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ECOSYSTEM ECOLOGY – ORIGINAL RESEARCH

Contrasting ecological impacts of geographically close invasive populations

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Abstract

Intraspecific trait variability is now well recognized as a key component of biodiversity explaining how individuals within a species can differentially interact with their environment. To date, however, this concept has rarely been incorporated in the study of biological invasions, despite its provision of new insights into invasive species management. Here, we used an experimental approach to investigate how invasive red swamp crayfish (*Procambarus clarkii*) derived from geographically close ecosystems can differentially impact prey community structure and relevant ecosystem processes. We also compared the magnitude of the effects induced by invasive species introduction with those induced by intraspecific variability. Our results showed that effects of intraspecific variability can be strong for direct interactions such as resource (e.g., leaf litter, snails) consumption and of similar magnitude to the effects induced by the introduction of the invasive species when considering indirect interactions (e.g., primary production, ecosystem metabolism). Overall, these results highlighted that invasive populations of the same species are not ecologically equivalent, with each population acting differently on their recipient ecosystem.

Keywords Biological invasions · Intraspecific variation · Ecosystem functioning · *Procambarus clarkii* · Ecological impacts

Introduction

Invasive species are a major threat to biodiversity and ecosystem services as they induce strong ecological impacts across all levels of biological organization (Clavero and García-Berthou 2005; Cucherousset and Olden 2011; Simberloff et al. 2013). This notably includes disruption of the native communities and alterations of ecosystem functioning through predation, competition or ecological engineering (Matsuzaki et al. 2009; Strayer 2010). The literature has primarily focused on evaluating species-specific impacts of invaders (Dunoyer et al. 2014; Jackson et al. 2014; Twardochleb et al. 2013), but an increasing number of studies have showed that both intrinsic (e.g., phenotypic traits; Phillips and Shine 2006; Cote et al. 2017) and extrinsic (e.g., environmental conditions; Jokela and Ricciardi 2008; Ruokonen et al. 2014) factors may modulate the effects of an invasive species. The context-dependence of invader impacts must be considered when developing a sound understanding of the consequences of novel biotic interactions and designing appropriate management strategies (Britton et al. 2011; Kumschick et al. 2014). Elucidating the reasons for spatial and temporal variation of impacts is of utmost importance if we are to predict when and where impacts might be most deleterious.

Recent studies have called for explicitly considering intraspecific phenotypic diversity in biological invasions (Forsman 2014; Juette et al. 2014; González-Suárez et al.

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2015; Cote et al. 2017; Závorka et al. 2018b). This intraspecific diversity may ensure successful establishment and rapid spread of newly introduced species because, during the multi-stage process of invasion (i.e., transport and introduction, establishment and spread), transition from one stage to another may be restricted to specific phenotypes (Chapple et al. 2012; Juette et al. 2014). Such non-random trait selection produces phenotypic variations among populations at large spatial scale as we move from where the invaders first established to the invasion fronts (Phillips et al. 2006; Brandner et al. 2013; Gruber et al. 2017). In addition, populations located in a restricted area often experience heterogeneous environments that may, in turn, produce local-scale patterns of within-species trait variability due to phenotypic plasticity or local adaptation (Bolnick et al. 2011; Violle et al. 2012; Richardson et al. 2014). Indeed, different levels of predation pressure and intraspecific competition are well-documented drivers of intraspecific variability (Araújo et al. 2011), highlighting the role of environmental conditions in mediating such variability at local scales (Jackson et al. 2017). Therefore, invasive populations located within a fairly narrow geographical range with divergent habitat characteristics would be composed of phenotypically distinct individuals. The logical next step is to examine whether these distinct populations differentially affect invaded ecosystems.

