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Changes in the aquatic macroinvertebrate communities throughout the expanding range of an invasive anuran

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ABSTRACT

Invasive species are among the most significant threats to biodiversity. They have direct and indirect effects on the colonized environments including the alteration of food webs structure by predation. Thus, the diet of invasive animal populations, and its effects on trophic networks, is a crucial factor that must be considered in the context of global change. In this study, we focused on the invasive population of the African clawed frog, *Xenopus laevis* in France, and compared the composition of the aquatic macroinvertebrate communities in colonized ponds of the core and the edge of the population range, as well as in surrounding areas. While previous studies recorded a broad diet of invertebrate and a low selectivity of prey items, they failed to identify the prey categories the most strongly affected. Here, we report a significant decrease in the proportion of nektonic macroinvertebrates in ponds occupied by *X. laevis*. Interestingly, this effect is not significant when evaluating the density of each taxonomic category of nektonic invertebrate separately. This result, combined with the existing literature, suggests that *X. laevis* preferably consumes large nektonic items first when it arrives at a new site and subsequently focuses on smaller planktonic or benthic prey after the proportion of nekton has been reduced.

The expansion of invasive species is one of the main drivers of the current biodiversity decline (Collins and Storfer, 2003). Native communities are impacted by invasive species through several mechanisms, *e.g.* predation, competition, the spread of new diseases, and habitat modifications (Ricciardi and Cohen, 2007). Discriminating the causes and consequences of a successful invasion by a species is a challenge in conservation biology (Pagnucco and Ricciardi, 2015). In this study, we compared the densities of the main prey classes of an invasive predator (Courant et al., 2017), the African clawed frog, *Xenopus laevis*, in relation to the duration of occupancy of this invasive species in the environment. This frog is currently known as one of the most harmful invasive amphibians (Kumschick et al., 2017). It is known to have negative effects on native amphibian populations in California (Wilson et al., 2017), Sicily (Lillo et al., 2011) and France (Courant et al., 2018). To date, this species has not been reported to alter the diversity or composition of aquatic invertebrate communities, although they represent their main prey classes (Courant et al., 2017). According to Courant et al. (2017) the species only consumes nektonic prey in large proportions in native populations, suggesting that a strong shift occurs in the proportions of ecological categories consumed by *X. laevis* in invasive populations. Thus, we put forward the hypothesis that, in the invaded areas, this shift is related to a preferential consumption of nektonic prey resulting in a decrease in the environment after the colonization by *X. laevis*.

The study took place in Western France where *X. laevis* was accidentally introduced during the late 1980s (Fouquet, 2001). It has colonized a part of the Deux-Sèvres and Maine-et-Loire departments and its range was estimated at 207 km^2 in 2012 (Measey et al., 2012). Data sampling occurred during May 2014, in the period of the year when most of the aquatic invertebrates are in their aquatic larval stage (Tachet et al., 2006). For this study, we selected 30 ponds, with 10 ponds at the range core, 10 ponds at the range edge, and 10 ponds outside of the range of *X. laevis* (Fig. 1). To reduce variability in the results due to external factors, we selected ponds according to their main characteristics (in pasturelands, with a surface under 500 m^2, with no fish detected, far from crop cultures, towns and large roads), which induced a reduced variability between the groups of ponds (Table 1). The presence/absence of *X. laevis* was checked with submerged fykes (60 cm length × 30 cm width, 6 mm mesh diameter) with a capture effort fixed at one trap per 50 m^2 of water during three consecutive nights, just after the collection of aquatic invertebrate data. The data collection of aquatic invertebrates consisted in a standardized hand net sampling (net dimensions: 30 cm width, 30 cm depth, 2 mm mesh), with a capture duration proportional to the accessible surface of the pond (10 min for 50 m^2). Invertebrates were immediately put in formaldehyde and left

