Freshwater invasive clams grow faster and reproduce earlier in recently introduced populations with reduced growth rates

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Abstract

Many species are shifting their ranges being forced to rapidly respond to novel stressful environmental conditions. Colonizing individuals experience a complex mixture of selective forces that favor rapid evolution of life history traits notably affecting dispersal and reproductive rates in newly invaded habitats. Limited information is currently available on trait variation within the invasive range despite is critical for understanding ecological and evolutionary factors that drive the process of range expansion of invasive species. Here we use the widely introduced Asiatic clam *Corbicula* to evaluate life history shifts within its invaded range. Through an exhaustive literature search, we obtained data for 17 invasive *Corbicula* populations from different ecosystems

worldwide, to test the relationship between population and individual parameters relevant to the process of range expansion. Our main results showed that (i) recently introduced *Corbicula* populations were characterized by low conspecific density and low population growth rate and (ii) clams grew faster and reproduced earlier in populations experiencing reduced growth rates. Our findings support the standpoint that individuals from recently established populations face strong *r*-selective forces that favor traits associated with high reproductive rates. These patterns could be interpreted as effective mechanisms to overcome difficulties associated with low densities and low population growth in newly colonized areas.

Key words: Asiatic clam, *Corbicula fluminea*, Invasive species, Growth rates, Front-edge populations, *r* selection.

INTRODUCTION

As a consequence of human-induced climate change and increasing global transport of people and goods, many species are shifting their ranges and are forced to rapidly respond to novel stressful environmental conditions (physical or biotic) (Bossdorf et al. 2005). These conditions can have a strong effect on species life histories through the selection of traits that optimize population growth and survival of offspring to maturity (e. g. reduced age of maturity and reproduction, increased growth rate, increased energy allocated to reproduction; Stearns 1976, 1977). Thus, individuals at the expanding edge of the species distribution experience a complex mixture of selective forces that can have profound impacts on the evolution of a species' life history traits affecting, for instance, dispersal and reproductive rates (Phillips 2009; Shine et al. 2011).

Colonization events are usually driven by a small number of individuals that are the first to arrive at an expanding front of the distribution, where they benefit from increased space open for colonization and low conspecific density, below carrying capacity (Cole 1954; Sakai et al. 2001; Phillips et al. 2010). Hence, the density gradient occurring at the expanding range (i. e. grading from zero to carrying capacity) creates different selective environments where individuals from a recently established population face stronger r selection compared to those from long established ones, which are exposed to selective K-type forces (e. g. Phillips et al. 2010). According to theory, low densities favor the evolution of life-history traits related with r-type selections (MacArthur & Wilson 1967; Phillips 2009; Burton et al. 2010), leading to exponential (non-density regulated) population growth in recently established populations while denser, long-established ones follow a density-regulated population growth (Brook and Bradshaw 2006).

Recently established populations are characterized by low conspecific density and low *per capita* rate of increase, leading to lag-times between initial colonization and the onset of rapid population growth (Sakai et al. 2001). The duration of the lag phase is mediated, among others, by a number of non-mutually exclusive ecological and evolutionary mechanisms (e. g. low encounter rate for reproduction, density-dependent effects, adaptation, and selection of new genotypes; Bossdorf et al. 2005; Davis 2005; Ricciardi 2012). An effective mechanism to increase the rate of population growth is early reproduction, which results from fast growing individuals (Cole 1954; Lewontin

1965; Roff 1993). Individuals that grow faster will attain reproductive sizes earlier and bring down generation times, promoting a rapid build-up of population numbers (Cole 1954; Lewontin 1965; Roff 1993; Phillips 2009) and accelerating primary invasion and secondary spread of invasive species (Skellam 1951; Phillips et al. 2006; Lockwood et al. 2007). Several studies have compared life-history traits between native and invaded ranges ('home-and-away' comparisons; reviewed in Phillips et al. 2010), but only few studies have looked for such trait changes on introduced species across their global invasive range (Gaston 2009). Thus, knowledge on life-history trait variation within the invasive range is critical for better understanding the process of species range expansion, largely induced by climate change and increasing global transport.

Here we investigated shifts in life history traits of the Asiatic clam *Corbicula* that may have resulted from its invasion dynamics within the introduced range. To do so, we searched for peer-reviewed articles providing enough information to estimate time since population introduction as well as different population and individual processes and characteristics including population density, population growth rate (*per capita* rate of increase), individual growth rate, age at first reproduction, and lifespan of global populations of this worldwide invader. We focus our predictions on life history strategies exhibited by individuals from recently established populations, which typically occur at the invasion front. We tested the hypotheses that *Corbicula*'s density and population growth rate increase with time since introduction, likely as compensatory responses to strong *r*-selective pressures in recently established populations. Although *Corbicula* is widely known to exhibit rapid population growth, being able to reach extremely high densities (reviewed in Mcmahon 2002), its dynamics are known to be chiefly influenced by environmental conditions (see Crespo et al. 2015 and references therein). Thus, density is predicted to have no effect on population growth, though high densities are considered likely to have a negative effect on individual growth rates. We also asked whether clams that grow faster and reproduce earlier are favored in populations with low *per capita* rate of increase. A related prediction is that clams that grow fast and reproduce early would have a shorter lifespan compared to individuals exhibiting slow growth.