Phenotypic variability is inherent to biological invasions and may be linked to variable ecological impacts (Cote et al. 2010, 2017; Raffard et al. 2017; Závorka et al. 2018b). Experimental studies have demonstrated the importance of intraspecific trait variability on community structure and ecosystem functioning (reviewed in Des Roches et al. 2018; Raffard et al. 2018). These effects of intraspecific variability can be as strong, or even stronger, than the ecological impacts of the removal or addition of the species itself (Des Roches et al. 2018) and can be transmitted by both trophic and non-trophic interactions. A recent study has found that trophic niche variation between invasive populations of pumpkinseed sunfish (*Lepomis gibbosus*) alter nutrient-mediated effects of individuals on ecosystem functioning (Evangelista et al. 2017). Altogether, these findings strongly suggest that, regardless of the mechanisms driving within-species variability, assessing the relative incidence of intraspecific variability compared to species introduction is particularly relevant in the context of biological invasions.

The aim of the present study was to investigate how the ecological impact of a global invader, the red swamp crayfish *Procambarus clarkii*, can vary among populations inhabiting lakes of contrasting environmental conditions. This omnivorous crayfish has strong impacts on recipient ecosystems through consumption of both primary producers and consumers (Twardochleb et al. 2013; Alp et al. 2016). We selected red swamp crayfish from four natural populations established along a gradient of lake maturity to experimentally quantify population-dependent ecological impacts in mesocosms. The process of ecosystem maturation was mainly characterized by increasing lake age and productivity, fish predation pressure and non-native species biomass. The abundance of crayfish decreased with ecosystem maturity (Zhao et al. 2016; Appendix A). Therefore, the more mature lakes had been colonized by invasive red swamp crayfish for longer. We predicted that the introduction of *P. clarkii* would impact the structure of prey communities and the functioning of the recipient ecosystem, but that the magnitude of these effects would vary between invasive populations. We compared the intensity of the impacts induced by invasive species introduction (invasion effect) to those induced by variability among populations (intraspecific effect). Although intraspecific effects are expected to be equivalent or even larger than species effects, their relative importance may depend on the phenotypic trait of interest (Palkovacs et al. 2015; Des Roches et al. 2018).

Materials and methods

Experimental design

In early September 2015, outdoor mesocosms (circular cattle tanks; 550 L, 0.63 m deep, 1.28 m diameter) were arranged in a 4 × 5 array. Each mesocosm was prepared with a 2 cm thick layer of clean gravel as a substrate, filled with 350 L of dechlorinated water and inoculated with 2 L of unfiltered water from a local gravel pit lake containing autotrophic and heterotrophic plankton. In each mesocosm, five pieces of PVC pipe (20 cm long, 5 cm outer diameter) and two halves of alveolar construction brick (15 cm deep, 50 cm long, 15 cm wide) were provided as shelters for crayfish. Mesocosms were supplied with freshwater snails (*Physa*; 16 individuals with similar size per mesocosm) from local ponds and litter-colonizing invertebrates (mainly Chironomidae and Caenidae larvae) collected by means of litterbags containing 5 g of air-dried leaf litter mixture (alder *Alnus glutinosa* and oak *Quercus robur*), submerged in a local gravel pit lake for 20 days. A floating macrophyte (*Ceratophyllum* sp.; mean = 20.50 ± 0.22 g fresh biomass) collected from local ponds and a mixture of dried leaves (mean = 20.32 ± 0.16 g air-dried mass) of *Alnus glutinosa* and *Q. robur* were added to the mesocosms. Two unglazed ceramic tiles (5 × 5 cm) were placed on the bottom to estimate benthic chlorophyll-*a* accrual (Steinman et al. 2006). Finally, each mesocosm was covered with a 0.5-mm nylon net and given 30 days to mature before the start of the experiment.

Experimental crayfish originated from four gravel pit lakes located in the Garonne river catchment (southwestern France; mean distance between lakes: 22 km ± 5 SE).

