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Conserved growth rate and age structure of *Xenopus laevis* in the edge and core of an expanding population

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Invasive species represent a unique opportunity to study the evolutionary mechanisms driving range expansions. Although range expansion is expected to be associated with increased reproduction and dispersal at the range edge, *Xenopus laevis* seems to decrease its reproductive investment and to enhance dispersal at the range edge. Evidence of increased dispersal at the edge of expanding populations occurring simultaneously with a faster growth rate has been reported for other organisms. Here, we focused on the growth rate and age structure at the range edge vs. the range core in an expanding population of *X. laevis*. We used skeletochronology to characterize the age of 250 individuals captured at the range core and edge of this expanding population. Using the Von Bertalanffy equation, we then compared individual growth rates between locations. We found no significant changes in growth rate or age structure between edge and core samples. This result suggests that the reduced investment in reproduction recorded in another study at the range edge might compensate for the increased dispersal without impacting growth in this population. This implies that the resource allocation in an expanding population might thus be more diverse than commonly assumed.

ADDITIONAL KEYWORDS: growth rate – invasive species – range expansion – resource allocation – *Xenopus laevis*.

INTRODUCTION

Studying population age structure is essential for understanding differences in the demography of both native and invasive populations (Barbault *et al.*, 1979; Francillon & Castanet, 1985: Järemo & Bengtsson, 2011). During range expansions, the resource allocation to life-history traits is expected to change, with an increased dispersal and reproductive investment and a reduced competitive ability at the range edge (Burton *et al.*, 2010). A faster individual growth rate at the range edge has also been reported in empirical studies (Sanford *et al.*, 2006; Lindström *et al.*, 2013). The association of a faster growth rate and greater resource abundance and/or quality is expected to lead to the enhancement of dispersal and the ability to defend newly colonized habitats (Brown *et al.*, 2013; Chuang & Peterson, 2016). However, a faster growth rate is commonly associated with a lower immune system performance (Van Der Most *et al.*, 2011) or a shorter lifespan (e.g. Amundsen *et al.*, 2012) and a more precocious reproduction (Dangremond & Feller, 2016). Yet, no consensus concerning the mechanisms driving these patterns has been reached (Metcalfe & Monaghan, 2003). Some authors consider these changes as consequences of an evolutionary process, i.e. spatial sorting, defined by a selection of individuals according to their dispersal potential and behaviour rather than their survival probability (Shine *et al.*, 2011). Furthermore, recent studies have shown that genetic and environmental factors (resource availability and competition) play a role in the phenotypic divergence observed in an expanding population through experiments (Van Petegem *et al.*, 2017) and field studies (Stuart *et al.*, 2019).

Here, we used skeletochronology to study the growth rate and age structure of an invasive population of

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Xenopus laevis. This species, native to austral Africa, was widely used in pregnancy tests (Gurdon & Hopwood, 2000) and as a biological model in development biology (Cannatella & De Sa, 1993). After accidental escapes from breeding facilities, populations have become established on four continents (Measey *et al.*, 2012). In the invaded areas, this species is known to impact native ecosystems (Lillo *et al.*, 2011; Courant *et al.*, 2018a, b), and it is considered to be one of the most important invasive amphibians in terms of impacts (Kumschick *et al.*, 2017). *Xenopus laevis* was introduced to Western France in the late 1980s through a series of escape events from a breeding facility (Fouquet, 2001). The range of the population has been estimated at 207 km^2 in 2012 (Measey *et al.*, 2012), and the colonization front is expanding every year. The individuals from the range edge of this population have been shown to reduce their allocation of reproductive resources (Courant *et al.*, 2017b) and to increase their locomotor abilities (Louppe *et al.*, 2017) and their allocation to dispersal (Courant J, Secondi J, Guillemet L, Vollette E and Herrel A, unpublished observations). Thus, resource allocation patterns of this species differ from theoretical predictions (Burton *et al.*, 2010). Following existing literature on growth patterns at the range edge of expanding populations (Phillips, 2009; Chuang & Peterson, 2016), we expected a significantly slower growth rate, associated with a longer lifespan, at the range core compared with the range edge.

