

Targeting clams: insights into the invasive potential and current and future distribution of Asian clams

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SUMMARY

Bivalves are among the main groups of invasive freshwater species, with the Asian clam genus *Corbicula* in particular being widely distributed. While global studies have focused on *Corbicula fluminea* (Müller, 1774), the invasive potential of *Corbicula largillierti* (Philippi, 1844) and *Corbicula fluminalis* (Müller, 1774) is still unknown. The spread of invasive species may be intensified by climate change. We estimated and compared environmentally suitable areas for these species under hypothetical climate scenarios, generating global maps of invasion risk. We found large climatically suitable areas for *C. largillierti* and *C. fluminalis* (under species distribution models) and that their invasive potential is currently underestimated. The analysis revealed many areas in which changing climate may favour the invasion of *Corbicula* spp.

Keywords: *Corbicula largillierti*, *Corbicula fluminalis*, *Corbicula fluminea*, invasive bivalves, species distribution model, areas of risk

INTRODUCTION

There has been increasing interest in the study of invasive species due to their strong impact on communities and ecosystems (Vilà *et al.* 2010). Freshwater ecosystems are particularly vulnerable to this threat: once a species has been introduced, it can spread using different vectors that facilitate passive dispersion among water bodies (Lucy *et al.* 2012). In particular, invasive bivalves are among the main groups of freshwater invaders with proven direct and indirect impacts on ecosystems, negatively affecting the native species and the biodiversity of invaded habitats (Sousa *et al.* 2014).

The negative effects of invasive species may be intensified by climate change, producing a positive feedback loop (Pyke *et al.* 2008). It has been predicted that climate change will

intensify during this century, accelerating global warming and changing precipitation patterns (IPCC 2014). This will affect aquatic systems by warming water temperatures, altering stream flow patterns and changing water chemistry characteristics (Poff *et al.* 2002). These changes are expected to produce profound effects on the distribution range and phenology of many species, altering community composition and aquatic ecosystem processes (Hellmann *et al.* 2008). Thus, climate change will force native species either to rapidly shift their distributional range or adapt to altered conditions (Williams *et al.* 2007). Given the particular life history characteristics of invasive species (including high fecundity, fast growth and early maturity), they can adapt faster to the new climate conditions than native species and potentially cause fundamental change to ecosystem structure (McMahon 2002).

One of the most problematic bivalve invasions is of the genus *Corbicula* (Mühlfeld, 1811). These clams may change the ecological condition of freshwater ecosystems, as they are able to alter biochemical cycles and food webs and to compete with native species (Sousa *et al.* 2008a, 2008b; Azevêdo *et al.* 2016). Additionally, their invasions have been associated with economic losses, since *Corbicula* can foul and obstruct filters and turbines, thus damaging cooling systems and affecting water reservoirs, power stations and water treatment plants, among others (Darrigran 2002; Rosa *et al.* 2011). The native distribution of the genus *Corbicula* covers areas of Asia, Europe, Africa and Australia (Lee *et al.* 2005; Sousa *et al.* 2008a). In the last century, natural and anthropogenic mechanisms have successfully dispersed the genus to many other areas (Sousa *et al.* 2007). Three species of the genus have become invasive beyond their native range. *Corbicula fluminea* is the most extended and problematic invasive species of the genus (Gama *et al.* 2016), and now is found in North, Central and South America (Karatayev *et al.* 2007). Gama *et al.* (2016, 2017) suggested that *C. fluminea* could still further extend its range. *Corbicula largillierti* has also been recorded as an alien species, with established populations in South and North America (Reyna *et al.* 2013; Tiemann 2014), while *Corbicula fluminalis* has been recorded as invasive in Europe and some countries of South America (Korniushin 2004; Martins *et al.* 2006). Despite these reports, the invasive potential of the latter two species is unknown and ignored.