In the studied area, the establishment of red swamp crayfish occurred approximately in 1995 (Changeux 2003) and this invasive species is the largest benthic invertebrate inhabiting lakes. In addition, colonization of gravel pit lakes by red swamp crayfish occurs relatively rapidly after the start of gravel extraction. Therefore, red swamp crayfish is often among the first macro-organisms to colonize these new ecosystems where it has been reported to induce conspicuous changes in ecosystem functioning (Alp et al. 2016). Gravel pit lakes usually formed a vast network of novel freshwater ecosystems highly variable in terms of age and particularly threatened by biological invasions (Zhao et al. 2016; Mollema and Antonellini 2016). Dredging activity has incrementally shaped the landscape creating a gradient of environmental conditions, with old lakes being typically more productive, shallower and more species-rich than recent lakes (Zhao et al. 2016; Appendix A). This gradient of lake ecosystem characteristics provided a unique opportunity to study whether spatially close populations were functionally different. The four studied lakes were selected to encompass different environmental conditions: lake A was the youngest and least productive, lake D was the oldest and most productive lake, while lakes B and C had intermediate characteristics (Appendix A). The more mature lakes were associated with fewer red swamp crayfish and higher biomass of predatory fish species due to management practices favouring sport fishing species (Appendix A; Zhao et al. 2016)

Adult crayfish were collected from 29 September 2015 to 30 September 2015 using baited traps set overnight. Specifically, traps with different mesh-size and shape were placed in different habitats of each lake to ensure collecting a representative body size distribution of crayfish within each population. The same sampling protocol was consistently used for the four populations to ensure comparability and to account for local environmental conditions (i.e., high turbidity). Individuals from each of the four lakes were kept in separate tanks until the beginning of the experiment (02 October 2015). The experiment consisted of four replicate blocks of five mesocosms randomly assigned to one of five treatments: crayfish originating from lakes A, B, C, and D, and no crayfish. A density of 3.1 ind. m^{-2} ($n = 4$ crayfish per mesocosm) was chosen to fall within the range of red swamp crayfish density reported in the wild (Gherardi and Lazzara 2006). Individuals used in the experiment were selected to minimize differences in carapace length (CL ± 0.1 mm) between mesocosms. However, due to differences in size structure between the focal populations, mean carapace length differed slightly among treatments ($CL_A = 44.8$ mm ± 0.8 SE; $CL_B = 46.6 \pm 0.8$ SE; $CL_C = 47.1 \pm 0.8$ SE; $CL_D = 48.4$ mm ± 1.3 SE), but the difference in mean carapace length was < 4 mm. Natural sex ratio variations also occurred between populations (% males: 82%, 30%, 83%, and 76% for lakes A, B, C, and D, respectively) and it was not possible to keep it constant across treatments. One female and three males were added in mesocosms assigned to treatments A, C, and D and three females and one male were used for treatment B. Although sex ratio variations can affect ecosystem functioning (Fryxell et al. 2015), further analyses indicated that this did not drive variation in the response variables in our study (Appendix B).

Five individuals died during the experiment and were immediately replaced with equivalent individuals. At the end of the experiment, three crayfish were found missing during the sampling procedure (5-Nov-2015) in three mesocosms (one from lake C and two from lake D) as they probably molted during the experiment and were eaten by conspecifics.

Sampling procedure and response variables

Community-level respiration (molC m^{-2} d^{-1}) was assessed 1 week before the end of experiment (from 28 October–30 October) using the diel oxygen technique (Staehr et al. 2010). HOBO® U26 dataloggers were set in mesocosms over the night-time periods to record dissolved oxygen concentration and water temperature every 15 min. As only five dataloggers were available, blocks of mesocosms were monitored one at a time on four consecutive days of dry weather. Piston velocity (i.e., the reaeration constant used to estimate the rate of gas exchange between water surface and atmosphere) was set to 0.036 m d^{-1}, a low value reflecting the fact that mesocosms were not influenced by wind.

Benthic and pelagic algal biomass were estimated at the end of the experiment using chlorophyll-*a* contents (µg chl-*a* cm^{-2} and µg chl-*a* L^{-1}, respectively). Benthic tiles were scrubbed and rinsed to detach algal mats which were immediately collected onto a Whatman GF/F filter (pore size 0.7 µm). Filters were stored in the dark at − 20 °C until analyses. Chlorophyll-*a* was then extracted with 90% acetone for 24 h and its concentration determined spectrophotometrically (Steinman et al. 2006). Pelagic chlorophyll-*a* was determined in situ using a portable fluorescent photometer (BBE-Moldaenke, Kiel, Germany).