MATERIAL AND METHODS

SAMPLING

Frogs were captured in 18 ponds from May to October 2014 and during spring 2016. The study sites were located in the expanding range of *X. laevis* in Western France (Fig. 1). The edge sites (N = 10) were selected in accordance with the knowledge of local landscape managers and were among the furthest colonized sites from the introduction locality in each direction. They were located between 13 and 55 km from the introduction site. To reduce as much as possible the effect of a different habitat on the individual growth or

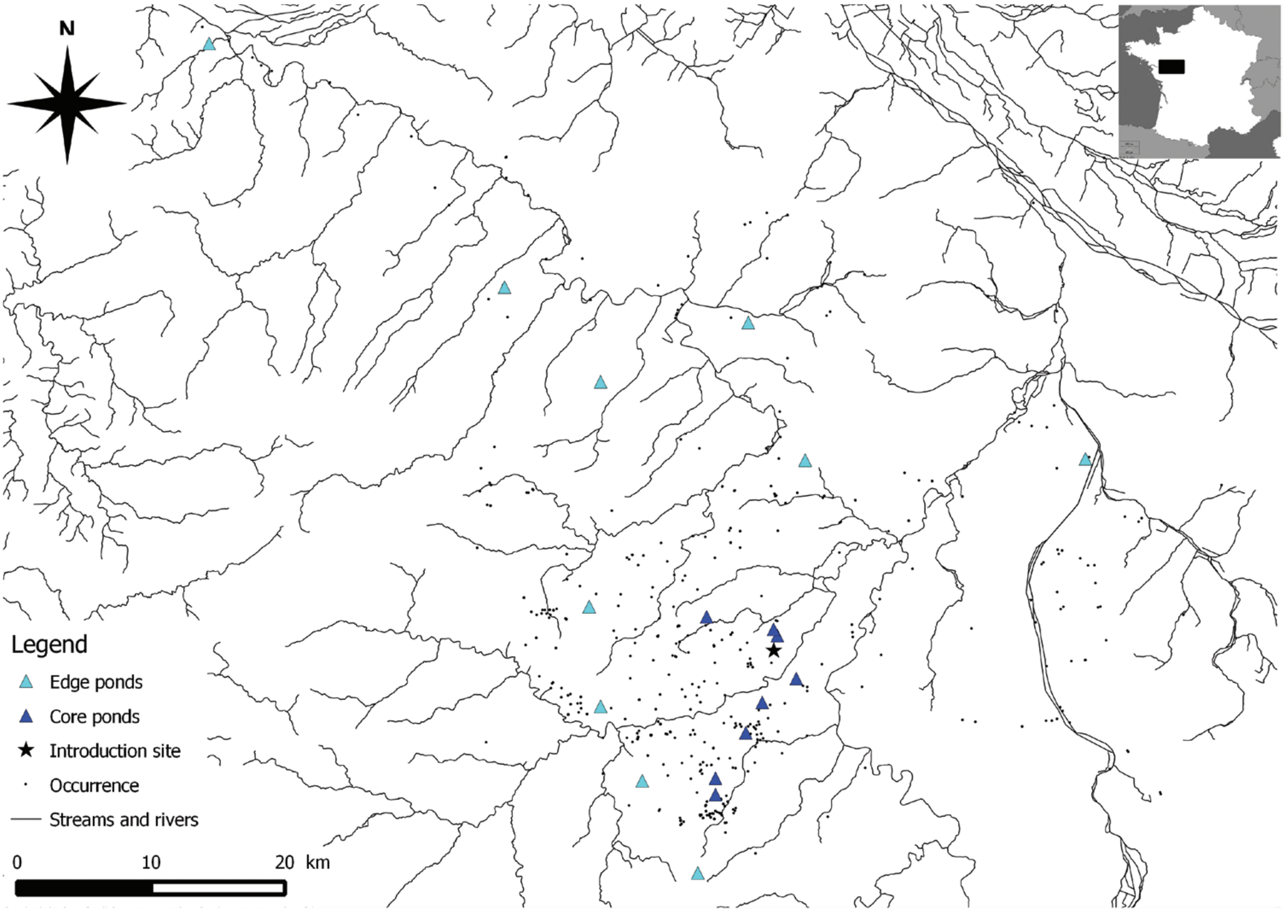

Figure 1. Sampled locations for the skeletochronological study of *Xenopus laevis* in the invasive population in Western France. Individuals were captured in ponds at the range edge (light blue triangles) and the range core (dark blue triangles).

the age structure, the man-made ponds were selected according to the following criteria: all of them were located in pasturelands and far from crop culture, towns and large roads, were not occupied by potential predator fish (according to the owner), and their size ranged between 200 and 500 m^2. The entire range of the species in France is subject to similar climatic conditions, with a climate defined as 'oceanic altered' (Joly *et al.*, 2010).