METHODS

Study organism

Bivalves of the genus *Corbicula* (Megerle Von Mühlfeld 1811) are native to Southeast Asia, the Middle East, Australia and Africa (Araujo et al. 1993) but they have colonized a large part of the Americas and Europe (Mouthon 2001; Schmidlin & Baur 2007; Crespo et al. 2015; Fig. 1). The successful invasion of *Corbicula* clams has been mainly attributed to their rapid growth and maturation, high fecundity, and high dispersal making this bivalve one of the most relevant faunal non-indigenous group in aquatic ecosystems (reviewed in Sousa et al. 2008). Invasive freshwater *Corbicula* populations are constituted by a small number of lineages composed of hermaphroditic individual clones where the most widespread and abundant lineage is the so-called Form A/R, widely known as *Corbicula fluminea* (Komaru et al. 1998; Pigneur et al. 2012, 2014). The current taxonomic status of the invasive *Corbicula* lineages in the Americas and Europe is still largely unresolved despite several morphological and genetic studies (reviewed in Pigneur et al. 2014). In the present paper, we deal with this form and refer to it as *Corbicula* to avoid entering unsettled taxonomic debates.

Literature search

We exhaustively searched the literature for peer-reviewed articles on *Corbicula* (*Corbicula fluminea sensu lato*) providing enough information to estimate the individual growth rate, population density, population growth rate, time since colonization, water temperature, and conductivity of global populations of this clam. To do this, we first identified relevant studies from ISI Web of Knowledge (Web of Science Core Collection, 1900 through 2017) by conducting a first search using the field tag “topic (TS)” in the “Advanced search” option and the search string: TS=“Corbicula fluminea” OR TS=“asia* clam” (search #1). We conducted a second search including topics TS=“population dynamic*” OR TS=“population size*” OR TS=“population densit*” OR TS=“population structure” (search #2). We ran a third search using TS=“growth” OR TS=“individual growth” OR TS=“population growth” (search #3). Finally, we combined searches #2 and #3 into search #4 (#4= #3 OR #2), and restricted the latter by search #1 to obtain a final set of candidate studies (search #5= #4 AND #1).

This literature search was finished on 27 September 2018 and this protocol identified 215 candidate studies (database search: 215 candidates; gray literature and unpublished data: 0 candidates). To identify papers potentially missing in this list, we subsequently

scanned the references in these papers and conducted a Google Scholar search using keywords mentioned above and added 8 studies to this candidate pool (Fig. S1). A total of 67 studies that belonged to research areas unrelated to the topic of the current study (*e. g.*, Chemistry Applied, Toxicology, Paleontology) were excluded from this candidate pool by refining the set based in 'Web of Science Categories'. The resulting studies (n = 156) were finally inspected individually in detail to assess their eligibility for our analyses according to the following inclusion criteria: i) Studies that assessed invasive populations of *Corbicula* clams (i. e. studies exclusively providing estimates for native populations were excluded); ii) Studies that reported or provided data enough to extract the population density and age/size distribution for >6-months (see below); iii) Studies that assessed populations in reasonably "average" natural environments, such that populations from heavily impacted sites (e. g. thermal plumes) were excluded (n = 140; see Fig. S1 for further details on screening and eligibility criteria). We finally retained a sample of n = 16 studies, covering 17 invasive populations of *Corbicula* from different ecosystems worldwide. We used the WebPlotDigitizer software (http://arohatgi.info/WebPlotDigitizer/) to extract data that was only graphically presented.

Population density and population growth rate

For each population selected from our literature search, we obtained the mean population density for the entire study period or extracted temporal values to estimate it whenever this value was missing in the text.

Population's *per capita* growth rate (*r*) can be derived from the exponential growth equation and expressed as:

$$r = \frac{\ln\left(\frac{Nt}{N0}\right)}{t}$$

Corbicula clams generally exhibit one or more high-density peaks related to recruitment events yearly. However, density in the field fluctuates almost constantly generating several peaks and valleys that do not necessarily indicated significant recruitment events. We therefore set a criterion to determine relevant recruitment peaks in each study by using the average density throughout the study period as a threshold. To estimate the *per capita* rate of increase (*r*), we considered the highest

peak above it (N_t), the lowest density value (N_0), and the time period elapsed between the peak and the valley (t). Intermediate density values comprised in each time period (i. e. defined by N_0 and N_t) were used to fit the growth equation and obtain r. Population growth rates were estimated using GraphPad Prism version 7.00 for Windows, GraphPad Software, La Jolla California USA, www.graphpad.com. Note that periods defined by non-relevant peaks (i. e. below the average density threshold) were discarded, as were also periods of progressive density decline between a relevant peak and the next N_0 value. We decided to do this because the aim of the present study was to compare population growth during periods of substantial growth across populations. When populations exhibited more than one relevant density peak throughout the study period, the population growth rate for such population was calculated as the average of single r estimations.

Individual growth rates and parameters

We calculate individual growth parameters from raw data using the same equations for all the studies considered to make sure results were fully comparable across studies. For each cohort present in each of the populations considered in this study, we fitted the von Bertalanffy-growth function with seasonal oscillations (hereafter SVBGF) proposed by Pauly and Gaschutz (1979), Hoenig and Hanumara (1982), and Somers (1988):

$$L_t = L_\infty (1 - exp^{-K[(t - t_0) + T_1 - T_2]}),$$

$$T_1 = C \sin (2\pi (t - t_s)) / 2\pi,$$

and

$$T_2 = C \sin (2\pi (t_0 - t_s)) / 2\pi,$$

where L_t is the predicted length at age t, L_∞ is the asymptotic length, K is the growth constant of dimension time (year^{-1} in most seasonally oscillating growth curves) expressing the rate at which L_∞ is approached, t_0 is the theoretical 'age' the clam have at length zero, C expresses the relative amplitude of the seasonal oscillation and varies between 0 and 1 (0 indicating lack of summer-winter differences in growth, it was constrained to be less than or equal to 1 during model fitting), and t_s is the starting point of the oscillation.