Coarse particulate organic matter (CPOM) remaining in mesocosms at the end of the experiment was collected using a hand net, and sorted to either macrophyte fragments or leaf litter, oven-dried (60 °C for 48 h) and weighed. Change in macrophyte mass (% dry mass change) was computed using initial dry mass values estimated from the relationship between air- and oven-dried masses from four extra batches of macrophytes. Daily decomposition rate of leaf litter (*k*, day^{-1}) was computed using the simple negative exponential decay model (Petersen and Cummins 1974).

Fine particulate organic matter (FPOM) and invertebrates were sampled once all of the other sampling procedures had been completed. First, deposited material was re-suspended and homogenized by stirring vigorously the water with a wooden handle for 30 s. A 2 L water sample was immediately collected in a plastic jar and then filtered onto a pre-ashed, pre-weighed glass fiber filter (Whatman GF/A). Filters were ashed (480 °C, 3 h) to determine the total amount of organic matter content (FPOM; g AFDM). Second, a representative sample of benthic invertebrates was collected from each mesocosm. The wall of the mesocosm was gently rubbed to dislodge attached invertebrates and the wooden handle was used to disturb the invertebrates of the bottom sediment. Organisms were kept suspended by stirring the water of the mesocosm while pulling the handnet circularly along the side of the mesocosm few centimeters above the bottom. Invertebrate samples were then preserved in ethanol and a total of eight taxa (Chironomidae, Ostracoda, Caenidae, Odonata, Corixidae, Trichoptera, Baetidae, and *Physa*) were identified under a stereomicroscope. The Shannon diversity index was then calculated based on abundance data.

Statistical analysis

The effects of invasion and intraspecific variations were quantified using orthogonal contrasts. The effect of invasion was assessed by comparing the control treatment (no crayfish) to the mean value of all the treatments containing crayfish (A through D). The effect of intraspecific variation was assessed using a set of orthogonal contrasts depicted using Helmert coding. Specifically, lakes were arranged according to their position along the environmental gradient ($A < B < C < D$; Appendix A) and each lake position was compared to the mean of the subsequent levels. Cohen's *d* was then calculated for each response variable and used to compare the magnitudes of the effects between those mesocosms containing crayfish and the controls (Palkovacs et al. 2015), with confident intervals computed following Nakagawa and Cuthill (2007).

Permutational multivariate analysis of variance (PERMANOVA, *adonis* function from R package 'vegan' v.2.4.3) was performed to test the effects of species invasion and intraspecific variability (i.e., the two contrasts), and a block effect was included to control for spatial variation among mesocosms. The response consisted of an Euclidean distance matrix including both community and ecosystem variables. Pelagic algal biomass, macrophyte mass change and decomposition rate were $\log_{10}$-transformed to reduce skewness of the data distributions. To standardize the dataset, all independent variables were centered to the mean and scaled to unit variance (Murray and Connor 2009). Statistical test indicated that there was no deviation from multivariate dispersion ($P = 0.939$; *betadisper* function from R package 'vegan' v.2.4.3, Oksanen et al. 2017).

To assess the influence of lake characteristics from which a crayfish originated on responses of direct resource consumption (i.e., invertebrate abundances, macrophyte mass change and leaf litter decomposition), the effect size was correlated with the first axis of a PCA of lake features which corresponded with lake maturity (i.e., higher TSI, total phosphorus and chlorophyll-*a* concentrations and lower Secchi depth; Appendix A) using Spearman rank correlations. All statistical analyses were performed using R v.3.4.3 (R Development Core Team 2017).