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One means of defining areas potentially vulnerable to invasion is to utilize correlative models to map regions that fall within abiotic tolerances of a given invasive species (see Peterson *et al.* 2011). It is then possible to modify those models to reflect hypothetical future climate conditions (e.g. Nori *et al.* 2011; Guisan *et al.* 2014). To define the climatic niche and the invasive potential of the genus *Corbicula* under current and possible future climate scenarios, we estimated and compared their climate niches and potential global distributions and finally assessed the potential effects of climate change on their distributions. Our main goal is to provide useful information to guide conservation policies regarding the management of these problematic species in freshwater ecosystems.

MATERIAL AND METHODS

Occurrence data of the native and invasive ranges for the three species were obtained from the Global Biodiversity Information Facility (GBIF.org 2017). To improve records, we obtained additional data from bibliographical reviews (Supplementary Appendix S1; available online). For South America, where the databases and literature are sparse, we also obtained records from the collections of the Museo de Ciencias Naturales de La Plata (MLP) and the Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN). Records with questionable taxonomy at the species level were excluded. To reduce the effect of spatial autocorrelation and to avoid over-represented areas (Beaumont *et al.* 2009), we removed duplicate records. We cleaned the database using the SpThin package of R (R Development Core Team 2011; Aiello-Lammens *et al.* 2015), leaving a single 40-km radius record. Our final database contained 79 records of *C. largillierti*, 85 records of *C. fluminalis* and 458 records of *C. fluminea* (see Supplementary Appendix S2 for details).

Environmental data for current and future scenarios were downloaded from the WorldClim database (Hijmans *et al.* 2005). Initially, we considered the 19 available bioclimatic variables (annual mean temperature, mean diurnal, isothermality, temperature seasonality, maximum temperature of warmest month, minimum temperature of coldest month, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation seasonality, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, precipitation of coldest quarter), plus altitude with a spatial resolution of 2.5 arc-minutes (*c.* 5 km). Variables were assigned to baseline conditions corresponding to the average conditions of the time period 1950–2000 (Hijmans *et al.* 2005). To avoid collinearity among bioclimatic variables, we calculated the Pearson correlation coefficient for each pair of variables. For the modelling procedure, we included only the following low-correlated variables ($r < 0.75$): mean diurnal range, minimum temperature of the coldest month, maximum temperature

of the warmest month, precipitation of the wettest quarter, precipitation of the driest quarter and altitude.

To establish suitable areas for present conditions and to study potential changes linked with climate change, we generated species distribution models (SDMs). First, SDMs were calibrated and projected for current climate conditions. Then, these SDMs were projected for the same variables, but considering different future hypothetical climate scenarios. For future climate variables, we considered an intermediate representative concentration pathway (RCP) for the year 2050 (RCP = 4.5). Due to the large uncertainty among different global circulation models (GCMs) in species range projections (Diniz-Filho *et al.* 2009) and in order to cover the wide variability among them, four different GCMs were used: INMCM4, MIROC5, IPSL-CM5A-LR and CCSM4. The future scenarios were compiled using the Intergovernmental Panel on Climate Change's (IPCC) Fifth Assessment Report (www.ipcc.ch/report/ar5/).

Since alternative SDM algorithms have different levels of accuracy under different circumstances and there is no single 'best' method, multiple algorithms were combined into ensembles (Araújo & New 2007). We built the ensembles based on four different algorithms, with different mathematical complexities (Rangel & Loyola 2012): generalized linear models, generalized additive models, generalized boosting methods and random forests. All algorithms were implemented using default settings in the biomod2 package (Thuiller *et al.* 2009) of R (R Development Core Team 2011). We generated 200 projections for each species (4 algorithms \times 5 climate scenarios \times 10 repetitions). Final ensembles for each climate scenario (current and four GCMs) corresponded to a weighted average of those projections with area under the receiver operating characteristic curve (AUC) values higher than 0.8 and true skill statistic (TSS) values higher than 0.6 (see description of evaluation parameters below). To generate a consensus ensemble for future predictions, we calculated the average raster of the ensembles of all GCMs in ArcGIS 10 (ESRI 2010). To analyse the effect of climate change on suitability patterns of both species, we calculated the difference between current and final ensembles using the 'Raster Calculator' tool in ArcGIS 10 (ESRI 2010).

