Fitness-related traits are maximized in recently introduced, slow-growing populations of an invasive clam: is this a response to strong *r*-selection?

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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 being critical for understanding ecological and evolutionary factors that drive the process of range expansion of invasive species. Here we evaluated life history shifts of the widely introduced Asian clam *Corbicula* 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 show that (i) recently introduced *Corbicula* populations are characterized by low conspecific density and low population growth rate, (ii) clams reproduce earlier in slow-growing populations, and (iii) density had no effect on population increase. Our findings support the standpoint that individuals from recently established populations of *Corbicula* face strong *r*-selective forces that favor traits associated with high reproductive rates, which could be interpreted as an effective mechanism to overcome difficulties associated with low densities and low population growth in newly colonized areas.

INTRODUCTION

The ongoing increase in frequency of extreme climatic events, caused by anthropogenic climate change, and global transport of people and goods is altering ecosystems by triggering a wide array of irreversible consequences (Walther et al. 2002; Bossdorf et al. 2005; Hoegh-Guldberg and Bruno 2010; IPCC 2014). Changes in local conditions, in particular those driven by human-induced climate change, are predicted to affect ecological processes across several levels of organization, likely over the coming decades. Such changes are altering the performance of individual organisms, the dynamics of populations and the distribution of species, ultimately modifying ecosystem properties and function (Hoffmann and Sgró 2011; Lonhart et al. 2019). Hence, many species are forced to rapidly respond to novel stressful environmental conditions when shifting their distribution and colonizing new areas.

If non-native species have difficulties in adapting to such conditions and fail to track projected environmental changes, populations become vulnerable to decline and extinction (Hill et al. 2011; Hoffmann and Sgró 2011; Strayer et al. 2017). These stressful conditions can have a strong effect on species life histories through the selection of traits that optimize population growth and survival from 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 through either continuous range expansion or jump dispersal are usually driven by a small number of individuals that are the first to arrive at a new point 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 and 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 rate of increase, often 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 that 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). Such comparisons could lead to erroneous interpretations of the patterns observed because it would be difficult to disentangle what were the processes (e.g. propagule bias and/or evolution in populations at spatial (dis)equilibrium) causing the shifts in life-history traits (Phillips et al., 2010 and references therein). Interestingly, only few studies have looked for such trait changes on introduced species across their global invasive range (Gaston 2009) despite 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.

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 and Baur 2007; Crespo et al. 2015). The successful invasion of *Corbicula* clams has been mainly attributed to their rapid growth and maturation, high fecundity, and high dispersal

making this bivalve genus one of the most relevant faunal non-indigenous groups in aquatic ecosystems (reviewed in Sousa et al. 2008a). Invasive freshwater *Corbicula* populations are constituted by a small number of lineages composed of hermaphroditic individuals, which reproduce through androgenesis, where the most widespread and abundant lineage is the so-called Form A/R, widely known as *C. 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.

Here we investigated how different life-history traits of the Asian clam *Corbicula* responded to different selective pressures occurring at varying population contexts within the introduced range: (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). 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 increase, individual growth rate, minimum age at sexual maturity, 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, and likely subjected to strong *r*-selective pressures with respect to those from older, long-established ones. We tested the hypotheses that population density and population growth increase with time since introduction. *Corbicula* is widely known to exhibit rapid population growth, being able to reach extremely high densities (reviewed in Mcmahon, 2002). Different studies suggest that *Corbicula*'s population dynamics are chiefly regulated by environmental conditions (e.g. Crespo et al., 2015, 2017; Gama et al., 2017), whereby population declines are typically driven by periodic mass mortality due to extreme hydro-meteorological events (Ilarri et al. 2011; McDowell et al. 2016; McDowell and Sousa 2019). This strongly suggests that invasive *Corbicula* populations primarily follows a non-density regulated population increase and, hence, they might not approach the carrying capacity as it happens with many other species (e.g. Brook and Bradshaw, 2006). In this sense, we expected density to have no

148 significant effect on population increase even within a wide range of densities in nature,
149 though high densities are considered likely to have a negative effect on individual
150 growth rates. We also asked whether clams that grow faster and reproduce earlier are
151 favored in slow-growing populations at the expanding front. A related prediction is that
152 clams that grow fast would have a shorter lifespan with respect to individuals exhibiting
153 slow growth.
154

155 # METHODS

156 **Literature search**

157 We exhaustively searched the literature for peer-reviewed articles on *Corbicula*
158 (*Corbicula fluminea sensu lato*) providing enough information to estimate the
159 individual growth rate, population density, population growth rate, time since
160 colonization, water temperature, and conductivity of global populations of this clam.
161 To do this, we first identified relevant studies from ISI Web of Knowledge (Web of
162 Science Core Collection, 1900 through 2017) by conducting a first search using the
163 field tag "topic (TS)" in the "Advanced search" option and the search string:
164 TS="Corbicula fluminea" OR TS="asia* clam" (search #1). We conducted a second
165 search including topics TS="population dynamic*" OR TS="population size*" OR
166 TS="population densit*" OR TS="population structure" (search #2). We ran a third
167 search using TS="growth" OR TS="individual growth" OR TS="population growth"
168 (search #3). Finally, we combined searches #2 and #3 into search #4 (#4= #3 OR #2),
169 and restricted the latter by search #1 to obtain a final set of candidate studies (search
170 #5= #4 AND #1).
171

