiment greatly differed among populations ($F_{3,135}$ = 11.38, p < 0.001), suggesting a strong contribution of G on larval growth rate. Larvae originating from the C population grew significantly less than larvae from all other populations (Tukey test, p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

During the mesocosm experiment, larvae growth rate did not vary among populations ($F_{3,34.32}$ = 0.97, p = 0.420) and among climatic conditions in the mesocosm ($F_{1,1.94}$ = 0.97, p = 0.412). The interaction between mesocosm temperature and the population of origin was also not significant ($F_{3,34.44}$ = 0.72, p = 0.545). Nonetheless, at the onset of the mesocosm experiment, the head width of larvae tended to be higher for populations A and D than for populations B and C ($F_{3,43.12}$ = 2.49, p = 0.072), whereas this was not the case at the end of the mesocosm experiment ($F_{3,38.41}$ = 0.82, p = 0.489). This suggests that populations B and C partly compensate the body size difference during the mesocosm experiment. After 60 days, survival rate in the mesocosm experiment was 73.3% (±0.04%, *SE*) and did not vary among treatments (GLM, all p-values > 0.05).

3.2 | Genetic and environmental contributions to ecological dynamics

Genetic (G), environmental (E_E and E_L) and interactive (G × E_E, G × E_L, E_E × E_L and G × E_E × E_L) contributions to the impact of dragonfly larvae on community and ecosystem dynamics were found for all ecological parameters, although not consistently (Figure 2, Supporting Information Appendix S1: Table S1). In particular, effect sizes of genetic contributions were significantly heterogeneous across ecological parameters (Q_G = 24.132, p = 0.044). A significant genetic effect (G) of dragonfly larvae on ecological

FIGURE 2 Mean (± 1 *SE*) residuals of the regression between the values for experimental and control mesocosms for pelagic chlorophyll concentration, benthic chlorophyll concentration and gross primary production (GPP) (a); for the number of Daphniidae, number of Cyclopidae, H Shannon diversity of the zooplankton and E Shannon evenness of the zooplankton (b); for the number of Asellidae, number of Physidae, H Shannon diversity of the benthic invertebrates and E Shannon diversity of the benthic invertebrates (c); for total nitrogen concentration, total phosphorous concentration, pH and decomposition rate (d); and for each *Crocothemis erythraea* population (G) at each of the early developmental environment (E_E) × late developmental environment (E_L) combinations. Mean value and 95% CI for each E_E × E_L combination are represented by a black horizontal line and a grey shaded area, respectively. The dotted grey line indicates that introducing larvae in the mesocosms has no effects compared to the control for a given response variable. Dots above these lines indicate that introducing larvae increases the value of a given response variable compared to the control tanks, and inversely for dots below that line


(a) Primary production
Pelagic chlorophyll
Benthic chlorophyll
GPP
pop A
pop B
pop C
pop D
(c) Benthic macro-invertebrates
Asellidae
Physidae
H Shannon invertebrates
E Shannon invertebrates
(b) zooplankton
Daphniidae
Cyclopidae
Hshannon zooplankton
Eshannon zooplankton
(d) Nutrient cycling
Total N
Total P
PH
Decompostion rate
Early developmental temperature (E_E)
Late developmental temperature (E_L)
LEGEND
Population (G)
pop A
pop B
pop C
pop D
Early developmental temperature (E_E)
24 °C
28 °C
Late developmental temperature (E_L)
14°C
18 °C

dynamics was found for six out of the fifteen ecological parameters. Early environmental (E_E) and late environmental (E_L) effects were found at lower occurrence, with three out of fifteen ecological parameters being significantly affected by E_E and E_L, respectively. Interestingly, late environmental contributions to variation in ecological dynamics were strongly dependent upon the population (six out of fifteen significant G × E_L interactions, Supporting Information Appendix S1: Table S1), which was not the case for early environment (one out of fifteen significant G × E_E interactions, Supporting Information Appendix S1: Table S1).