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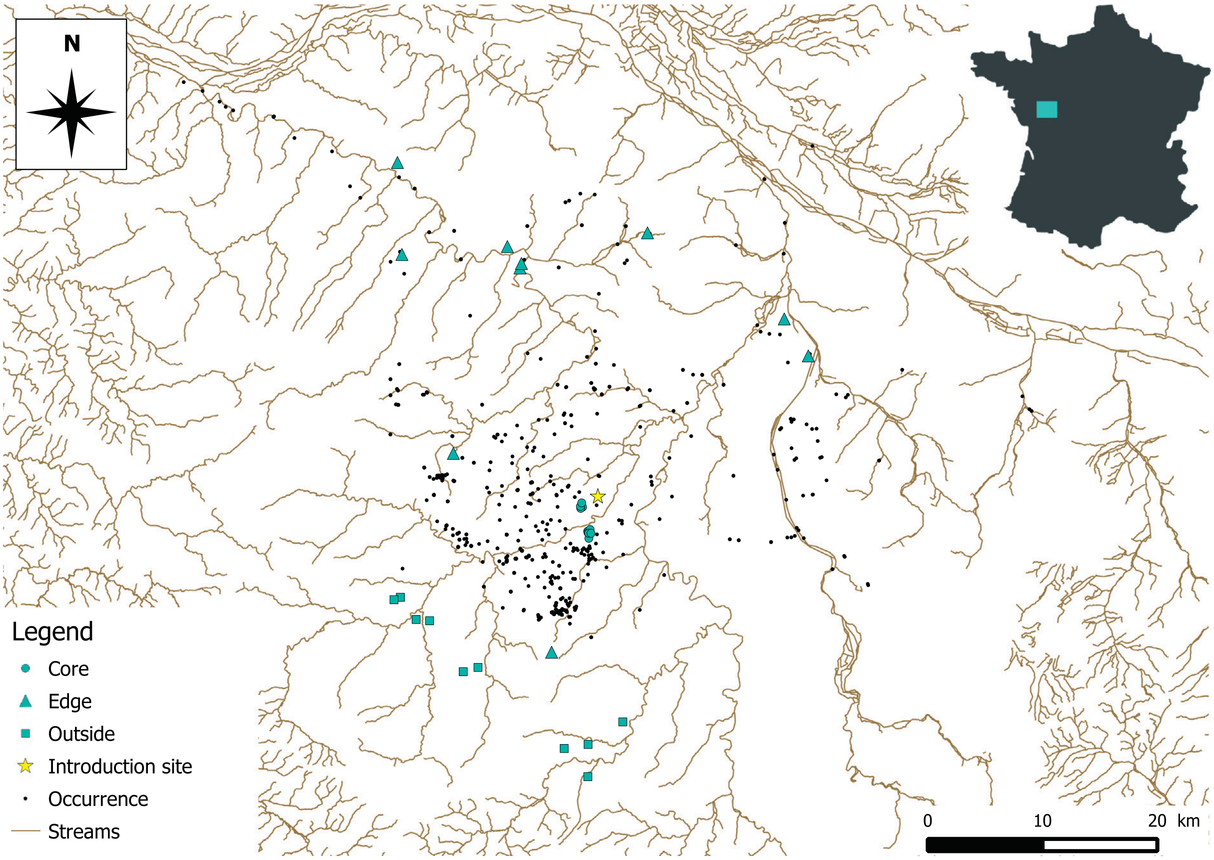

Fig. 1. Location of the sites used in this study at the range core (blue circles), the range edge (blue triangles), and outside (blue squares) of the invasive population of *Xenopus laevis* in France. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

there for 24 h, before being transferred in 70% ethanol. Samples were transferred to the laboratory and identified using a binocular microscope (Leica Wild M3Z). Aquatic invertebrates were identified to the lowest taxonomic level possible, using the identification key of Tachet et al. (2006). This identification key was also used to classify the macroinvertebrates into two ecological classes: the benthos (Acheta, Bivalvia, Diptera, Ephemeroptera, Gastropoda, Isopoda and Trichoptera) and the nekton (Coleoptera, Heteroptera and Odonata). During invertebrate identification, we retained the lowest common taxonomic level (*i.e.* the Order) that could be identified for all prey items. The significance of the changes in normalized densities of nektonic and benthic categories between areas was tested using a linear mixed model, with the area and the ecological class as predictors, and the pond nested in the area (core, edge, outside) as random variable. Densities were normalized by dividing the density of each prey category at each site by the maximal density of the sample. Fisher exact tests were performed to assess the significance of the changes in proportions, calculated as the sum of each ecological category (nekton and benthos), between each area. All statistical analyses were performed with R (R Core Team, 2017) and the linear mixed models were built with R and the "nlme" package (Pinheiro et al., 2013).