172 This literature search was finished on 27 September 2018 and this protocol identified
173 215 candidate studies (database search: 215 candidates; gray literature and unpublished
174 data: 0 candidates). To identify papers potentially missing in this list, we subsequently
175 scanned the references in these papers and conducted a Google Scholar search using
176 keywords mentioned above and added 8 studies to this candidate pool (Fig. S1). A total
177 of 67 studies that belonged to research areas unrelated to the topic of the current study
178 (*e. g*., applied chemistry, toxicology, paleontology) were excluded from this candidate
179 pool by refining the set based in 'Web of Science Categories'. The resulting studies (n =
180 156) were finally inspected individually in detail to assess their eligibility for our
181 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. We finally retained a sample of 16 studies, covering 17 invasive populations of *Corbicula* from different ecosystems worldwide (n = 140 out of 156 were excluded; see Fig. S1 for further details on screening and eligibility criteria). Whenever population data was only graphically presented, we contacted directly the authors. However, if data were no longer available or authors did not respond, we used the WebPlotDigitizer software (http://arohatgi.info/WebPlotDigitizer/) to extract data and accurately estimate population density and growth rates.

Population density and population increase

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. *Corbicula* clams generally exhibit a bivoltine juvenile release pattern (i.e. producing two generations a year; Mcmahon, 2002; Sousa et al., 2008a), leading to 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. *Corbicula* populations exhibit rapid growth (Mcmahon 2002; Sousa et al. 2006, 2008a; Franco et al. 2012). Hence, the rate of population increase of *Corbicula* can be expressed by deriving the classical exponential growth equation:

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

To estimate the rate of increase (r), we set a criterion to determine relevant recruitment peaks in each study by using the average density throughout the study period as a threshold. We considered the lowest density value (N_0), the highest peak above it (N_t), and the time period elapsed between the valley and the peak (t). Intermediate density values comprised in each period (i. e. defined by N_0 and N_t) were used to fit the growth equation and obtain r. Population rates of increase 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 (see Fig. S2 for further details on the step-by-step procedure to estimate population increase). 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 increase rate for such population was calculated as the average of single *r* estimations. Then, we standardized estimates by a year to make them comparable.

Individual growth rates and parameters

For studies that only presented data on length-frequency distributions, we identified age cohorts using that information and applied the Bhattacharya's method available in FISAT II software (Version 1.2.0, FAO-ICLARM Fish Assessment Tools; (Gayanilo et al. 2002). To confirm each component of normal distributions from the modal progression analysis, we used the NORMSEP method also available in the FISAT II software (Pauly and Caddy 1985). Once we had cohorts identified for all the studies, we calculated individual growth parameters 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):

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

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

and

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

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).

Minimum age at sexual maturity

The minimum age at sexual maturity was estimated as the time (months) elapsed until clams reach the minimum size (shell length) at which invasive *Corbicula* clams become sexually mature, which, on average, is 10.0 mm ± 0.8 SE (n = 13 reported sizes). This value was obtained from shell sizes reported in the literature (Heinsohn 1958; Gardner et al. 1976; Kraemer and Lott 1977; Aldridge and Mcmahon 1978; Eng 1979; Kraemer 1979; Ituarte 1985; Kennedy and Van Huekelem 1985; French and Schloesser 1991; Rajagopal et al. 2000; Mcmahon 2002; Cao et al. 2017). We acknowledge that in some conditions and populations, clams might mature at a different pace and thus introduce a degree of error in such cases. While this error is unavoidable until more detailed data is available, we are confident that the 10-mm estimate applies to many real-life situations and thus our results based on it are robust.