Meta-regressions revealed that the overall contributions (across all ecological parameters) of G, E_E, E_L and their interactions significantly differed among these types of contributors (Table 2, Figure 3), with the strongest overall contributions being detected for the G, the G × E_L and, to a lesser extent, G × E_E and G × E_E × E_L interactions. In contrast, the lowest overall contributions were detected for E_E, E_L and E_E × E_L for which the 95% confidence intervals (CIs) included 0. Nonetheless, these differences among types of contributors differed between the position of the ecological parameters in the ecosystems (pelagic vs. benthic) and the functional group being measured (primary productivity, zooplankton, benthic macro-invertebrates and nutrient cycling), as shown by significant interaction terms (Table 2). For instance, E_L contributions tended to be higher for benthic ecological parameters than for pelagic ecological parameters (Figure 3). Further, the contributions of both G × E_E and G × E_L were stronger for parameters related to primary production and zooplankton dynamics than for parameters related to the dynamics of benthic invertebrates and nutrient cycling.

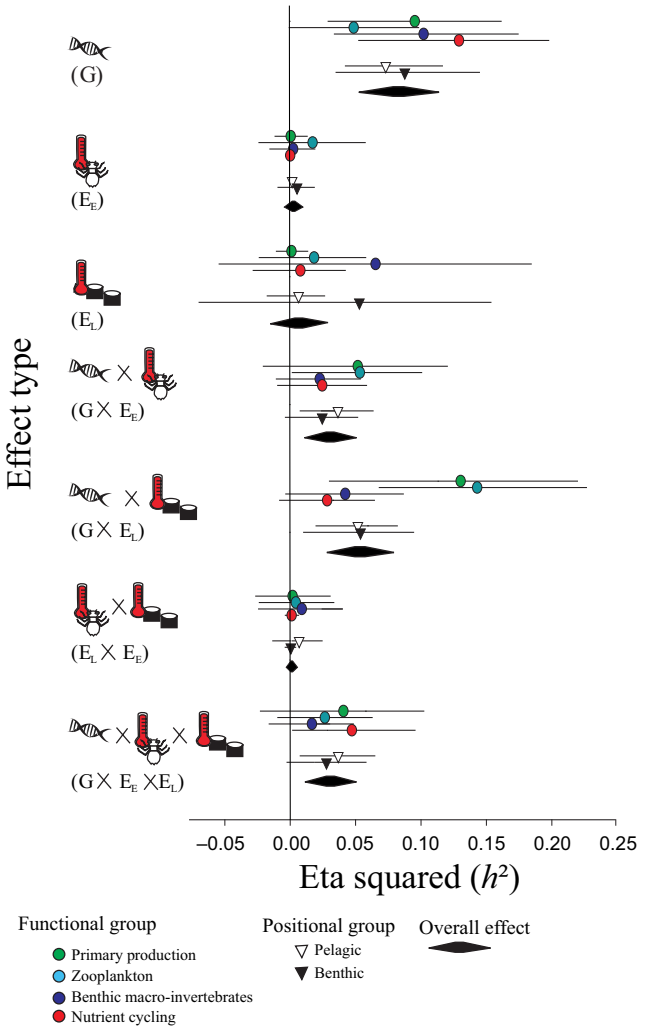


FIGURE 3 Eta-squared effect sizes for the genetic (G), early developmental environment (E_E), late developmental environment (E_L) and interactive (G × E_E, G × E_L, E_E × E_L) contributions to the effects induced by *Crocothemis erythraea* larvae on the community and ecosystem properties measured in the mesocosms. For each effect type, the combined effect size with 95% CI is given, together with the 95% CIs of the effect sizes split up according to the positional group (pelagic vs. benthic) and according to the functional group (primary production, zooplankton, benthic macro-invertebrates or nutrient cycling) of the variables quantified in the mesocosms

4 | DISCUSSION

Phenotypic and genetic differentiation between populations can take place when populations are exposed to contrasting selection pressures and/or when genetic drift is strong enough to generate significant differentiation (Chuang & Peterson, 2016; Hoffmann & Sgrò, 2011; Lowe et al., 2017). A growing number of studies documented that intraspecific trait variation arising from evolutionary processes (selection and/or drift) can affect the dynamics of communities and ecosystems, leading to *evo-to-eco* feedbacks (El-Sabaawi et al., 2015; Harmon et al., 2009; Lundsgaard-Hansen et al., 2014; Matthews et al., 2011; Pantel et al., 2015; Rudman et al., 2015; Lowe et al., 2017). In this study, we disentangled the genetic and environmental contributions of intraspecific trait variation in a range-expanding predator to the dynamics of communities and the functioning of ecosystem. We demonstrated that community