The parameters of the function were estimated by the modeling method available in

JMP statistical software (v9.0 SAS Institute). When preliminary results of the SVBGF failed to converge to estimate the asymptotic shell length (L_∞), we used the maximum shell length (*Lmax*) observed or reported at/for each study site to calculate the asymptotic shell length following the equation suggested by Taylor (1958):

$$Lmax / 0.95 = L_\infty$$

These values were fixed when we performed a second fit.

Because of the negative correlation between growth parameters (K and L_∞) prevents making comparisons based on individual parameters (Vakily 1992; Ramón et al. 2007), we used the growth-performance index (*GPI*), which reflects the growth rate of a given organism of unit length. In other words, *GPI* can be viewed as the (theoretical) value of K that would occur in organisms with a L_∞ value of 1 unit of length (Munro and Pauly 1983), and it was defined by Pauly and Munro (1984) as:

$$GPI = 2 \log_{10} L_\infty + \log_{10} K$$

We calculated the *GPI* values for cohorts from each study site based on growth parameters (L_∞ and K) obtained after fitting the SVBGF using the *Growth Performance Indices* application of the FISAT II software (Gayanilo et al. 2002).

Age at first reproduction and lifespan

Age at first reproduction can be estimated as the time (months) elapsed until clams reach the minimum size at first reproduction or maturity, which can be assumed to be 10 mm (Aldridge and McMahon 1978; Mcmahon 2002).

As *t0* is the theoretical 'age' the clam have at length zero, *tmax* can be defined as the theoretical 'age' the clam reaches its maximum length (*Lmax*). Since *Lmax* is dependently related to a maximum point in time (years), it is assumed that *Lmax* implicates *tmax* (*Lmax* ⇒ *tmax*) (Bonel and Lorda 2015). Thus, the theoretical maximum lifespan of a clam cohort can be approximately express as:

$$Lifespan = tmax - t0$$

Time since colonization and key environmental variables

For the same 17 populations and sites studied, we calculated the time elapsed since

population foundation (hereafter time since colonization) as the difference between the sampling dates in the first ecological survey and the first report of introduction. Moreover, we obtained water temperature and conductivity values for each site averaging monthly mean values for the same period used to estimate growth rates in each study. We considered these two environmental variables in the analyses because they have been reported to play a key role on bivalve's biology and ecology (Magnusen, 2007; Franco et al. 2012; Crespo et al. 2015). In order to keep values seasonally unbiased, only entire years were used in subsequent calculations. Whenever these parameters were not reported in the original paper, we obtained values for the same sites and years from the literature and reliable online databases (e. g. https://waterdata.usgs.gov/nwis/qw). When data was only graphically presented, we extracted it following the procedure mentioned above.

Statistical analyses

We ran separate linear regressions using the inverse of the variance to weigh response variables. Although we were mainly interested in testing individual effects of predictors (hereafter reduced models), we added annual mean water temperature and conductivity as quantitative variables in each model (hereafter full models). We used the partial *F*-test to compare nested models—that is, full *versus* reduced models. As we had strong *a priori* hypotheses as to the direction of effects, we used one-tailed tests. Density and growth estimates (except *GPI*) were Ln-transformed, whereas time, temperature, and conductivity were square-root transformed to fulfill the models' assumption of normality. All analyses were carried out in R version 3.4.3 (R Development Core Team 2017).

RESULTS

Literature search

Populations belonged to a broad range of freshwater and estuarine habitats including lakes, rivers, estuaries, manmade canals, and reservoirs in Europe, North and South America (Fig. 1; Table 1). These included 8 populations in the United States, 3 in France, 3 in Argentina, and 3 in Portugal (see Table 1 for detailed location, bibliographic source, and code number used herein to refer to the populations, for each of the 17 *Corbicula* populations selected, and Table S1 for additional information).

Density, growth, time since colonization, and key environmental variables

Overall, mean density of *Corbicula* from 17 locations worldwide spanned 32 to *ca*. 9,500 ind. m^{-2}, population growth rate (*r*) varied from 0.68 to 8.26%, individual growth rate (*GPI*) ranged 2.53-3.49, age at first reproduction 3.1-22.7 months, and lifespan 2.3-8.0 years (Table 1). On the other hand, time since introduction ranged 2 to 28 years in the populations studied (Table 1) and yearly water temperature range from 13.2 to 20.7 ºC and conductivity from 68 to 8,457 µS/cm (see Table S1 of the Supporting Information for details). In all cases, we found no evidence that adding temperature and conductivity in each model significantly increased its predictive power (for details see '*Model comparison*' in Supporting Information). We therefore report estimates and statistics from the reduced models in Table 2.

We found that *Corbicula*'s density (R^2 = 0.22, P=0.028) and population growth rate (R^2 = 0.26; P=0.018) were positively correlated with time since colonization (Fig. 2a,b), which is consistent with our expectation that recently established populations are characterized by low density and low *per capita* rate of increase. We found no significant relationship between *r* and population density, suggesting that *Corbicula* populations grow independently from density (R^2 = 0.03; P=0.245; Fig. 2c).