Lifespan

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. The accuracy of the introduction date is generally very difficult to know, however, many of the studies used report range expansions of a conspicuous invader across well studied regions, where the appearing of the species might have been anticipated and readily detected by ongoing monitoring actions in the initial stages of invasion. Therefore, we consider that the possible error introduced should be moderated to low and the value obtained can be view as a good approximation. 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. Other biotic and abiotic variables are known to interact with temperature to drive growth rates of invasive bivalves (e.g. food availability, dissolved oxygen, heavy metal concentration; e.g. (Vohmann et al. 2010; Bonel and Lorda 2015). However, we only considered water temperature and conductivity in the analyses because they have been reported to play a key role on the *Corbicula*'s biology and ecology (Magnussen 2007; Franco et al. 2012; Crespo et al. 2017). Indeed, temperature has emerged as the most important variable explaining the current distribution and, also, predicting that climate change will favor the expansion of *Corbicula*'s into colder areas at higher latitudes (Gama et al. 2017). Likewise, salinity has been considered a key factor influencing the success and velocity of the invasion of new estuarine ecosystems (e.g. Sousa et al., 2006). As *Corbicula* populations considered herein belonged to a broad range of freshwater and estuarine habitats, we therefore included conductivity, which serve as a *proxy* of salinity levels. 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 five separate multivariate weighted linear regressions in order to test ecological processes and characteristics at three different (but non-mutually exclusive) levels: 1) population level, 2) population and individual level, and 3) individual level. In this sense, a response variable at the population level can be considered as an explanatory variable when analyzing a response at the individual level. In all cases, we computed the variance of the effect size from different populations, which were then used as weights in linear regressions. The inverse-variance weighting allows combining the results from independent measurements giving more importance to the least noisy measurements and *vice versa* (Borenstein et al. 2009).

We were interested in testing individual effects of predictors, which are related to life-history traits of *Corbicula* (hereafter reduced models). However, we added annual mean water temperature and conductivity as quantitative variables in each model (hereafter full models). Preliminary analyses showed that latitudinal effects are strongly correlated with water temperature ($r = -0.84$). Hence, it was excluded from the models to avoid multicollinearity. In some cases, we also included interaction terms between explanatory variables. We used the partial F-test to compare models—that is, full models with and without the interaction term, and full *versus* reduced models. As we had strong *a priori* hypotheses as to the direction of effects, we used one-tailed tests. Variables were Ln-transformed to fulfill the models' assumption of normality and homoscedasticity, which were tested using the *gvlma* package (Peña and Slate 2006). Prior to analyses, we standardized explanatory variables to zero mean and a unit of variance in order to get directly comparable effects. All analyses were carried out in R version 3.6.1 (R Development Core Team 2019). Values are given as means ± SE unless otherwise stated.

RESULTS

Literature search

Populations analyzed in this study belonged to Europe, North and South America (Fig. 1; Table 1). These included eight populations in the United States, three in France, three in Argentina, and three 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 rate of increase (*r*) varied from 0.37 to 189%, 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 colonization ranged 2 to 28 years in the populations studied (Table 1) and yearly water temperature ranged 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 an interaction term with variables of interest nor did temperature and conductivity in each model significantly increase its predictive power (for details see '*Model comparison*' in Supporting Information). We therefore report estimates and statistics from the reduced models in Table 2.

At the population level, we found that younger *Corbicula* populations (i.e. newly established) were characterized by low density and slow population growth rate with respect to older, long established ones (Fig. 2a, b). We found that density had no significant effect on population increase (Fig. 2c). When analyzing responses at the interaction between population and individual processes and characteristics, we found that clams tended to grow faster (marginally non-significant) in low-dense and slow-growing populations (Fig. 2d, e). In contrast, we observed a strong positive response of the minimum age at sexual maturity as a function of population increase, clearly indicating that clams reproduce earlier in slow-growing populations (Fig. 2f). This is directly linked to processes occurring at the individual level, where clams with higher growth rates reach the minimum reproductive size earlier (10 mm) and live less than clams that grow more slowly (Fig. 2g, h).

DISCUSSION

382 This is the first study that evaluates how population and individual parameters, involved
383 in the process of range expansion, varied in response to different selective pressures
384 occurring within the introduced range of the worldwide invasive Asian clam *Corbicula*.
385 Our main results showed that (i) recently introduced *Corbicula* populations are
386 characterized by low density and reduced rate of increase, (ii) clams reproduce earlier in
387 slow-growing populations, and (iii) population growth was unfettered by density
388 (summarized in Fig. 3).
389
390 Density of *Corbicula* populations increased with time since colonization, which is
391 consistent with the standpoint that recently established populations typically occur at
392 low conspecific density, below the carrying capacity (Cole 1954; Sakai et al. 2001).
393 Likewise, we found that population growth increased with time since colonization,
394 suggesting that, in newly colonized areas, populations could have experienced stronger
395 *r*-type selection favoring fitness-related traits effectively increasing the rate of
396 population growth, as it was observed in long established populations (MacArthur and
397 Wilson, 1967; Phillips, 2009; Burton et al., 2010). Population density did not predict
398 changes in the rate of population increase, as variation in population growth remained
399 relatively low even at high-density values. By definition, long established and denser
400 populations tend to be density regulated as they approach to carrying capacity (logistic
401 population growth; e. g. Phillips et al. 2010). Considering the so-called *r*/K selection
402 continuum, this implies that such population is predicted to shift from the *r*- towards the
403 K-endpoint (MacArthur and Wilson 1967)—that is, selection shifts a population from
404 density-independent to density-dependent regulation. However, *Corbicula*'s population
405 growth rate did not decrease with increasing density despite the fact that some of the
406 populations included in this study exhibit extremely high densities exceeding, in some
407 cases, 100,000 individuals per square meter (e. g. Eng 1979; Table 1).
408
409 Why population growth was unfettered by density regulation? A large number of
410 studies have analyzed density dynamics of *Corbicula* and commonly assumed that,
411 following exponential growth, the clam population achieves densities approaching the
412 carrying capacity of the environment (e.g. Sousa et al., 2006). However, to our
413 knowledge, no study have ever conducted (field or laboratory) experiments to test
414 whether population growth is limited by increasing conspecific density, which, in turn,
415 is expected to reduce local biotic resources. In other words, there is a complete lack of