Individuals were captured in ponds using baited funnel traps with a closed empty bottle as a float to avoid drowning. Traps were placed in each pond with an effort of one trap per 50 m^2 of accessible surface. Traps were placed during three consecutive nights and were checked each morning 1 h after sunrise.

For each individual, the snout–vent length (SVL) was measured with digital callipers (Mitutoyo Absolute IP67; precision, 0.01 mm). Immediately after euthanasia by immersion in MS222, the second phalanx of the second finger was collected from each individual and placed into 70% ethanol before being sent to the laboratory and analysed a few weeks later. A research permit for the capture and euthanasia was provided by the Préfet of the Deux-Sèvres department.

AGE ESTIMATES

To estimate the age of individuals, we used a skeletochronological method, which has been confirmed to estimate the age of amphibians accurately, especially in Palaearctic and subtropical species (reviewed by Sinsch, 2015), such as *X. laevis*. The age of individuals was estimated by making histological cross-sections (2 μm thick) of the second phalanx with a microtome (Microm HM360, with Diatome histoknife 8 mm) according to the protocol of Castanet & Smirina (1990). Some minor modifications were applied to this protocol, such as the use of Toluidine Blue (C.I.52040 VWR34187.185) for colouring instead of Haematoxylin and the use of an epoxy embedding medium (epoxy embedding medium: FLUKA 45345, Sigma; DDSA: FLUKA 45346, Sigma; MNA: FLUKA 45347, Sigma; Accelerator :FLUKA 45348, Sigma) instead of paraffin. Sections were observed using a Leica DM2700M microscope and photographs were taken using the software and camera of the microscope (LAS v.4.6).

We counted lines of arrested growth (LAGs; see Fig. 2) in 20 sections per individual (ten per slide, two slides per individual) to ensure that there was no bias in any of the sections. Endosteal resorption could not be assessed in our study but was probably not present given the presence of hyaline cartilage at the core of the bone in most individuals. Double LAGs or false LAGs (i.e. LAGs that are fainter and do not form a complete ring) are likely to be attributable to acyclical events (e.g. scarcity of food resources, disease) occasionally inducing low rates of growth or the arrest of osteogenesis. We did not consider these false LAGs, as suggested previously (Castanet *et al.*, 1993). When double lines were found, we considered them as a double single line, following Castanet *et al.* (1993). We considered that the number of LAGs is equivalent to the age of individuals. Indeed, for this species, most individuals are born between April and September (Courant *et al.*, 2017a), and the metamorphosis generally occurs before autumn. The first LAG appears during the first winter of the life of individuals, and when individuals are active in ponds during the following spring/summer they are 1 year old with one LAG. Similar reasoning applies to older individuals. In amphibians, skeletochronology methods seem to become inaccurate when individuals exhibit more than eight LAGs, because it becomes difficult to make the distinction between close LAGs and double lines (Sinsch, 2015). According to previous studies performed on other populations of *X. laevis* and using skeletochronology and capture–mark–recapture (Measey, 2001), we expect that a large majority of individuals will exhibit fewer than eight LAGs. This means that skeletochronology can be an accurate method to estimate growth rate and age structure for this species.

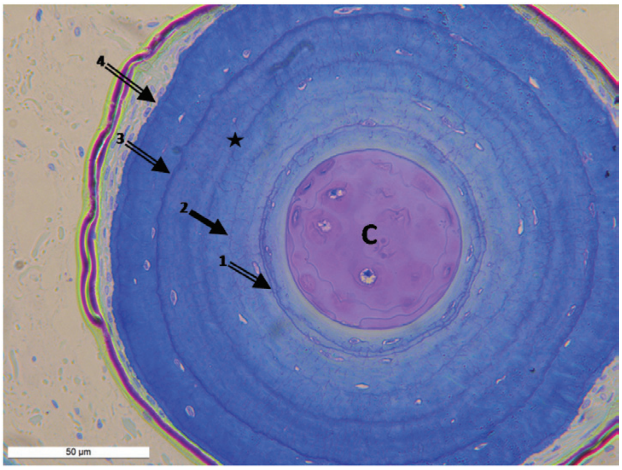

Figure 2. Example of a phalangeal cross-section of *Xenopus laevis*. Arrows indicate lines of arrested growth (LAGs); double arrows indicate double LAGs; and star indicates a false LAG. Abbreviation: C, hyaline cartilage.