In contrast, population density had a negative effect (marginally non-significant) at the individual level, suggesting that individual clams grew faster in low-density populations whereas clam growth slowed down as density numbers built up (P=0.069; Fig. 3a). We also observed that that clams tended to grow faster (P=0.053; Fig. 3b) and reproduce earlier in populations with reduced growth rates (P=0.015; Fig. 3c), which supports the standpoint that individuals with faster grow and early reproduction are favored in populations with low *per capita* rate of increase.

At the individual level, clam growth rates (*GPI*) had a strong effect on the age at first reproduction (P=0.009; Fig. 4a) and lifespan (P=0.002; Fig. 4b), as individuals with higher growth rates reach minimum reproductive size earlier (*ca*. 10 mm) and live less than clams with lower growth rates. Accordingly, we observed a strong positive relationship between the age at first reproduction and lifespan, meaning that individuals that reproduce earlier live less compared to those with late maturation (P<0.001; Fig. 4c).

DISCUSSION

This is the first study that provides a comprehensive test for relationships between different population and individual parameters involved in the process of range expansion of the worldwide invasive Asiatic clam. Our main results show that (i) recently introduced *Corbicula* populations are characterized by low conspecific density and low *per capita* rate of increase and (ii) clams grow faster and reproduce earlier in populations experiencing reduced growth rates.

Growth rate and density of invasive *Corbicula* populations increased with time since colonization. Considering the most recent (2 years) and the longest time since colonization (28 years) in our review, these increases can be as much as 66% and 90% in density and population growth rate, respectively. These responses are in line with the standpoint that recently established populations typically occur at low conspecific density, below the carrying capacity, as colonization events are usually driven by a small number of individuals and a low *per capita* rate of increase (Cole 1954; Sakai et al. 2001). In addition, the increase in population growth rate with time suggests that recently established populations experienced stronger *r*-type selection that favor life history traits and strategies that effectively increase the rate of population growth, which was observed in long established populations (MacArthur and Wilson, 1967; Phillips, 2009; Burton et al., 2010).

Low-density *Corbicula* populations experiencing low growth rates (*r*) exhibited the fastest individual growths. Likewise, clams reproduce earlier in populations with reduced grow rate. In recently introduced populations, periods of negligible population growth can be driven by non-mutually exclusive ecological and evolutionary adjustments such as Allee effect, changing abiotic conditions, and adaptation and selection of new genotypes imposed by novel environments conditions at the newly habitat (Sakai et al. 2001; Bossdorf et al. 2005; Davis 2005; Ricciardi 2012). Such conditions can have a strong effect on life-history traits that are selected for optimizing population growth and survival to maturity of offspring (Stearns 1976, 1977). As predicted by life-history theory, individuals from recently established populations (typically occurring at the invasion front) face stronger *r* selection relative to conspecifics from older populations (MacArthur and Wilson 1967), favoring traits that

accelerate the range expansion. For instance, some empirical observations have revealed that individuals from recently colonized areas grow faster, and thus, reproduce earlier, than do conspecifics from older, long-established populations (e. g. tallow trees: Siemann and Rogers 2001; butterflies: Hanski et al. 2006; Australian cane toads: Phillips 2009). Accordingly, our results for *Corbicula* clams showing fast growth and early reproduction support the standpoint that such populations faced strong *r* selection, which favored traits associated with high reproductive rates in recently introduced populations with reduced growth rates.

The increased in individual growth and early reproduction are associated with a decrease of the clams' life span, supporting the idea of compensatory responses (i. e. trade-off) between different life-history traits. Such trade-offs can be interpreted as an effective mechanism to bring down generation times, promoting a rapid build-up of population numbers, which increases the rate of population growth in newly colonized areas (Cole 1954; Lewontin 1965; Roff 1993) and accelerate primary invasion and secondary spread of invasive species (Skellam 1951; Phillips et al. 2006; Lockwood et al. 2007). Collectively, our results suggest that reduced population growth of the current *Corbicula* population triggers the shortening of the time that the clams need to reach maturity by favoring clams that grow the fastest. Hence, as early-maturing clams reproduce earlier, this has the effect of fostering the growth of the future population. In this way, incipient *Corbicula* populations can increase their chances of overcoming the difficulties associated with low densities and survive to the population establishment stage, which can clearly subsidize the bivalve's invasive abilities in newly colonized areas.

The Asiatic clam is widely known as a worldwide successful invader capable of rapidly respond to novel stressful environmental conditions as a result of *r*-selected life history traits that favor exponential population growth once the population is established (Mcmahon 2002; Sousa et al. 2008a). Our results show how different life-history traits of individuals responded to different selective pressures occurring at varying population contexts: (i) newly *vs*. long-established, (ii) low *vs*. high density, and (iii) low *vs*. high population growth rates; all of them being linked to the geographic range shifting of species' distribution (i. e. front/core populations). The differences observed in *Corbicula*'s optimal life-history strategies suggest that traits of individuals from a

recently established population experienced a strongly *r*-selective environment as compared to long established ones. Considering the so-called *r*-K selection continuum, this implies that such population is predicted to shift from the *r*- towards the *K*-endpoint (MacArthur and Wilson 1967)—that is, selection shifts a population from density-independent to density-dependent regulation. However, *Corbicula*'s population growth was unfettered by density regulation.