416 knowledge on the true effect of density on population growth. On the contrary, different
417 studies have shown that *Corbicula*'s dynamics are chiefly influenced by environmental
418 variables (e. g. water temperature, conductivity, pH, and/or dissolved oxygen) and seem
419 to be less influenced by population's density (e. g. Crespo et al., 2015; Gama et al.,
420 2016). Indeed, periodic mass mortality due to extreme hydro-meteorological events (e.g.
421 extremely high or low temperatures, drought) could play an important role with
422 infrequent, but catastrophic population declines (>99% in some cases; Mouthon and
423 Parghentanian 2004; Ilarri et al. 2011; McDowell et al. 2016). These events have been
424 described (though not quantified) in several other systems as well (e.g. Vaughn et al.
425 2015; McDowell and Sousa 2019). Despite a given *Corbicula* population might
426 approach or even grow beyond the carrying capacity of the ecosystem, evidence from
427 previous studies (and those cited herein) suggests that population size significantly
428 varies with time. This means that the population is at non-equilibrium and that such
429 fluctuations (or boom-bust dynamics; e.g. Strayer et al., 2017) are likely driven by
430 density-independent factors, as the above-mentioned hydro-meteorological events.
431 Thus, it does seem reasonable to infer that *Corbicula*'s population growth rate is non-
432 density-regulated and do not level off at carrying capacity, as expected from a highly
433 invasive organism as the Asian clam (Mcmahon 2002). Our results suggest that this
434 bivalve seems to be far from approaching carrying capacity, even at extremely high
435 densities, supporting the idea that individuals from long established denser populations
436 do not face a *K*-selective environment but a less strongly *r*-selective pressure.
437
438 Clams tended to grow faster in low-density populations experiencing low rates of
439 increase. Likewise, *Corbicula* clams reproduce earlier in slow-growing populations. In
440 recently introduced populations, periods of negligible population increase can be driven
441 by non-mutually exclusive ecological and evolutionary adjustments such as Allee effect,
442 changing abiotic conditions, and adaptation and selection of new genotypes imposed by
443 novel environments conditions at the newly habitat (Sakai et al. 2001; Bossdorf et al.
444 2005; Davis 2005; Ricciardi 2012). Such conditions can lead to a strong selection on
445 life-history traits that optimize population increase and survival to maturity of offspring
446 (Stearns 1976, 1977). As predicted by life-history theory, individuals from recently
447 established populations (typically occurring at the invasion front) face stronger *r*-
448 selection relative to conspecifics from older populations (MacArthur and Wilson 1967),
449 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, thus, early reproduction support the standpoint that such populations faced strong *r*-selection, which favored traits associated with high reproductive rates in recently introduced, slow-growing populations.

The increase in individual growth is 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 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 increase 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 increase in size 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.

One can argue that the issues associated to low densities (e.g. Allee effect) would not apply to *Corbicula* populations as it has been largely assumed that this invasive bivalve reproduces mainly by self-fertilization, meaning that they do not need to find a partner to mate. However, cross-fertilization seems to be the norm in *Corbicula* clams whereas self-fertilization takes place on a less regular basis (see pp. 200, Kraemer et al., 1986), suggesting that this bivalve is rather a facultative selfer. In line with their findings, Hünicken et al. (2019) reported extremely low population densities at the southernmost invasion front in Patagonia where *Corbicula* has been established in the area for more than 15 years. This suggests that this clam would be predominately outcrosser, and not selfer because, otherwise, they would have shown an increase in density with time since colonization, which was not the case. Notably, despite the evidence found by Kraemer