STATISTICAL ANALYSES

A non-linear regression of the estimated age on SVL was performed following the von Bertalanffy (1938) equation, for each sex and each area. This equation is often used with amphibians because it fits the asymptotic growth of these animals (Cogălniceanu &

Miaud, 2003). We used this equation in a non-linear regression to estimate its components, i.e. the maximal SVL (SVL_{max}), the growth constant (K) and the theoretical age when there is no LAG (t_0), as follows:

$$\text{SVL} = \text{SVL}_{\text{max}} \times \left\{1 - \mathrm{e}^{[-K\times(\text{Age}-t_0)]}\right\}$$

The non-linear regression was performed for each sex and each population using the nls function in R (R Core Team, 2017). To improve the accuracy and the realism of the estimates, t_0 was constrained to vary between zero and the maximal age using the 'algorithm', 'lower' and 'upper' arguments of the nls function. For the same purpose and with the same R code, the maximal SVL was constrained to be superior to the maximal rounded SVL recorded in each subsample (core males, edge males, core females and edge females). The residuals of each non-linear regression were analysed by looking at their autocorrelation and the normal quantile–quantile plot vs. the standardized residuals. The parameter estimates of the equations obtained for each sex and each area (core or edge) were compared using Student's paired t-tests.

We performed a linear mixed model, with the age structure as the tested variable, the sex and areas as covariates, and the pond nested in the areas as a random effect. All statistical analyses were performed using R (R Core Team, 2017) with the nlme package (Pinheiro *et al.*, 2013).

RESULTS

A total of 250 individuals (123 females and 127 males) were captured for this study, with the number of individuals per site ranging from 11 to 46, depending on the capture success. A total of 116 and 134 individuals were captured at edge and core sites, respectively. In the total sample, the estimates of age varied between 1 and 9 years (Fig. 3), with the majority of individuals exhibiting an estimated age of 2 (45.67% of males and 39.84% of females) or 3 years (37.01% of males and 21.95% of females).

Non-linear regressions performed for the core and edge individuals of each sex led to estimates of growth parameters (Table 1), following the von Bertalanffy equation (Fig. 4). We tested for differences between these parameters and found no significant differences, either between the sexes in the core (t-test: $t_2 = 0.925$, $P = 0.45$) or the edge area (t-test: $t_2 = 0.91$, $P = 0.46$) or between areas for males (t-test: $t_2 = -0.67$, $P = 0.57$) and females (t-test: $t_2 = 0.96$, $P = 0.44$). Age structure was not significantly different between sexes (linear mixed model: $t_{230} = -0.642$, $P = 0.52$) or locations (linear mixed model: $t_{16} = -1.022$, $P = 0.32$). The interaction of sex and location was not significant either (linear mixed model: $t_{230} = -1.519$, $P = 0.13$).

DISCUSSION

In this study, the estimated age structure and growth rate were similar at the range core compared with the range edge. Resource allocation to reproduction at the edge of the range is decreased by reducing relative gonad size (Courant *et al.*, 2017a). On the contrary, resource allocation to dispersal is enhanced at the range edge of the same population, as suggested by the higher endurance capacity and the longer limbs (Louppe *et al.*, 2017), estimates of dispersal rates and distances in the field (Courant J, Secondi J, Guillemet L, Vollette E and Herrel A, unpublished observations). Our results show that, contrary to other expanding populations, where an increased dispersal was associated with faster growth and a shorter lifespan (Phillips, 2009; Amundsen *et al.*, 2012), individual growth/lifespan trade-off has remained unaltered