Environmental conditions within the distribution range of invasive species provide essential information for the implementation of SDMs, and SDMs exclusively calibrated with data from the native range are prone to misrepresent potential distributions of species (Broennimann *et al.* 2007; Jiménez-Valverde & Lobo 2007; Beaumont *et al.* 2009). Therefore, our models were calibrated including records from native and non-native ranges worldwide. Additionally, calibration areas have important implications in model calibration and evaluation (Lobo *et al.* 2008; Barve *et al.* 2011) and must be carefully thought out for each study. In these particular cases, given the ability of the species to disperse throughout the world by human transport, pseudo-absences were randomly generated worldwide. We used 70%

Table 1 *Corbicula* spp. evaluation statistics and levels of variable importance (mean \pm SD). TSS = true skill statistic; AUC = area under the receiver operating characteristic curve; ALT = altitude; MDR = mean diurnal range; MTW = maximum temperature of warmest month; MTC = minimum temperature of coldest month; PWQ = precipitation of wettest quarter; PDQ = precipitation of driest quarter.

	<i>Corbicula largillierti</i>	<i>Corbicula fluminalis</i>	<i>Corbicula fluminea</i>
TSS	0.82 \pm 0.07	0.81 \pm 0.05	0.74 \pm 0.04
AUC	0.94 \pm 0.04	0.95 \pm 0.03	0.93 \pm 0.02
ALT	0.07 \pm 0.08	0.11 \pm 0.10	0.17 \pm 0.04
MDR	0.12 \pm 0.17	0.16 \pm 0.21	0.06 \pm 0.02
MTW	0.28 \pm 0.23	0.12 \pm 0.12	0.14 \pm 0.07
MTC	0.34 \pm 0.24	0.37 \pm 0.12	0.46 \pm 0.08
PWQ	0.18 \pm 0.13	0.19 \pm 0.14	0.03 \pm 0.02
PDQ	0.09 \pm 0.11	0.22 \pm 0.22	0.19 \pm 0.06

of occurrences to calibrate and the remaining 30% were used to evaluate each model (Guisan & Thuiller 2005).

For model evaluation, we implemented the TSS (Allouche *et al.* 2006) and the AUC (Fielding & Bell 1997). In addition, biomod2 allowed us to evaluate the importance of the variables (from 0 (poor) to 1 (very important)) by randomizing one variable at a time and calculating the correlation between the randomized and the true model (Thuiller 2003).

Finally, in order to explore and compare the climate requirements of each species, we estimated the overlap between their climate niches, specifically calculating Schoener's D statistic (Schoener 1968). From these overlaps, a similarity test was performed (Warren *et al.* 2008). This test shows whether species niches are more similar (or dissimilar) than expected at random (Warren *et al.* 2008). To carry out these tests, we implemented the PCA-env approach proposed by Broennimann *et al.* (2012) in the Escopat package in R (Di Cola *et al.* 2017), with the five climate variables selected to model and 100 replicates to infer the statistical significance.

RESULTS

Projections for the three species performed well, with overall mean AUCs of 0.94, 0.95 and 0.93 and mean TSSs of 0.82, 0.81 and 0.74 for *C. largillierti*, *C. fluminalis* and *C. fluminea*, respectively (Table 1). Although the minimum temperature of the coldest month was the most important predictor for all species, other predictors differed in importance among species (Table 1). Variation in the distributions of the three species under different minimum and maximum temperature ranges, as well as different altitudes worldwide, is given in Supplementary Appendix S3.

For current conditions, the SDM projections showed a high concordance with geographic records of the species. Additionally, we detected new suitability areas where the species has not yet invaded. For *C. largillierti*, these

include south-eastern North America, the whole of Central America, central and southern Europe, southern Africa and eastern Australia. Other areas in northern and south-western New Zealand and southern Asia were also detected as suitable for this species (Fig. 1(a)). For *C. fluminalis*, large suitable areas were detected in Europe, south-western Asia, southern Australia and south-eastern South America (Fig. 1(b)). Finally, highly suitable areas for *C. fluminea* were located in New Zealand, south-eastern Australia and Europe, a small zone in northern and southern Africa, Madagascar, south and south-eastern South America and central and south Asia (Fig. 1(c)).