Population density did not predict changes in population growth rate, as variation in *r* remained relatively low even at high-density values. By definition, long established and denser populations tend to be density regulated as they approach to carrying capacity (logistic population growth; e. g. Phillips et al. 2010). However, *Corbicula*'s population growth rate did not decrease with increasing density despite the fact that some of the populations included in this study exhibit extremely high densities exceeding, in some cases, 100,000 individuals per square meter (e. g. Eng 1979; Table 1). *Corbicula*'s dynamics are chiefly influenced by environmental variables (e. g. water temperature, conductivity, pH, and/or dissolved oxygen) and seem to be less influenced by population's density (e. g. Crespo et al. 2015). Thus, it does seem reasonable to infer that *Corbicula*'s population growth rate is non-density-regulated and do not level off at carrying capacity, as expected from a highly invasive organism as the Asiatic clam (McMahon 2002). Overall, our results suggest that this bivalve seems to be far from approaching carrying capacity, even at extremely high densities, supporting the idea that individuals from long established denser populations do not face a *K*-selective environment but a less strongly *r*-selective pressure.

All invasive *Corbicula* populations analyzed in this study are constituted by hermaphroditic individual clones belonging to the same lineage (Form A/R), which are distributed all across Europe and the Americas and characterized by an extremely low genetic diversity (see Pigneur et al. 2012, 2014 for further details). One fundamental principle of evolutionary biology is that the rate of change in response to natural selection is proportional to the amount of additive genetic variation present (Fisher 1930). Decrease in genetic diversity results in reduced evolutionary potential required to rapidly adapt to the novel habitat conditions of the invaded range, among other issues related to critical invasion phases (e. g. initial colonization, leading edges of range expansion; (Schrieber and Lachmuth 2017). It is still puzzling how *Corbicula*'s

genetically depleted populations succeed in their invasion process, which represents a case of genetic paradox (Pigneur et al. 2014). Acknowledging the implications of rapid evolution of life histories during shift is of high concern as a steadily increasing number species are shifting their ranges—and forced to rapidly respond to novel abiotic and biotic conditions—as a consequence of human-induced climate change and increasing global transport (Bossdorf et al. 2005). Further work on *Corbicula* can cast light on these important processes.

In conclusion, the approach proposed in this study provides a clear evidence of how different life-history traits associated with species' reproductive rate, such as individual growth rate and age at first reproduction, are maximized in recently established populations with reduced growth rates. Notably, these trait responses emerge across a broad range of sites and environmental conditions, which could be interpreted as a holistic mechanism to increase growth of the population and decrease the risk of stochastic extinction at initial stages of newly introduced populations.

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TABLES

Table 1. Summary of ecological and growth variables (mean ± SD) of worldwide invasive populations of the Asiatic clam *Corbicula* reviewed from the literature. *Density* is the estimated abundance of clams at the study site (ind. m^{-2}), *Population growth rate (*r*)* is the *per capita* rate of increase (%), *Time* is the number of years elapsed since population colonization at the time of the original study (years), *GPI* is the growth performance index (a *proxy* for individual growth rate), *AFR* is the age at first reproduction (months), and *LS* is the lifespan (years), *ID#* is a number assigned arbitrarily for identification purposes. The country, specific study location, and reference to the source paper of the original study used to build the information are shown for each population. NA, data not available. See the main text for details on how data was collected and variables were built from the literature. For extended information on each population, see Table S1 of the Supporting Information.

Country	Study location	*Density*	*Population growth rate* (*r*)	*Time*	*GPI*	*AFR*	*LS*	*ID#*	*Reference*
Argentina	Punta Atalaya, Río de la Plata	339±405	0.85±0.04	3.5	2.87±0.07	4.30±0.13	3.83±0.57	1	Ituarte (1985)
	Paraná de las Palmas River	1,053±768	3.23±0.05	25.5	2.73±0.01	9.23±1.17	6.82±0.05	2	Cataldo and Boltovskoy (1999)
	Río Negro estuary	94±8.3	0.99±0.16	15.5	2.94±0.23	5.32±1.66	3.55±0.41	3	Hünicken et al. (2018)
France	Saone River	302±186	1.46±0.02	12.5	2.54±0.13	12.73±2.42	7.55±2.17	4	Mouthon (2001)
	Loire Lateral Canal	992±1209	5.77±0.27	17.0	2.80±0.24	8.93±5.95	5.17±3.00	5	Mouthon and Parghentanian (2004)
	Canal of Roanne	626±897	4.17±0.04	17.0	2.77±0.16	8.25±3.43	4.27±1.58	6	Mouthon and Parghentanian (2004)
Portugal	River Minho estuary	840±387	1.17±0.00	16.5	3.32±0.05	3.06±1.20	2.28±0.30	7	Sousa et al. (2008b)
	Mondego estuary	5,017±5,489	1.63±0.09	6.9	NA	NA	NA	8	Franco et al. (2012)
	Casal de São Tomé	3,255±1,115	0.84±0.09	10.3	3.14±0.12	3.83±1.69	2.75±0.51	9	Rosa et al. (2014)
USA	Altamaha River	712±1,613	0.68±0.06	4.5	NA	NA	NA	10	Gardner et al. (1976)
	Lake Arlington	32±11	1.44±0.05	2.0	3.49±0.05	5.80±0.60	2.59±0.20	11	Aldridge and McMahon (1978)
	Delta-Mendota canal	9,470±7067	1.18±0.15	28.0	2.77±0.17	9.69±4.07	8.03±2.75	12	Eng (1979)
	New River (Station 1)	316±654	4.74±0.11	2	NA	NA	NA	13	Graney et al. (1980)
	Clear Fork, Trinity River	4,474±3,899	3.06±0.08	7.0	3.00±0.16	6.76±3.62	7.07±2.83	14	McMahon and Williams (1986)
	Mechums River	669±636	8.26±0.27	10.5	2.56±0.15	9.20±4.41	3.31±1.21	15	Hornbach (1992)
	Ogeechee River	1,398±1,096	1.54±0.02	10.0	2.52±0.12	22.72±9.17	6.85±1.63	16	Stites et al. (1995)
	Lake Tahoe	1,809±723	2.10±0.08	8.0	2.80±0.12	6.90±1.90	2.70±1.32	17	Denton et al. (2012)

Table 2. Summary of results from reduced models of weighted linear regression analyses of invasion and growth variables of global invasive populations of *Corbicula*. Parameter values are means ± SE. We report one-tailed *P* values indicating significant results in bold characters. Note natural logarithmic and square-root transformations of variables. Variable names as per Table 1. For details on descriptive statistics of full models and results on partial *F*-tests see the Supporting Information.