Results

Community and ecosystem response variables were significantly affected by the introduction of invasive crayfish (PERMANOVA; $P = 0.001$, $R^2 = 0.24$; Table 1). Invasion effect sizes (grand mean $d_{\text{inva}} = 1.56 \pm 1.02$ SE) were usually > 0.8 (Fig. 1) and varied over a 11-fold range. The introduction of invasive crayfish induced resource depletion as suggested by the significant reduction of invertebrate prey abundance (snail and chironomid: $d_{\text{inva}} = -1.17$; 95% CI -2.18 to -0.17 and -2.17 to -0.17, respectively) and macrophyte ($d_{\text{inva}} = -3.38$; 95% CI -4.83 to -1.94), and by the increase in both leaf litter decomposition rate ($d_{\text{inva}} = +3.05$; 95% CI $+1.69$ to $+4.42$) and FPOM production ($d_{\text{inva}} = +1.28$; 95% CI $+0.26$ to $+2.30$), in mescososms with invasive crayfish compared to those without (Fig. 2). Primary production increased with addition of invasive crayfish (pelagic primary production: $d_{\text{inva}} = +1.28$; benthic primary production: $d_{\text{inva}} = +0.73$) but only the pelagic production was significantly affected by crayfish (95% CI $+0.60$ to $+2.75$ and -0.23 to $+1.69$, respectively). Finally, the introduction of invasive crayfish significantly decreased community respiration ($d_{\text{inva}} = -1.26$; 95% CI -2.27 to -0.24) but had no significant effect on Shannon diversity index ($d_{\text{inva}} = +0.59$; 95% CI -0.62 to $+1.24$).

The effect of invasive crayfish on both prey community and ecosystem responses significantly varied between populations (PERMANOVA; $P = 0.022$, $R^2 = 0.20$; Table 1). The

Table 1 Summary of PERMANOVA results

Source	*df*	Mean square	*F*	R^2	*P*
Invasion	1	42.8	7.12	0.24	**0.001**
Intraspecific	3	12.1	2.02	0.20	**0.022**
Block	3	9.6	1.59	0.16	0.112
Residuals	12	6.0	–	0.40	–
Total	19	–	–	1.00	–

Significant *P* values are displayed in bold. 'Invasion' contrast tests the effect of invasive species introduction; 'Intraspecific' contrast tests for the effect of intraspecific variability on response variable matrix

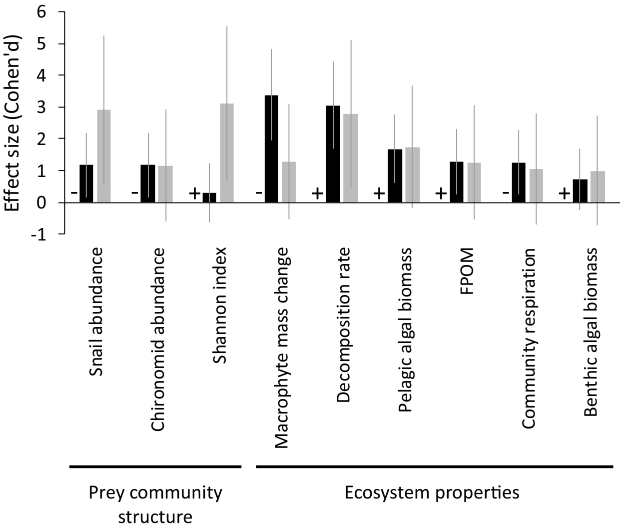


Fig. 1 Magnitude (Cohen's *d*, unsigned value) of the ecological changes induced by red swamp crayfish invasion (black bars) vs. intraspecific variability (i.e., the maximal difference across populations, grey bars). The direction of the effect size of crayfish invasion is indicated with positive or negative symbols next to black bar. Response variables for prey community and ecosystem properties are sorted based on the value of the invasion effect sizes (from the highest to the lowest value). Error bars indicate the 95% confidence interval (CI) for the mean effect size calculated following Nakagawa and Cuthill (2007)

magnitude of this intraspecific difference compares well with the magnitude of the effect of crayfish invasion (mean $d_{\text{intra}} = 1.81 \pm 0.87$ SE vs. mean $d_{\text{inva}} = 1.56 \pm 1.02$ SE). For prey community responses, the effect sizes for intraspecific variability were up to ten times greater than for crayfish invasion (mean $d_{\text{intra}} = 2.39 \pm 1.06$ SE; mean $d_{\text{inva}} = 0.88 \pm 0.50$ SE). For ecosystem responses, effect sizes revealed that intraspecific differences (mean $d_{\text{intra}} = 1.52 \pm 0.68$ SE) were, except for macrophyte mass change, equivalent to those induced by crayfish invasion (Fig. 1).