TABLE 2 Meta-regression assessing the effect of contribution type (G, E_E, E_L, G × E_E, G × E_L, E_E × E_L or G × E_E × E_L), positional group (pelagic vs. benthic) and functional group (primary production, zooplankton, benthic invertebrates or nutrient cycling) on eta-squared effect sizes of the impact of *Crocothemis erythraea* larvae on community and ecosystem properties

Factor	*df*	*F*	*p*
Effect_type	6, 63	9.19	**<0.001**
Group_position	1, 63	0.03	0.864
Group_functional	3, 63	0.75	0.526
Effect_type × Group_position	6, 63	2.42	**0.036**
Effect_type × Group_functional	18, 63	2.63	**0.002**
Group_position × Group_functional	1, 63	0.13	0.712
Effect_type × Group_position × Group_functional	6, 63	0.81	0.548

Note. Bold values indicate significant *p*-values.

and ecosystem dynamics were more influenced by populations of origin than by developmental thermal conditions experienced early and late in life, suggesting a stronger genetic contribution to the overall ecological dynamics than plastic contributions. Nonetheless, the genetic contributions were partially modulated by late (and to a lesser extent early) thermal environments and varied among the functional groups and different compartments of the ecosystem. This study allowed to better estimate the relative contribution of intraspecific trait variation due to either genetic or environmental factors to the ecological impact of a predator, and therefore of the eco-evolutionary dynamics.

Abiotic and biotic environmental gradients can generate strong adaptive phenotypic differentiation among populations within a species distribution range. In range-expanding species, colonization and invasion processes often strengthen phenotypic clines along spatial gradients as found with behaviours and pace-of-life (Chuang & Peterson, 2016; Phillips, 2009; Therry, Nilsson-Oertman, et al., 2014). Additionally, range-expanding species are characterized by series of founder effects that can also generate rapid phenotypic differentiation (due to drift) among colonizing populations. In this later case, spatial patterns of phenotypic differentiation should be independent from environmental clines. However, genetic and environmental differentiations are often confounded in range-expanding species. For example, *C. erythraea* expanded its range from south to north, and therefore, populations at the expanding edge are at higher latitude and encounter—among others—colder conditions. In this study, we collected egg clutches to limit environmental influences as much as possible, and we manipulated developmental thermal conditions at different important life stages. This protocol allows estimating the relative contribution of heritable and environmental determinants of trait variation in this range-expanding species. It must be acknowledged that—because of field constraints—eggs from one of the populations were collected one month after the others, which may limit clear-cut conclusions related to the pure effect of range expansion on trait diversity. However, either with or without this specific population, we found large population differentiation in the growth rate of *C. erythraea* larvae reared in standardized conditions from eggs and additional differences in growth rate induced by temperature at early stages of development. These effects suggest both heritable and plastic determinants of growth rate. Given that eggs have been fecundated in the wild, our design cannot rule out the possibility that both non-genetic (yet heritable such as maternal effect or epigenetic marks) and genetic processes explained phenotypic differentiation observed between populations. While we did not quantify them, differences in growth rate likely encompass differences among populations in many other response traits (e.g., behaviour and metabolism, Chuang & Peterson, 2016; Stoks, Swillen, & De Block, 2012) and effect traits (e.g., nutrient excretion, consumption rate, Raffard et al., 2017; Tilman, 2001; Vanni, 2002), which is actually sustained by a companion study showing that patterns of trait covariation strongly varied in this species along the expansion gradient (L. Therry, F. Finn, K. Koch, T. Brodin, S. Blanchet, & J. Cote, unpublished data). Covariation between effect and response traits (the functional syndrome) might actually contribute to differential ecological impacts across a species range (Raffard et al., 2017). Surprisingly, growth rate did not vary linearly with latitudes as it was expected (Kivelä, Välimäki, Carrasco, Mäenpää, & Oksanen, 2011; Therry, Lefevre, et al., 2014). This suggests that variation among populations does not result (only) from climatic conditions or from population colonization history, but probably from other environmental differences and/or from founder effects inducing population divergence in heritable traits.