Response variable	Predictor variable	Estimate	Intercept	R^2	*F*-statistics	*df*	*P*
Ln(*Density*)	sqrt(*Time*)	0.604 ± 0.293	3.423 ± 0.941	0.221	4.25	1, 15	**0.028**
Ln(*r*)	sqrt(*Time*)	0.277 ± 0.120	-0.418 ± 0.400	0.261	5.29	1, 15	**0.018**
Ln(*r*)	Ln(*Density*)	0.075 ± 0.106	-0.007 ± 0.700	0.032	0.50	1, 15	0.245
GPI	Ln(*Density*)	-0.087 ± 0.054	3.463 ± 0.367	0.174	2.53	1, 12	0.069
GPI	Ln(*r*)	-0.200 ± 0.114	3.029 ± 0.108	0.204	3.07	1, 12	0.053
Ln(*AFR*)	Ln(*r*)	0.400 ± 0.162	1.633 ± 0.128	0.338	6.13	1, 12	**0.015**
Ln(*AFR*)	*GPI*	-1.010 ± 0.368	4.777 ± 1.085	0.386	7.54	1, 12	**0.009**
Ln(*LS*)	*GPI*	-1.113 ± 0.285	4.695 ± 0.841	0.559	15.21	1, 12	**0.002**
Ln(*LS*)	Ln(*AFR*)	0.728 ± 0.172	0.041 ± 0.338	0.599	17.95	1, 12	**<0.001**

FIGURES

Figure 1. Global distribution of invasive *Corbicula* clams indicating the native range of the genus (dark grey), the distribution of of *Corbicula* inside (black/grey shading and black dots) and outside of the genus' native range (color dots), which are mostly represented by forms A/R (formerly designed as *Corbicula fluminea sensu lato*; see main text for detailed explanation). Numbered stars are invasive worldwide populations reviewed in the present study. Years indicate estimated date of first introduction. See Table 1 and main text for references and details on the invasive populations reviewed here. See the Supporting Information for detailed criteria and data used to build the genus native and invasive distributions.