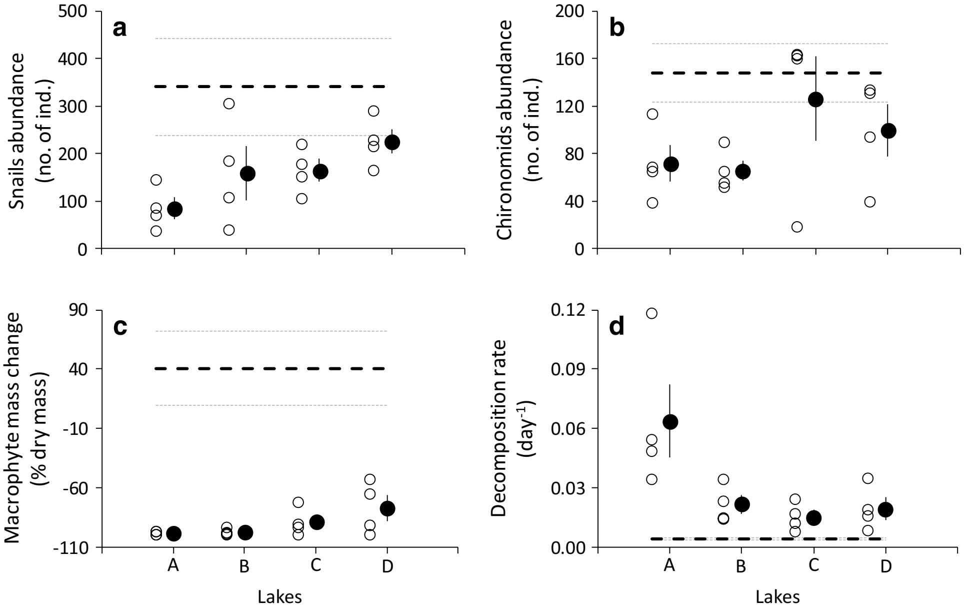
The abundance of snails and macrophyte mass change significantly increased along the environmental gradient formed by the lakes where crayfish originated (Spearman correlations; $\rho = 0.64$, $P = 0.007$ and $\rho = 0.53$, $P = 0.037$, respectively; Fig. 2). The rate of leaf decomposition significantly decreased along this gradient ($\rho = -0.56$, $P = 0.025$) whereas no trend was observed for the abundance of chironomids ($\rho = 0.32$, $P = 0.225$; Fig. 2b).

Discussion

The present study provides, to our knowledge, the first evidence for strong variations in the ecological impacts of invasive populations inhabiting contrasting environments within a narrow geographical range (i.e., within a radius of 20 km). Resource depletion, for instance, varied widely among experimental populations, presumably as a result of variable rates of direct consumption. Our results also showed that the effects of intraspecific variability on prey community were often greater than overall species effects, while intraspecific effects on ecosystem responses were mainly of similar magnitude to overall species affects.

Only one (i.e., macrophyte mass change) out of the 9 variables measured here displayed an unambiguously stronger response to crayfish introduction than intraspecific effects. This aligns well with the main trend reported by Des Roches et al. (2018) who summarized data from 25 different studies