Overall, genetic (adaptive and/or non-adaptive) effects towered over temperature-driven plastic effects on community and ecosystem dynamics, as found for the effects of white fish's ecotypes on aquatic ecosystems (Lundsgaard-Hansen et al., 2014). As stated above, we cannot exclude that non-genetic heritable processes are also part of these *evo-to-eco* links. Future studies should aim at tackling the respective role of genetic and non-genetic heritable processes on *evo-to-eco* links, notably given that eco-evolutionary feedbacks might vary in their dynamics depending on the underlying processes driving trait variation. The observed *evo-to-eco* links were related to a broad range of ecosystem variables, ranging from the zooplanktic and benthic prey species to primary production and nutrient cycling. Nonetheless, ecological effects sizes of trait variation arising from genetic contributions and (to a lesser extent) from the interaction between genetic contributions and late developmental conditions ($G \times E_L$) were not homogeneous among ecological parameters. For example, $G \times E_L$ had stronger effects on zooplanktic species and on primary production, than on benthic prey species and nutrient cycling. This variability of effects makes difficult to predict precisely differences in ecosystem functioning across the species range. However, it appears that all ecological parameters are more strongly influenced by genetic background, directly or environmentally mediated, than by the sole effect of developmental thermal conditions. In aquatic ecosystems, predators often have strong top-down impacts by directly controlling prey species and indirectly primary production and nutrient cycling (Bestion, Cucherousset, Teyssier, & Cote, 2015; Shurin et al., 2002). This may explain why (heritable) trait variation in predators such as *C. erythrea* has substantial consequences on several ecosystem parameters (see also El-Sabaawi et al., 2015; Harmon et al., 2009; Raffard et al., 2018).

It further shows that the temperature-mediated plastic contributions to ecological dynamics were largely dependent on the genetic contribution as indicated by $G \times E_E$ and $G \times E_L$ interactions. These interactions could have been caused by adaptive plastic evolution. Accordingly, reaction norms have been shown to differ between populations subjected to different selection pressures (Ghalambor, McKay, Carroll, & Reznick, 2007), and to evolve during species range expansion (Aubret & Shine, 2009; Ducatez, Crossland, & Shine, 2016). However, while population latitudes should reflect larvae thermal adaptation, it does not explain well the $G \times E$ interactions in our case. On the contrary, the southern and northern populations display more similar reactions to late and early developmental temperatures than the two intermediate populations. These differences

among populations match the differences in growth rate and body size before the mesocosm experiment. The similar dependency to thermal conditions could have therefore resulted from the differences in growth rate, body size or growth compensation during the experiment. The comparison between effects sizes controlled or not by body size however does not provide strong support for this hypothesis. Additionally, linear models computed for each response variable (Supporting Information Appendix S1: Table S1) did not highlight strong and significant effects of body size of larvae on community and ecosystem dynamics. This suggests that other phenotypic traits may differ among populations and explain both differences in growth rate and in the impacts on ecosystem functioning. In this study, we failed at uncovering the proper phenotypic trait involved in these *evo-to-eco* links, probably because the ecological effects of intraspecific trait variation might rather arise from a suite of correlated traits varying among these populations (L. Therry, F. Finn, K. Koch, T. Brodin, S. Blanchet, & J. Cote, unpublished data). Future studies should focus on whether a single trait or a suite of traits can predict the observed *evo-to-eco* links, as this will be the key for providing quantitative predictions on the ecological consequences of evolution at the intraspecific level.

Finally, the contributions of early and late thermal environment, alone or in interaction, to the impacts of dragonfly larvae on ecosystems were particularly low, while we could have expected that the temperature an organism experienced during early stages of development can shape its thermal performance in later stages (Schulte, Healy, & Fangue, 2011) and hence its impact on ecosystems. The finding that plasticity has an overall weak effect on ecological dynamics contrasted with previous findings (e.g., Lundsgaard-Hansen et al., 2014), hence indicating that the respective roles of genetic and plastic contributions to ecological dynamics are probably context and/or species dependent. The benthic variables tended however to be more impacted by the environmental conditions encountered late in the life of the dragonfly larvae than the pelagic variables. Temperature may differently impact species across trophic levels and ecological compartments, and via these mechanisms alter prey–predator dynamics (Grigaltchik, Ward, & Seebacher, 2012). Sensitivity to climatic conditions may indeed depend on position within food webs (Thackeray et al., 2016). Across a food web, species vary for example for their thermal performance curves, for microclimatic conditions in habitats and for the strength of bottom-up effects and top-down they endure. A different response of pelagic and benthic organisms to temperature (e.g., activity budget) may explain the observed higher impact of the environmental contribution of the dragonfly larvae to the benthic variables compared to the pelagic variables. A major future objective will be to elucidate what makes the balance shifting from genetic to plastic (and vice versa) contributions to ecological dynamics, so as to improve our predictive capabilities.