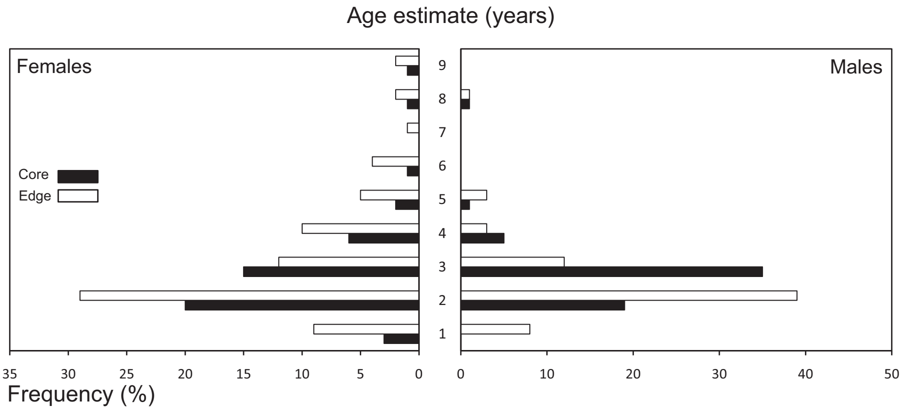

Figure 3. Age structure of the edge and core individuals of *Xenopus laevis* for females and males from the invasive population in Western France.

in the case of *X. laevis* in France. In Australia, the expansion of the invasive cane toad, *Rhinella marina*, is driven by shifts in dispersal (Phillips *et al.*, 2008) and increased individual growth rate, leading to an enhanced population growth rate at the range margins (Phillips, 2009). According to our study, the expansion of the population of *X. laevis* in France seems to occur without any accelerated individual growth rate and despite the reduced reproductive investment at the range edge (Courant *et al.*, 2017a). The differences in the observed patterns for *R. marina* and *X. laevis* might be related to ecological factors, such as food availability. Aquatic macroinvertebrates are the main item in the diet of *X. laevis* in France and elsewhere (Courant *et al.*, 2017b). Despite a significant decrease in nektonic macroinvertebrates in ponds occupied for decades (Courant *et al.*, 2018b), the density of *X. laevis* does not decrease significantly in the aquatic habitats of the range core (Courant J, Secondi J, Guillemet L, Vollette E and Herrel A, unpublished observations). Thus, the remaining prey items (benthic macroinvertebrates and zooplankton) at the range core seem to provide a sufficient quality and quantity of resources to result in a similar growth in the entire population. These resources are indeed sufficient to guarantee the expansion of other invasive populations of *X. laevis* in Europe and America (Courant *et al.*, 2017b). In contrast, the invasive *R. marina* in Australia seems to impact a much more diverse range of species, including prey, competitors and potential predators (Shine, 2010; Jolly *et al.*, 2015). This could result in decreased resource availability at the range core (Brown *et al.*, 2013) that would participate in a decrease of growth rate in the area colonized by *R. marina* for decades. Thus, it would be interesting to assess how the niches of these species drive the changes in individual growth rates and age structures in different ecological contexts; for example, through

Table 1. Parameters of the non-linear regressions performed with the von Bertalanffy equation for the age of individuals relative to their snout–vent length (SVL), with the maximal SVL (SVL_{max}) and the growth constant (K)

Sex	Area	SVL_{max} (± SE)	K (± SE)
Females	Core	120 ± 15.026	0.460 ± 0.193
	Edge	120 ± 18.876	0.425 ± 0.209
Males	Core	95 ± 11.235	0.499 ± 0.234
	Edge	91 ± 11.741	0.611 ± 0.292

The theoretical age when there is no line of arrested growth, t_0, was null for each sex and area.