Fig. 2 Response of prey community and ecosystem properties to red swamp crayfish originating from lakes (A, B, C, and D) ordered by increasing level of ecosystem maturity (see "Materials and methods"). **a** Snails and **b** chironomids abundances (number of individuals), **c** macrophyte mass change (% dry mass) and **d** leaf litter decomposition rate (day^{-1}). Open circles represent each mesocosm and solid circles represent the mean values (± SE) for each treatment. The black dashed line represents the mean value ($n = 4$) of the control mesocosms (no crayfish); the grey band represents the standard error of the mean



and found that intraspecific effects were not negligible compared to species effects. Macrophyte depletion by crayfish in mesocosms was likely due to direct resource consumption (Twardochleb et al. 2013), a type of interaction whose strength is thought to be more dependent on species effects than intraspecific effects (Des Roches et al. 2018). By contrast, snail abundance and litter decomposition rate were strongly affected by intraspecific variability, indicating that direct resource consumption is not always associated with the prevalence of species effects. Therefore, considerable efforts should be pursued to quantify the relative importance of intraspecific vs. species effects in shaping the ecological impacts of invaders. To go further, it would be interesting to investigate the magnitude of species-specific effects to those induced by intraspecific variability. This would be particularly relevant to study in organisms such as crayfish which display well-documented intraspecific trait variability (e.g., Pintor et al. 2008; Biro et al. 2014; Raffard et al. 2017), as well as clear species-specific effects on recipient ecosystems (e.g., Dunoyer et al. 2014; Jackson et al. 2014; Twardochleb et al. 2013).

Intraspecific variability of per capita rate of resource consumption can have produced the population-dependent effects of red swamp crayfish on invertebrate community structure and ecosystem functioning. This hypothesis is based on observations reporting substantial inter-individual variations (> fourfold range) in predation rate and leaf consumption rate in this crayfish species (Raffard et al. 2017). These authors further demonstrated that intraspecific variability in resource consumption rate was largely independent of body size. Although trophic niche variability can occur among adult crayfish through changes in diet composition (Jackson et al. 2017), our results suggested that diet variability was likely related to different levels of voracity since individuals from the four studied populations reduced stocks of all three main resource items (i.e., snails, macrophytes, and leaf litter). However, accurate estimation of diet composition cannot be derived from our data, precluding conclusions about intraspecific trophic niche variability.

Metrics depicting the consumption of snails, macrophytes, and leaf litter by crayfish indicated that, as lakes get more mature, crayfish consumed resources at slower rates. This trend is expected if the lake gradient correlated with the time since invasion as red swamp crayfish is an early colonizer. The success of invaders depends on their assertiveness in a recently invaded environment, suggesting that first colonizers would have strongest abilities to invade and impact the recipient habitat (Duckworth and Badyaev 2007). When new invaders successfully establish in a novel habitat, population size rapidly increases in the first generations following invasion and this would require phenotypic traits that provide access to a large amount of resources (e.g., aggressiveness and high foraging activity) (Cote et al. 2017). Such a fast-paced lifestyle may prevail in younger and less productive lakes also because of low predator abundance. In contrast, phenotypes associated with low individual energy expenditure and foraging activity conceivably confer fitness advantage in mature lakes wherein predation pressure is high (Réale et al. 2010; Zhao et al. 2016). Intraspecific variability may also be driven by different levels of intraspecific competition and resource availability across lakes (Araújo et al. 2011; Costa-Pereira et al. 2018).

Our study indicated that intraspecific variability in invasive species can mediate the impacts of invaders on recipient ecosystems and this intraspecific effect was far from being negligible. Crayfish from young and recently invaded lakes had greatest impacts on the aquatic ecosystem than those from lakes invaded for a longer time. This suggests that traits selected for during invasion process (i.e., functional response traits) and those that modulate the ecological impacts of invasive species (i.e., functional effects traits) vary in a coordinated manner (Díaz et al. 2013; Raffard et al. 2017; Závorka et al. 2018a). Achieving a better understanding of patterns and determinants of covariations between response and effect traits should enhance our ability to predict where and when an invader will have the strongest ecological impacts.

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Author contribution statement CE, AL and JC conceived and designed the experiment. CE led the experiment. CE and AL performed the statistical analyses. CE, AL and JC wrote the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethics Authorizations to perform this study were provided by the "Arrêté Préfectoral—from 18/09/2015 to 30/10/2015".

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