The densities of aquatic macroinvertebrates are listed in Table 2. Their normalized values were significantly different according to the ecological class (Mixed model: $F_{1,537} = 12.35$; $p = 0.0005$), but not according to the area alone (Mixed model: $F_{2,57} = 0.74$; $p = 0.48$). Finally, there was a significant interaction effect between the area and the ecological class (Mixed model: $F_{2,537} = 3.49$; $p = 0.03$). The summed proportions of benthic macroinvertebrates significantly increased (Fisher exact test: $p = 0.0002$) from the outside of the range to its core (Fig. 2). Yet, the proportions of benthic and nektonic macroinvertebrates were not significantly different at the range core compared to the range edge (Fisher exact test: $p = 0.391$). The proportion of these classes was, however, significantly different when comparing ponds at the range edge to ponds outside of the range (Fisher exact test: $p = 0.0042$), with a lower proportion of the nekton at the range edge. It also significantly differed between ponds at the range core and ponds outside of the range (Fisher exact test: $p = 0.0001$), with a lower proportion of the nekton at the range core.

In this study, we documented the availability in aquatic macroinvertebrates in ponds located at the range core, the range edge, and outside of the range of *X. laevis* in France. Even if the normalized densities of aquatic macroinvertebrates did not significantly decrease from outside of the range to its core, significant changes in the proportions of the ecological classes of aquatic macroinvertebrates between ponds occupied by *X. laevis* and ponds outside of its range were detected. Because we were not able to detect another factor than the presence of *X. laevis* in the ponds, such as a predator or an abiotic factor, that could possibly explain these changes, we consider this result as the first report of a

Table 1
Habitat characteristics of the ponds used during the study. For each parameter, the mean values for each group – Core, Edge and Outside – and the Standard Error are shown. The distances to the closest road and to the closest stream are coded as D_{road} and D_{stream}, respectively.

	Core	Edge	Outside	Total
D_{road}	146.8 (±25.5)	76.8 (±29.6)	142.5 (±68.5)	123.3 (±19.2)
D_{stream}	267.3 (±56.9)	443.7 (±83.4)	310.4 (±78.1)	331.6 (±41.8)
Pond surface	176.0 (±34.9)	386.5 (±92.1)	226 (±46.1)	252.5 (±36.6)
Water depth	163.9 (±17.8)	177.7 (±14.4)	145 (±11.0)	165.5 (±10.3)
Mud depth	7.1 (±1.5)	6.7 (±2.0)	7.4 (±1.9)	7.04 (±1.0)
Vegetation cover	24.3 (±6.0)	12.4 (±4.7)	28.1 (±12.7)	21.0 (±4.0)

Table 2
Densities of macroinvertebrates captured in the study sites.

Ecological class	Order	Area	Mean density	Standard error
Benthos	Acheta	Core	0.31	0.2
		Edge	0.0	0.0
		Out	0.2	0.1
	Bivalvia	Core	0.1	0.1
		Edge	0.5	0.3
		Out	0.1	0.1
	Diptera	Core	8.0	2.0
		Edge	5.0	2.1
		Out	1.4	0.7
	Ephemeroptera	Core	11.0	5.2
		Edge	4.7	1.6
		Out	10.6	6.1
	Gastropoda	Core	4.1	1.4
		Edge	2.0	0.9
		Out	2.3	1.7
	Isopoda	Core	2.6	1.1
		Edge	1.3	0.9
		Out	0.1	0.1
	Trichoptera	Core	0.7	0.2
		Edge	0.2	0.1
		Out	0.0	0.0
Nekton	Coleoptera	Core	5.7	1.1
		Edge	6.4	2.8
		Out	3.7	1.6
	Hemiptera	Core	3.6	0.8
		Edge	4.1	1.1
		Out	19.7	9.4
	Odonata	Core	7.7	2.6
		Edge	1.0	0.4
		Out	5.6	3.7