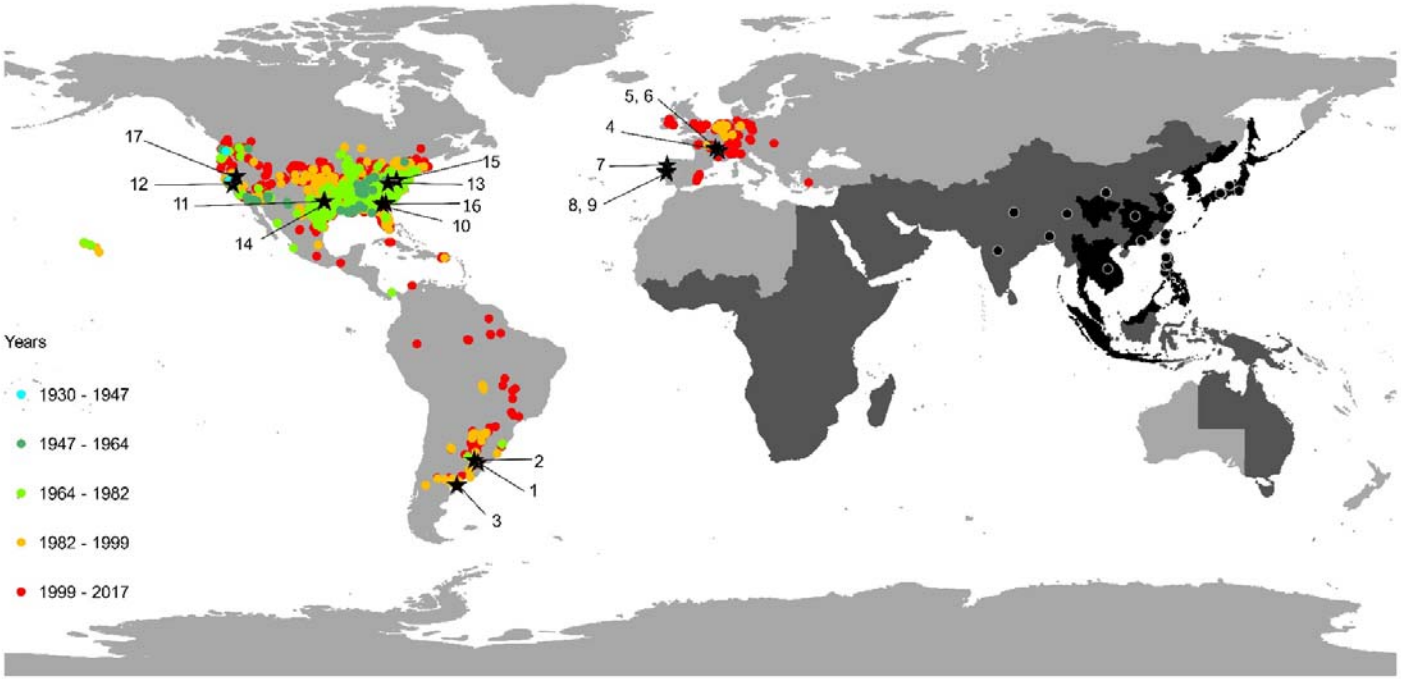

Figure 2. Density (a), growth rate (b) of 17 global invasive populations of *Corbicula* as a function of time since colonization and population density (c). The size of circles correspond to the inverse of the variance of mean value of each observation of the response variable, used to weigh effect sizes in the regression analyses (see main text for details). Population density and growth rate increased significantly with time since colonization (R^2 = 0.22, P = 0.028 and R^2 = 0.26, P = 0.018, respectively), while the relationship between growth rate and density was not significant (R^2 = 0.03, P = 0.245). Note natural logarithmic and square-root transformation of variables. Variable names as per Table 1.

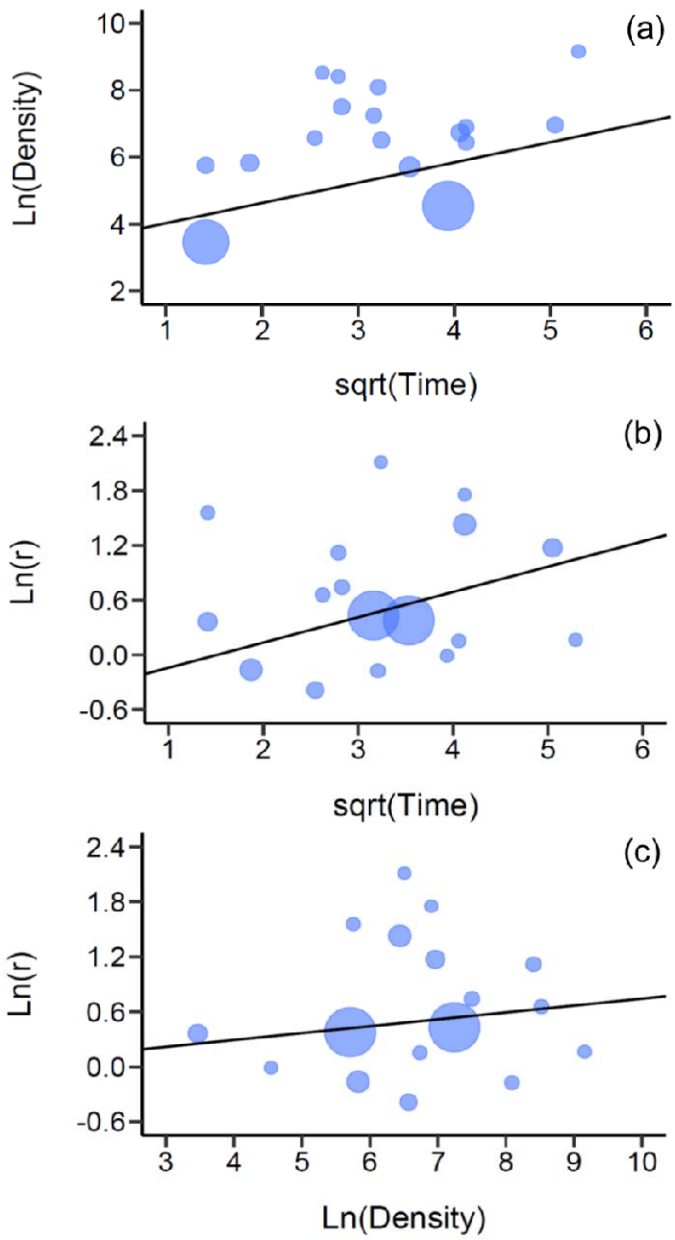

Figure 3. Individual growth performance index of the same global invasive *Corbicula* populations in Fig. 2 as a function of population density (a), growth rate (b), and age at first reproduction as a function of population growth rate (c). The size of circles correspond to the inverse of the variance of mean value of each observation of the response variable, used to weigh effect sizes in the regression analyses (see main text for details). Individual growth was higher (marginally not significantly) in low-dense, slow-growing populations (R^2 = 0.17, P = 0.069 and R^2 = 0.20, P = 0.053, respectively), while age at first reproduction was higher in fast-growing populations (R^2 = 0.34, P = 0.015). Note natural logarithmic transformation of some variables. Variable names as per Table 1.