5 | CONCLUSIONS

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

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AUTHORS' CONTRIBUTIONS

L.T., J.Cu., J.Co. and S.B. conceived and designed the experiment; L.T., F.F. and Y.B. collected the data and performed laboratory analyses; L.T., J.Co. and S.B. analysed the data; L.T., J.Co. and S.B. wrote the first drafts of the manuscript; J.Cu., F.F. and Y.B. commented and corrected the manuscript.

DATA ACCESSIBILITY

Data used in this manuscript are available at https://doi.org/10.6084/m9.figshare.7409561.v1 (Therry et al., 2018).

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REFERENCES

Alford, R. A., Brown, G. P., Schwarzkopf, L., Phillips, B. L., & Shine, R. (2009). Comparisons through time and space suggest rapid evolution of dispersal behaviour in an invasive species. *Wildlife Research*, *36*(1), 23–28. https://doi.org/10.1071/wr08021

Alp, M., Cucherousset, J., Buoro, M., & Lecerf, A. (2016). Phenological response of a key ecosystem function to biological invasion. *Ecology Letters*, *19*(5), 519–527. https://doi.org/10.1111/ele.12585

Aubret, F., & Shine, R. (2009). Genetic assimilation and the postcolonization erosion of phenotypic plasticity in Island Tiger Snakes. *Current Biology*, *19*(22), 1932–1936. https://doi.org/10.1016/j.cub.2009.09.061

Bassar, R. D., Marshall, M. C., Lopez-Sepulcre, A., Zandona, E., Auer, S. K., Travis, J., & Reznick, D. N. (2010). Local adaptation in Trinidadian guppies alters ecosystem processes. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(8), 3616–3621. https://doi.org/10.1073/pnas.0908023107

Bestion, E., Cucherousset, J., Teyssier, A., & Cote, J. (2015). Non-consumptive effects of a top-predator decrease the strength of the trophic cascade in a four-level terrestrial food web. *Oikos*, *124*(12), 1597–1602. https://doi.org/10.1111/oik.02196

Brockhaus, T. (2015). Findings of *Crocothemis erythraea* (Brullé, 1832) and *Orthetrum albistylum* (selys, 1848) in northern Poland. *Odonatrix*, *11*(2), 59–60.

Brunner, F. S., Anaya-Rojas, J. M., Matthews, B., & Eizaguirre, C. (2017). Experimental evidence that parasite drive eco-evolutionary feedbacks. *Proceedings of the National Academy of Sciences of the United States of America*, *114*, 3678–3683. https://doi.org/10.1073/pnas.1619147114

Chuang, A., & Peterson, C. R. (2016). Expanding population edges: theories, traits, and trade-offs. *Global Change Biology*, *22*(2), 494–512. https://doi.org/10.1111/gcb.13107

Corbet, P. S. (1999) *Dragonflies: Behaviour and ecology of Odonata*. Ithaca, NY: Cornell University Press.

Danchin, É., Charmantier, A., Champagne, F. A., Mesoudi, A., Pujol, B., & Blanchet, S. (2011). Beyond DNA: integrating inclusive inheritance into an extended theory of evolution. *Nature Reviews Genetics*, *12*(7), 475–486. https://doi.org/10.1038/nrg3028

De Block, M., Slos, S., Johansson, F., & Stoks, R. (2008). Integrating life history and physiology to understand latitudinal size variation in a damselfly. *Ecography*, *31*(1), 115–123. https://doi.org/10.1111/j.2007.0906-7590.05313.x

Des Roches, S., Post, D. M., Turley, N. E., Bailey, J. K., Hendry, A. P., Kinnison, M. T., … Palkovacs, E. P. (2018). The ecological importance of intraspecific variation. *Nature Ecology & Evolution*, *2*(1), 57. https://doi.org/10.1038/s41559-017-0402-5.

Dijkstra, K. D. B., & Lewington, R. (2006). *Field guide to the dragonflies of Britain and Europe: including western Turkey and north-western Africa*. Dorset, UK: British Wildlife Publishing.