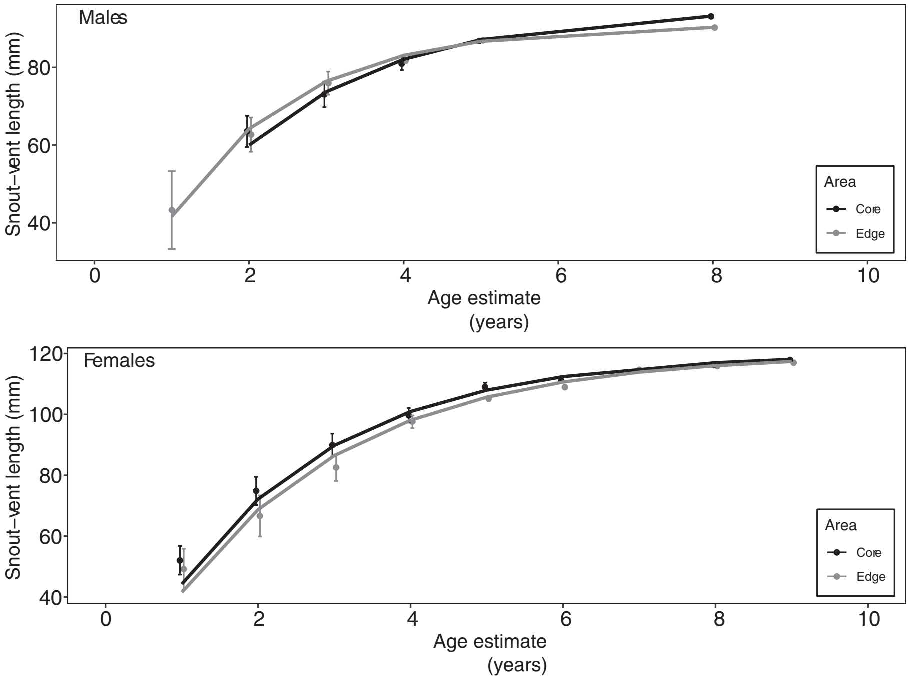

Figure 4. Non-linear regressions (lines) performed for each sex on the age estimates and the snout–vent length of individuals from the range core (black) and edge (grey) of the expanding population of *Xenopus laevis* in France. The mean snout–vent lengths are shown with black and grey dots with standard error for the range core and edge, respectively.

experiments simulating different environmental conditions and availability of resources.

In our study, the age estimates varied from 1 to 9 years, which is in accordance with a previous study on the age structure of *X. laevis* in the population introduced in Wales (Measey, 2001). During a capture–recapture survey performed in Wales, the maximal longevity recorded for this species in the wild was 14 years (Measey & Tinsley, 1998). In this population, recruitment did not appear to occur every year, inducing an age structure with many 1-year-old individuals and a low frequency of the older age categories (Measey, 2001). In other populations, recruitment appeared to occur each year (Ferreira ACO, pers. comm.; De Villiers FA, pers. comm.), but the dominant age classes varied from one population to another. These differences in longevity between populations might be explained, in part, by ecological factors, such as the presence of predators and competitors, or differences in resource availability and climate. The climate of the native population is classified as Mediterranean (Peel *et al.*, 2007). In France and Wales, the climate is classified as temperate (Peel *et al.*, 2007), which might impact the growing season and the available resources in the habitat of *X. laevis*.

In experimental conditions, water temperature has been suggested to have a small influence on *X. laevis* growth rate (Hilken *et al.*, 1995). In contrast, Measey (2001) suggested that water temperature might have a significant effect on growth rate, because growth occurred year-round in California (McCoid & Fritts, 1989), where the water temperature is always > 20 °C. In Wales, growth was restricted to only the warmest months (Measey, 2001). The differences between the conclusions of laboratory and field studies are likely to be explained by food availability: in the laboratory, food is constantly provided to individuals irrespective of temperature, whereas invasive *X. laevis* feeds mainly on aquatic invertebrates (Measey, 1998; Courant *et al.*, 2017b), which are mainly available during spring and summer (Tachet *et al.*, 2006). This suggests that growth and reproduction (Courant *et al.*, 2017a) might occur only when the water temperature is high enough to provide sufficient food resources to *X. laevis*. Thus, climate and, consequently, climate change, might play a significant role in future expansions of the species (Ihlow *et al.*, 2016). Studying the effects of climate on the longevity of individuals appears crucial given the demonstrated impacts of this species in invaded areas (Lillo *et al.*, 2011; Courant *et al.*, 2018a, b) and the relevance of this issue to conservation biology.

CONCLUSION

Our results show that, beyond the well-documented case of the cane toad in Australia, other species use different strategies and exhibit various patterns of resource allocation in expanding populations. These patterns are likely to be the result of differences in ecological contexts, but they can also result from the niche that the invasive species occupies in these contexts. The model in our study, *X. laevis* is, with the cane toad, *R. marina*, amongst the most important invasive amphibians in terms of ecological impacts (Kumschick *et al.*, 2017). These species represent only two examples amongst the many species with expanding invasive populations, but they clearly show that the eco-evolutionary mechanisms driving range expansions are more diverse and complex than commonly assumed.

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AUTHOR CONTRIBUTIONS

J.C. and A.H. conceived the study. J.C. collected the data in the field. B.D.K. and D.A. performed the cross-sections. L.A. and A.H. analysed the cross-sections. L.A. and J.C. performed the statistical analyses. All authors contributed to the writing of the manuscript.

CONFLICTS OF INTEREST

None.

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