484 et al. (1986) and their conclusions, somewhat the idea of self-fertilization as the norm
485 (and not as the exception), has been spread in the literature as an effective mechanism
486 by which a single individual would be capable of founding new populations (reviewed
487 in Mcmahon, 2002). Thus, experimental assays are needed to clearly determine under
488 which conditions invasive *Corbicula* would reproduce by selfing.
489
490 Is evolutionary adaptation to local conditions possible in *Corbicula*? All invasive
491 *Corbicula* populations analyzed in this study are constituted by androgenetic individuals
492 belonging to the same lineage (Form A/R), which are distributed all across Europe and
493 the Americas and characterized by an extremely low genetic diversity (see Pigneur et al.
494 2012, 2014 for further details). The question that arises is whether there is scope for
495 evolution in genetically depleted populations of *Corbicula*. One fundamental principle
496 of evolutionary biology is that the rate of change in response to natural selection is
497 proportional to the amount of additive genetic variation present (Fisher 1930). Decrease
498 in genetic diversity results in reduced evolutionary potential required to rapidly adapt to
499 the novel habitat conditions of the invaded range, among other issues related to critical
500 invasion phases (e.g. initial colonization, leading edges of range expansion; Schrieber
501 and Lachmuth 2017). It is still puzzling how *Corbicula*'s genetically depleted
502 populations succeed in their invasion process, which represents a case of genetic
503 paradox (Pigneur et al. 2014). One possible explanation is that invasive *Corbicula*
504 might exhibit a certain degree of genetic polymorphism linked to androgenesis (Pigneur
505 et al. 2012). Indeed, androgenesis in *Corbicula* clams combines features of clonal
506 reproduction and the ability of rare genetic material exchange through 'egg parasitism'.
507 Among other processes, egg parasitism enables a mixing of different nuclear genomes
508 when the maternal nuclear genome is incompletely extruded creating triploid
509 individuals (invasive freshwater *Corbicula* clams produce unreduced spermatozoa; i.e.
510 sperm cells are diploids; Pigneur et al. 2014).
511
512 The invasive lineage (Form A/R) considered in our study includes both diploid and
513 triploid populations, with triploidy being predominant (further details in Pigneur et al.,
514 2014 and references therein; Etoundi et al., 2019). As polyploidy can buffer deleterious
515 mutations and can lead to hybrid vigor (heterosis) with increased fitness (e.g. Otto 2007;
516 Selmecki et al. 2015), polyploid *Corbicula* clams with genotypes associated with broad
517 tolerance to environmental stressful conditions (usually found at the invasion front) may

be favored during an invasion process, and in the long term a general-purpose genotype may evolve (Pigneur et al. 2012). Therefore, evolved adaptation to local stressful conditions in newly colonized areas might be possible, though evolved responses might be limited by low levels of quantitative genetic variation (e.g. Dybdahl and Drown, 2011). Hence, further studies should focus on analyzing the level of ploidy within the most common invasive lineage (From A/R) and determine whether front/newly established populations show a higher frequency of triploids individuals, and thus, higher fitness, relative to those from core/long-established populations.

In conclusion, in this study we provide evidence supporting that different life history traits of individuals can respond to different selective pressures occurring at varying population contexts (e.g. time elapsed since the population foundation, low vs. high population density, and low vs. high rates of increase). Our results show that fitness-related traits, such as individual growth rate and minimum age at sexual maturity, are maximized in recently established, slow-growing populations, which experience a stronger *r*-selective environment with respect to long established ones. While these responses might be interpreted as an effective mechanism to decrease the risk of stochastic extinction associated with low densities at the invasion front, population increase seems to be independent of population density in a wide range of environmental conditions within *Corbicula*'s invasive range. Whether trait shifts resulted from plasticity or genetically based evolutionary change remain as an open question that could be addressed by conducting laboratory experiments under common-garden conditions. Although other relevant variables could not be considered in our models, this study represents a first step in the attempt to understand in a wide geographical perspective whether evolvability of fitness-related traits increases invasiveness of *Corbicula* during processes of range shift. Knowledge of rapid evolutionary adaptation is of high concern as a steadily increasing number species are forced to rapidly respond to novel stressful conditions as consequence of increasing global transport and human-induced climate change.