Ducatez, S., Crossland, M., & Shine, R. (2016). Differences in developmental strategies between long-settled and invasion-front populations of the cane toad in Australia. *Journal of Evolutionary Biology*, *29*(2), 335–343. https://doi.org/10.1111/jeb.12785

El-Sabaawi, R. W., Bassar, R. D., Rakowski, C., Marshall, M. C., Bryan, B. L., Thomas, S. N., & Flecker, A. S. (2015). Intraspecific phenotypic differences in fish affect ecosystem processes as much as bottom–up factors. *Oikos*, *124*(9), 1181–1191. https://doi.org/10.1111/oik.01769

Fussmann, G. F., Loreau, M., & Abrams, P. A. (2007). Eco-evolutionary dynamics of communities and ecosystems. *Functional Ecology*, *21*(3), 465–477. https://doi.org/10.1111/j.1365-2435.2007.01275.x

Ghalambor, C. K., McKay, J. K., Carroll, S. P., & Reznick, D. N. (2007). Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional Ecology*, *21*(3), 394–407. https://doi.org/10.1111/j.1365-2435.2007.01283.x

Grigaltchik, V. S., Ward, A. J. W., & Seebacher, F. (2012). Thermal acclimation of interactions: differential responses to temperature change alter predator-prey relationship. *Proceedings of the Royal Society B-Biological Sciences*, *279*(1744), 4058–4064. https://doi.org/10.1098/rspb.2012.1277

Hardie, D. C., & Hutchings, J. A. (2010). Evolutionary ecology at the extremes of species' ranges. *Environmental Reviews*, *18*, 1–20. https://doi.org/10.1139/a09-014

Harmon, L. J., Matthews, B., Des Roches, S., Chase, J. M., Shurin, J. B., & Schluter, D. (2009). Evolutionary diversification in stickleback affects ecosystem functioning. *Nature*, *458*(7242), 1167–1170. https://doi.org/10.1038/nature07974

Hoffmann, A. A., & Sgrò, C. M. (2011). Climate change and evolutionary adaptation. *Nature*, *470*(7335), 479–485. https://doi.org/10.1038/nature09670

Hudson, J., & Berrill, M. (1986). Tolerance of low pH exposure by the eggs of Odonata (dragonflies and damselflies). *Hydrobiologia*, *140*(1), 21–25. https://doi.org/10.1007/BF00006725

Kivelä, S. M., Välimäki, P., Carrasco, D., Mäenpää, M. I., & Oksanen, J. (2011). Latitudinal insect body size clines revisited: a critical evaluation of the saw-tooth model: Insect body size clines revisited. *Journal of Animal Ecology*, *80*(6), 1184–1195. https://doi.org/10.1111/j.1365-2656.2011.01864.x

Lowe, W. H., Kovach, R. P., & Allendorf, F. W. (2017). Population genetics and demography unite ecology and evolution. *Trends in Ecology and Evolution*, *32*, 141–152. https://doi.org/10.1016/j.tree.2016.12.002

Lundsgaard-Hansen, B., Matthews, B., & Seehausen, O. (2014). Ecological speciation and phenotypic plasticity affect ecosystems. *Ecology*, *95*(10), 2723–2735. https://doi.org/10.1890/13-2338.1

Matthews, Blake, Aebischer, T., Sullam, K. E., Lundsgaard-Hansen, B., & Seehausen, O. (2016). Experimental evidence of an eco-evolutionary feedback during adaptive divergence. *Current Biology*, *26*(4), 483–489. https://doi.org/10.1016/j.cub.2015.11.070

Matthews, B., Narwani, A., Hausch, S., Nonaka, E., Peter, H., Yamamichi, M., & Turner, C. B. (2011). Toward an integration of evolutionary biology and ecosystem science. *Ecology Letters*, *14*(7), 690–701. https://doi.org/10.1111/j.1461-0248.2011.01627.x

Neyeloff, J. L., Fuchs, S. C., & Moreira, L. B. (2012). Meta-analyses and forest plots using a microsoft excel spreadsheet: Step-by-step guide focusing on descriptive data analysis. *BMC Research Notes*, *5*(1), 52. https://doi.org/10.1186/1756-0500-5-52

Ott, J. (2007). The expansion of Crocothemis erythraea (Brullé, 1832) in Germany – an indicator of climatic changes. In Odonata – Biology of Dragonflies. (Scientific Publishers). Indi: Tyagi BK.