potential effect of *X. laevis* on the native aquatic invertebrates. In previous studies on the diet of *X. laevis* most of the main prey categories belonged to the zooplanktonic or benthic ecological classes (McCoid and Fritts, 1980; Measey, 1998; Lobos and Measey, 2002; Courant et al., 2017). The nektonic class has only been reported as an important prey class in the native range of this species in South Africa, and represented less than 5% of the prey items elsewhere (Vogt et al., 2017; Courant et al., 2017). This statement, combined with the significant decrease in nektonic macroinvertebrates after the colonization by *X. laevis*, suggests that this class may be preferentially consumed when *X. laevis* colonizes a new habitat. Once it has consumed most of the large nektonic prey items, it may then fall back on other categories such as zooplankton and benthic categories as observed in invasive populations (Courant et al., 2017). This result may necessitate qualifying because the sampling method used in this study might not enable a complete and homogenous recording of the diversity of prey occupying the ponds (Kerans et al., 1992). They still highlight the importance of taking into account the relative abundance of the potential prey categories in the environment. Moreover, it highlights the importance of considering the changes in the environment before and after the colonization by an alien species for conservation biology. Behavioral and experimental studies are needed to confirm the suspected preferential consumption of large nektonic prey by *X. laevis*, for example by assessing which category of prey it consumes when the availability of each category is equivalent. Our study questions the long term consequences of the changes in the macroinvertebrate community we report here: how the trophic network will respond to these changes through time appears as a crucial element. Thus, regarding the results described in this study, and those described in Courant et al. (2017, 2018), we would recommend a long term survey the invasive populations of *X. laevis* and their effects on the colonized environments.

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Declarations of interest

All the authors declare that they have no conflict of interest to declare in relation with this study.

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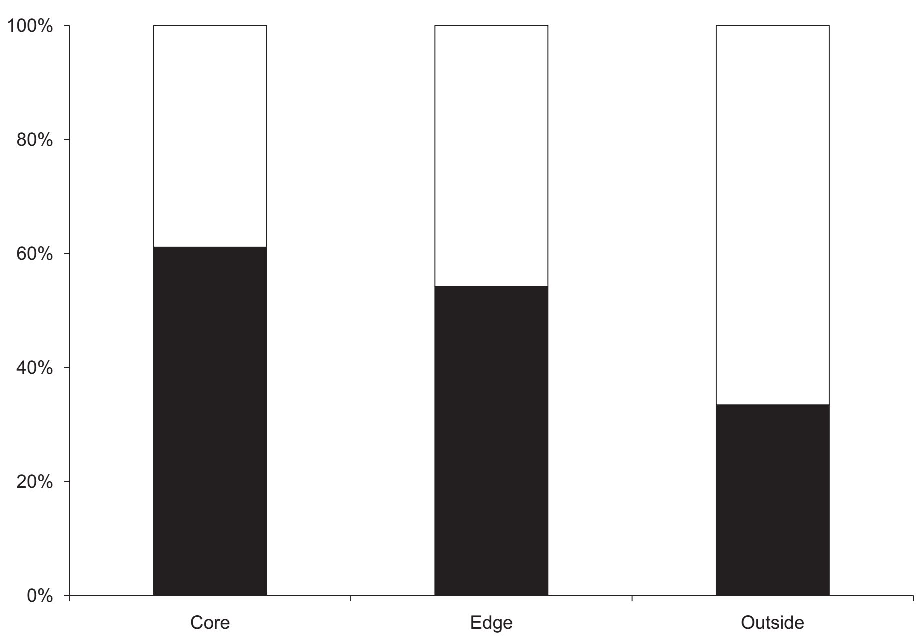

Fig. 2. Proportions of nektonic (white) and benthic (black) macroinvertebrates captured in ponds at the range core, the range edge, and outside of the range of *Xenopus laevis* in France.

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