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TABLES

Table 1. Summary of ecological and growth variables (mean ± SD) of worldwide invasive populations of the Asian clam *Corbicula* reviewed from the literature. *Density* is the estimated abundance of clams at the study site (ind./m^2), *Pop.growth* is the rate of increase (%), *Time* is the number of years elapsed since population colonization at the time of the original study (years), *Ind.growth* is the individual growth rate (*GPI*, a *proxy* for individual growth rate), *mASM* is the minimum age at sexual maturity (months), and 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. 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	*Time*	Population parameters		Individual parameters			*ID#*	*Reference*
			Density	*Pop.growth*	*Ind.growth*	*mASM*	*Lifespan*		
Argentina	Punta Atalaya, Río de la Plata	3.5	339±405	2.20±0.01	2.87±0.07	4.30±0.13	3.83±0.57	1	Ituarte (1985)
	Paraná de las Palmas River	25.5	1,053±768	14.44±0.31	2.73±0.01	9.23±1.17	6.82±0.05	2	Cataldo and Boltovskoy (1999)
	Río Negro estuary	15.5	94±8.3	7.85±0.10	2.94±0.23	5.32±1.66	3.55±0.41	3	Hünicken et al. (2019)
France	Saone River	12.5	302±186	14.65±0.01	2.54±0.13	12.73±2.42	7.55±2.17	4	Mouthon (2001)
	Loire Lateral Canal	17.0	992±1209	41.17±0.12	2.80±0.24	8.93±5.95	5.17±3.00	5	Mouthon and Parghentanian (2004)
	Canal of Roanne	17.0	626±897	25.50±0.01	2.77±0.16	8.25±3.43	4.27±1.58	6	Mouthon and Parghentanian (2004)
Portugal	River Minho estuary	16.5	840±387	11.89±0.06	3.32±0.05	3.06±1.20	2.28±0.30	7	Sousa et al. (2008b)
	Mondego estuary	6.9	5,017±5,489	7.67±0.04	–	–	–	8	Franco *et al.*, 2012
	Casal de São Tomé	10.3	3,255±1,115	4.06±0.04	3.14±0.12	3.83±1.69	2.75±0.51	9	Rosa et al. (2014)
USA	Altamaha River	4.5	712±1,613	0.37±0.00	–	–	–	10	Gardner et al. (1976)
	Lake Arlington	2.0	32±11	11.94±0.03	3.49±0.05	5.80±0.60	2.59±0.20	11	Aldridge and McMahon (1978)
	Delta-Mendota canal	28.0	9,470±7067	4.53±0.03	2.77±0.17	9.69±4.07	8.03±2.75	12	Eng (1979)
	New River (Station 1)	2	316±654	9.40±0.02	–	–	–	13	Graney et al. (1980)
	Clear Fork, Trinity River	7.0	4,474±3,899	19.34±0.04	3.00±0.16	6.76±3.62	7.07±2.83	14	McMahon and Williams (1986)
	Mechums River	10.5	669±636	188.52±0.62	2.56±0.15	9.20±4.41	3.31±1.21	15	Hornbach (1992)
	Ogeechee River	10.0	1,398±1,096	6.23±0.00	2.52±0.12	22.72±9.17	6.85±1.63	16	Stites et al. (1995)
	Lake Tahoe	8.0	1,809±723	16.64±0.04	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 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	Estimate ± SE	Intercept ± SE	R^2	*F*-statistics	*num.df, den.df*	*one-tailed P*-value
Ln(*Density*)	Ln(*Time*)	0.454 ± 0.196	-0.906 ± 0.241	0.263	5.34	1, 15	**0.018**
Ln(*Pop.growth*)	Ln(*Time*)	0.936 ± 0.323	-0.518 ± 0.216	0.376	4.03	2, 14	**0.006**
	Ln(*Density*)	-0.522 ± 0.407					0.220†
Ln(*Ind.growth*)	Ln(*Density*)	-0.422 ± 0.265	0.098 ± 0.264	0.283	2.17	2, 11	0.070
	Ln(*Pop.growth*)	-0.473 ± 0.344					0.099
Ln(*mASM*)	Ln(*Ind.growth*)	-0.505± 0.179	-0.192 ± 0.171	0.601	8.28	2, 11	**0.008**
	Ln(*Pop.growth*)	0.460 ± 0.208					**0.024**
Ln(*Lifespan*)	Ln(*Ind.growth*)	-0.718± 0.184	-0.056 ± 0.192	0.559	15.20	1, 12	**0.001**

† two-tailed *P*-value.

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.