Pantel, J. H., Duvivier, C., & De Meester, L. (2015). Rapid local adaptation mediates zooplankton community assembly in experimental mesocosms. *Ecology Letters*, *18*(10), 992–1000. https://doi.org/10.1111/ele.12480

Phillips, B. L. (2009). The evolution of growth rates on an expanding range edge. *Biology Letters*, *5*(6), 802–804. https://doi.org/10.1098/rsbl.2009.0367

Raffard, A., Lecerf, A., Cote, J., Buoro, M., Lassus, R., & Cucherousset, J. (2017). The functional syndrome: Linking individual trait variability to ecosystem functioning. *Proceedings of the Royal Society B*, *284*(1868), 20171893. https://doi.org/10.1098/rspb.2017.1893

Raffard, A., Santoul, F., Cucherousset, J., & Blanchet, S. (2018). The community and ecosystem consequences of intraspecific diversity: A meta-analysis. *Biological Reviews*. In press. https://doi.org/10.1111/brv.12472

Rosenberg, M. S., Adams, D. C., & Gurevitch, J. (2000). *MetaWin: Statistical software for meta-analysis with resampling tests*. Sunderland, MA: Sinauer Associates.

Rudman, S. M., Rodriguez-Cabal, M. A., Stier, A., Sato, T., Heavyside, J., El-Sabaawi, R. W., & Crutsinger, G. M. (2015). Adaptive genetic variation mediates bottom-up and top-down control in an aquatic ecosystem. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1812), 20151234. https://doi.org/10.1098/rspb.2015.1234

Schmitz, O. J., Beckerman, A. P., & O'Brien, K. M. (1997). Behaviorally mediated trophic cascades: Effects of predation risk on food web interactions. *Ecology*, *78*(5), 1388–1399. https://doi.org/10.1890/0012-9658

Schulte, P. M., Healy, T. M., & Fangue, N. A. (2011). Thermal performance curves, phenotypic plasticity, and the time scales of temperature

exposure. *Integrative and Comparative Biology*, *51*(5), 691–702. https://doi.org/10.1093/icb/icr097

Shurin, J. B., Borer, E. T., Seabloom, E. W., Anderson, K., Blanchette, C. A., Broitman, B., & Halpern, B. S. (2002). A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters*, *5*(6), 785–791. https://doi.org/10.1046/j.1461-0248.2002.00381.x

Stoks, R., Swillen, I., & De Block, M. (2012). Behaviour and physiology shape the growth accelerations associated with predation risk, high temperatures and southern latitudes in Ischnura damselfly larvae. *Journal of Animal Ecology*, *81*(5), 1034–1040. https://doi.org/10.1111/j.1365-2656.2012.01987.x

Suhling, I., & Suhling, F. (2013). Thermal adaptation affects interactions between a range-expanding and a native odonate species. *Freshwater Biology*, *58*(4), 705–714. https://doi.org/10.1111/fwb.12074

Tachet, H., Richoux, P., Bournaud, M., & Usseglio-Polatera, P. (2010) *Invertébrés d'eau douce: Systématique, biologie, écologie*. CNRS Edition.

Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., & Burthe, S., … Wanless, S. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, advance online publication *535*, 241–245. https://doi.org/10.1038/nature18608

Therry, L., Cote, J., Cucherousset, J., Finn, F., Buoro, Y., & Blanchet, S. (2018). Data from: Genetic, plastic and environmental contributions to the impact of a range-expanding predator on aquatic ecosystems. *Figshare*, https://doi.org/10.6084/m9.figshare.7409561.v1

Therry, L., Lefevre, E., Bonte, D., & Stoks, R. (2014). Increased activity and growth rate in the non-dispersive aquatic larval stage of a damselfly at an expanding range edge. *Freshwater Biology*, *59*(6), 1266–1277. https://doi.org/10.1111/fwb.12346

Therry, L., Nilsson-Oertman, V., Bonte, D., & Stoks, R. (2014). Rapid evolution of larval life history, adult immune function and flight muscles in a poleward-moving damselfly. *Journal of Evolutionary Biology*, *27*(1), 141–152. https://doi.org/10.1111/jeb.12281

Tilman, D. (2001). An evolutionary approach to ecosystem functioning. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(20), 10979–10980. https://doi.org/10.1073/pnas.211430798

Vanni, M. J. (2002). Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology and Systematics*, *33*(1), 341–370. https://doi.org/10.1146/annurev.ecolsys.33.010802.150519

Yoshida, T., Jones, L. E., Ellner, S. P., Fussmann, G. F., & Hairston, N. G. J. (2003). Rapid evolution drives ecological dynamics in a predator–prey system. *Nature*, *424*(6946), 303–306. https://doi.org/10.1038/nature01767

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