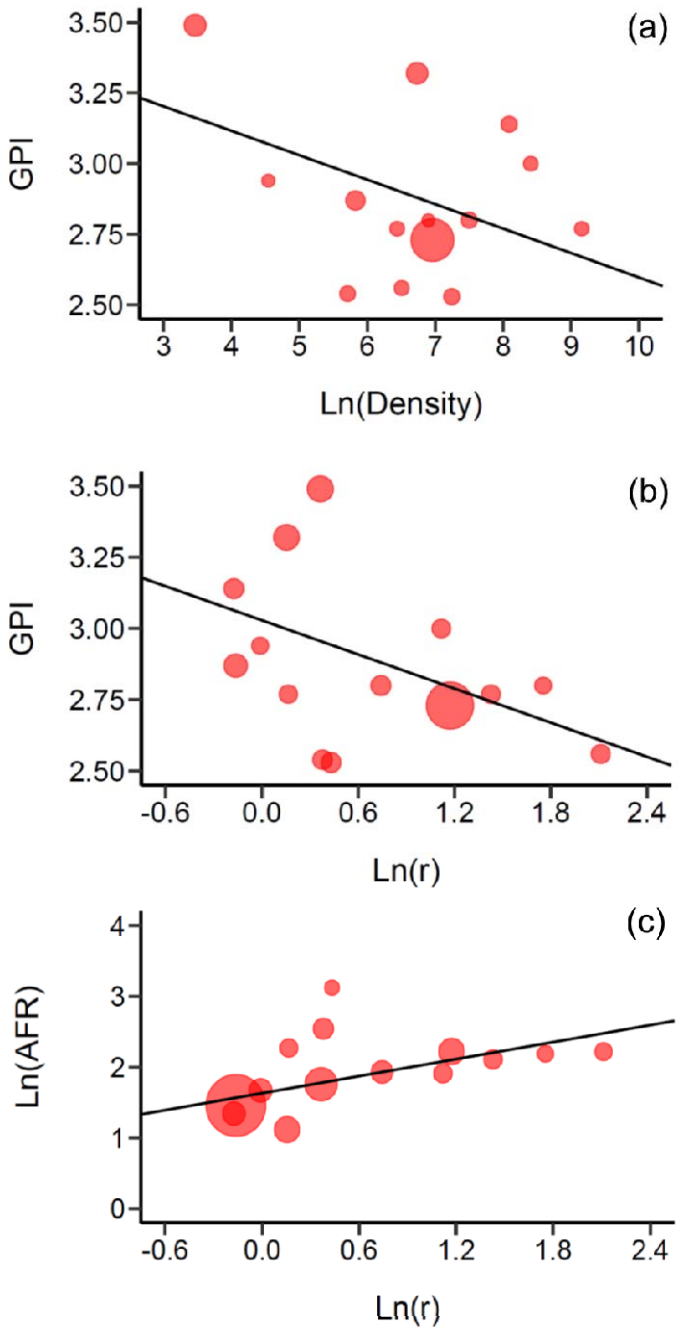
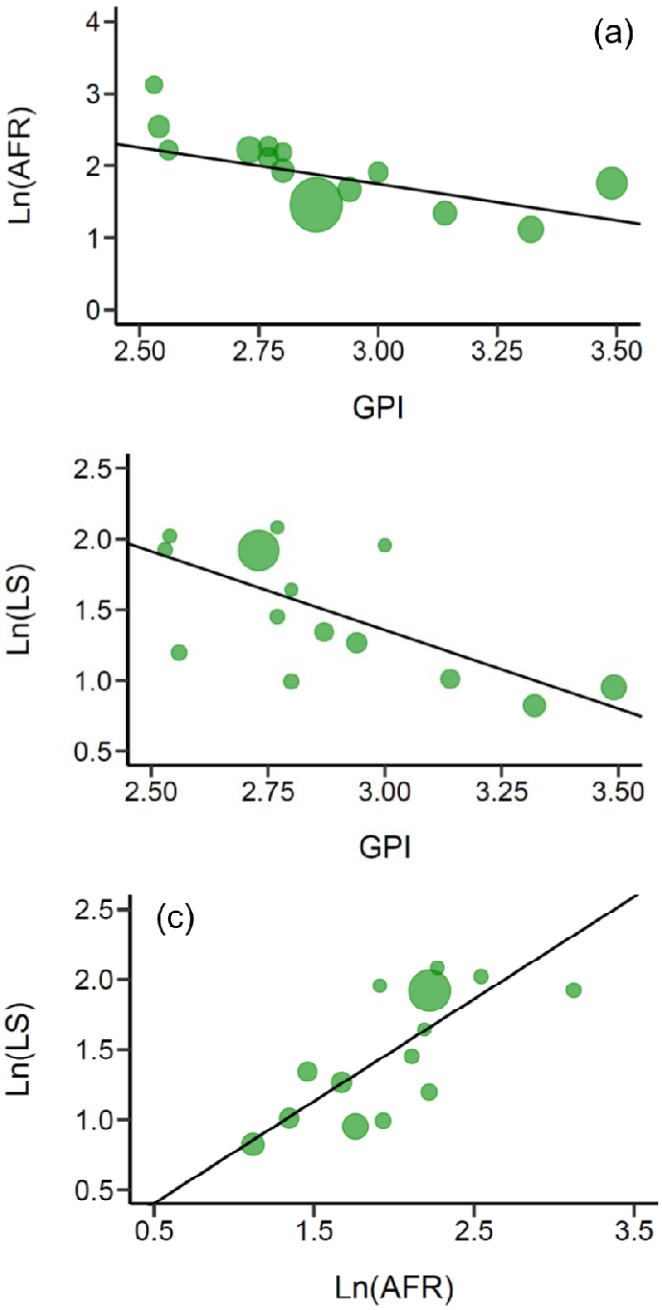
Figure 4. Relationship of age at first reproduction and lifespan of the same global invasive *Corbicula* populations in Fig. 2 with individual growth performance index (a, b) and with each other (c). The size of circles correspond to the inverse of the variance of mean value of each observation of the response variable, used to weigh effect sizes in the regression analyses (see main text for details). Age at first reproduction and lifespan were higher in populations with slow individual growth (R^2 = 0.39, P = 0.009 and R^2 = 0.56, P = 0.002, respectively), and lifespan was higher in populations exhibiting late reproduction (R^2 = 0.56, P <0.001). Note natural logarithmic transformation of some variables. Variable names as per Table 1.