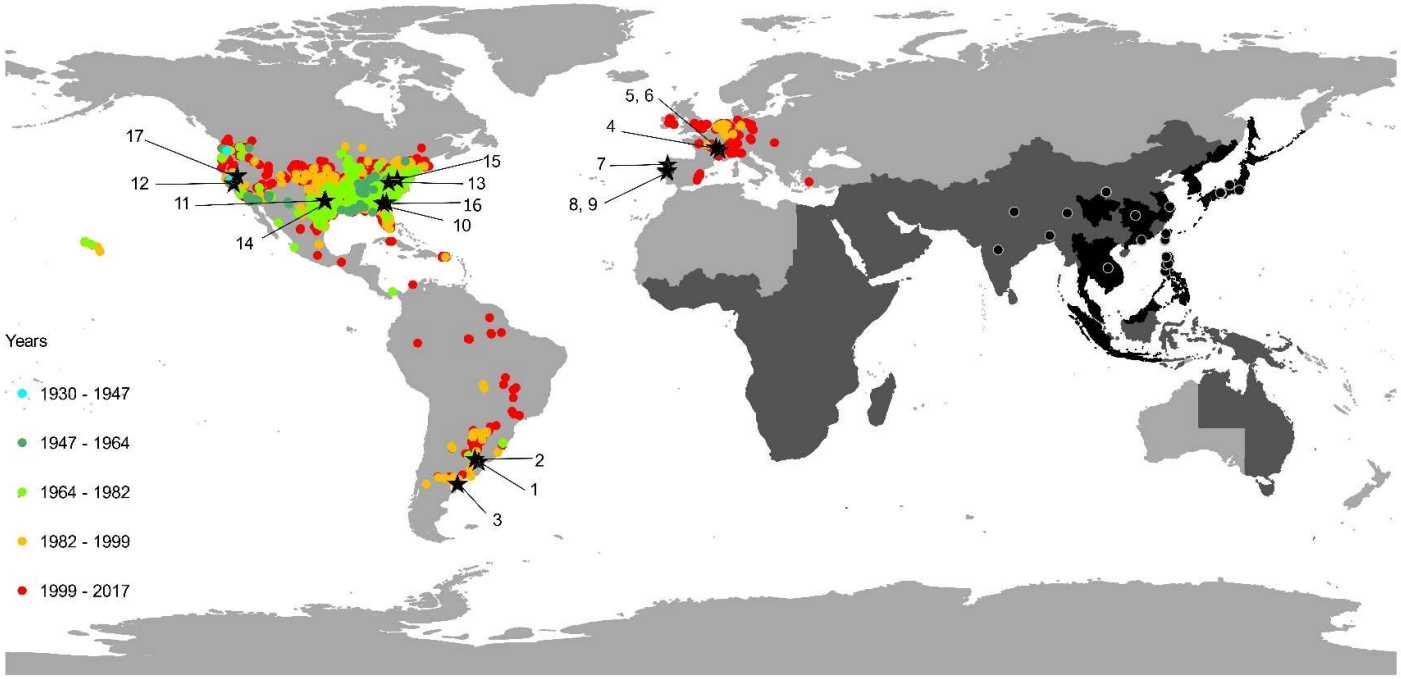

Figure 2. Relationships between processes and characteristics at different levels of organization of 17 global invasive populations of the Asian clam *Corbicula*. At the population level: a) the effect of time since colonization (*Time,* years) on population density *(Density*, ind./m^2*)* and b, c) the simultaneous effect of *Density* and *Time* on population increase (*Pop.growth*¸% rate of increase). At the interaction between population and individual level: d, e) the simultaneous effect of density and population increase on individual growth (*Ind.growth*, GPI), and f) the effect of population increase on the minimum age at sexual maturity (*mASM*, months). At the individual level: g) the effect of individual growth on the minimum age at sexual maturity, and h) on the *Life span* (years). When plotting the fit for one variable after testing for simultaneous effects, we removed the effect of the variable not considered (b, c, d, e). Dashed lines show fits when marginally significant 0.05> α <0.10. Solid lines show linear regression fits when statistically significant at α < 0.05. 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). Note natural logarithmic transformation of variables.

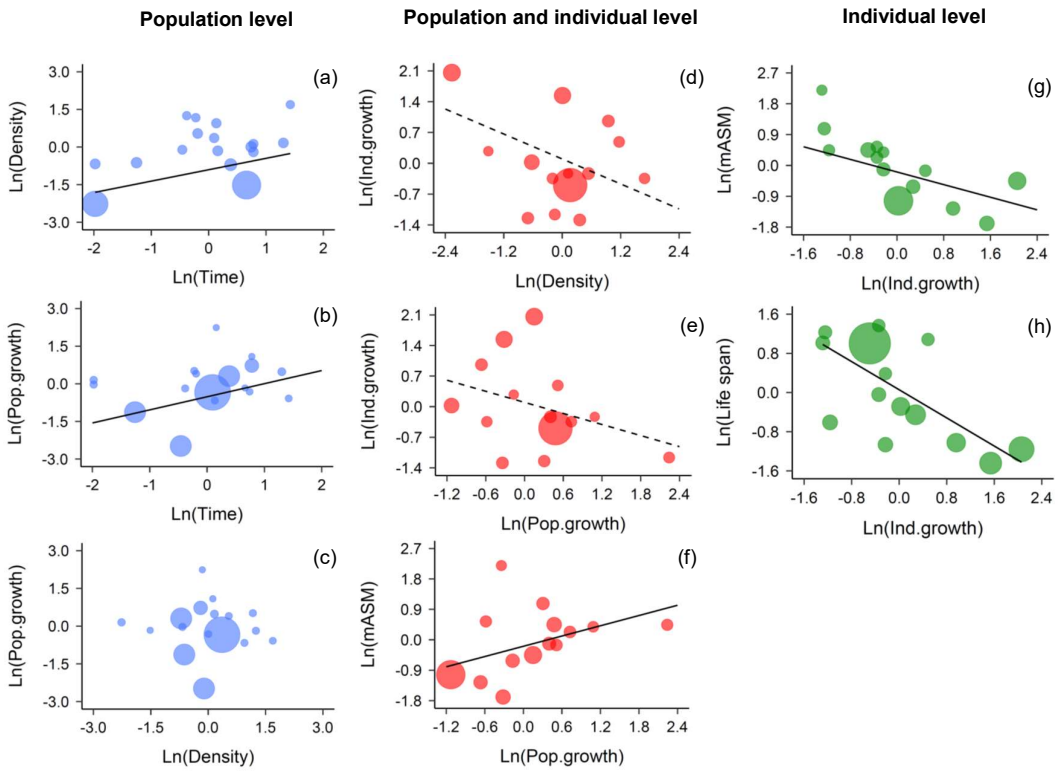
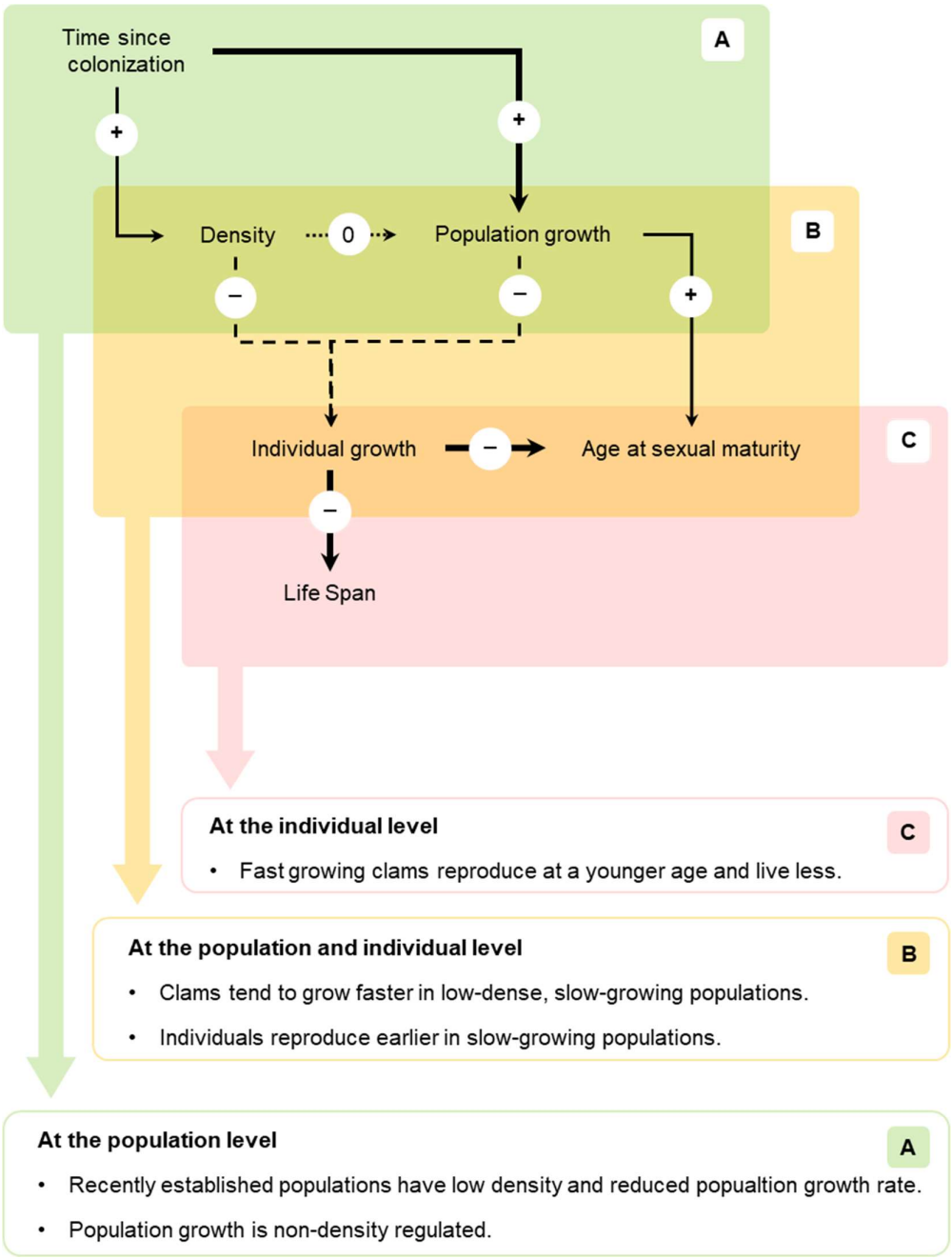
Figura 3. Summary of the relationships between processes and characteristics at different levels of organization of 17 global invasive populations of the Asian clam *Corbicula*, showing positive (+), negative (–), and no relationships (0) after fitting weighted linear regressions.Thick solid lines (➡) show linear regression fits when statistically significant at $\alpha < 0.01$. Thin solid lines (⟶) show linear regression fits when statistically significant at $\alpha < 0.05$. Dashed lines (– –➤) show fits when marginally significant $0.05 > \alpha < 0.10$. Dotted line (·····➤) show no significant relationship $\alpha > 0.10$. Relationships are shown at three different levels: A) at the population level, B) the interaction between processes and characteristics at the population and individual level, and C) at the individual level.