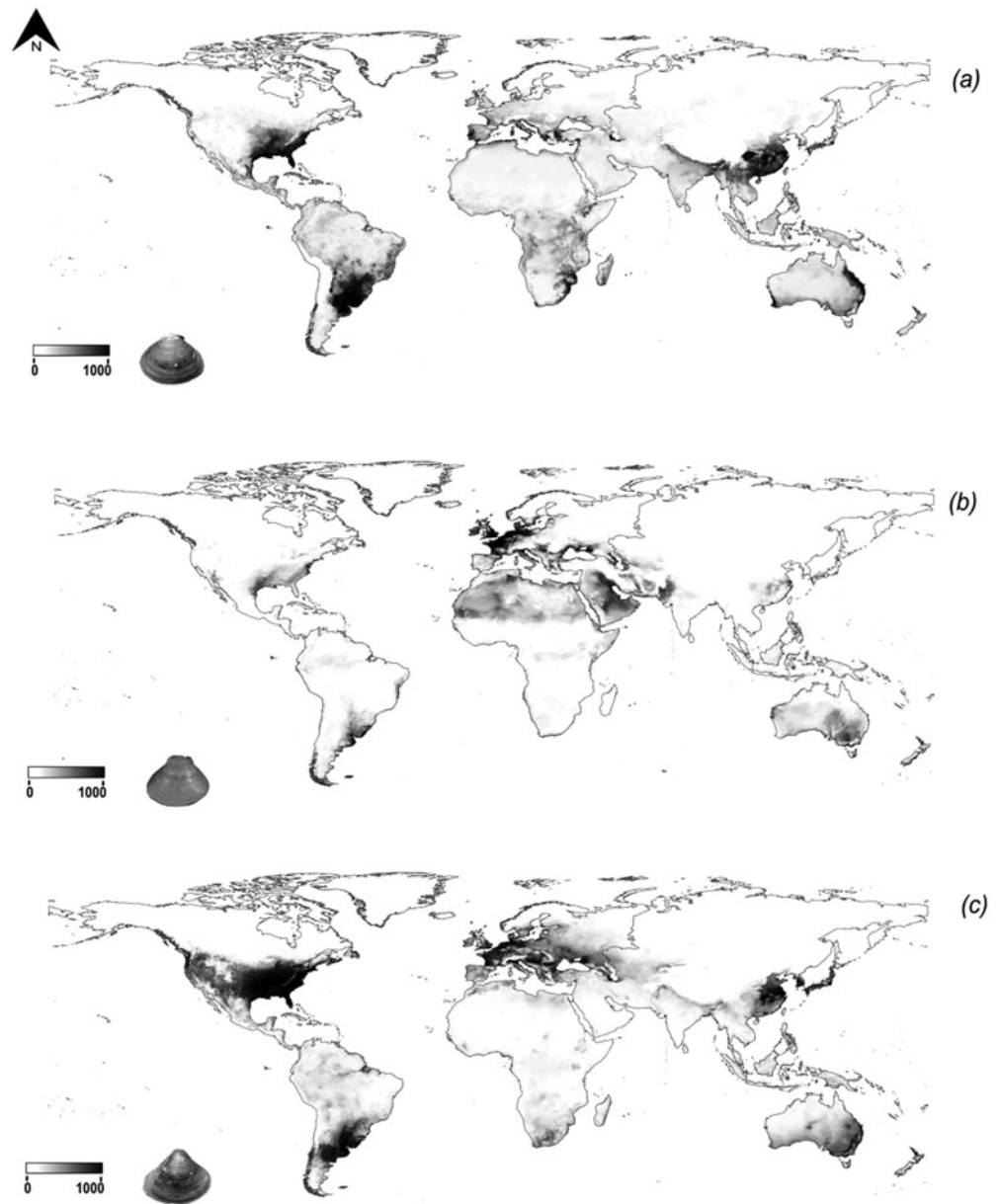
While most areas would remain relatively stable for the three species, future projections revealed potential areas of significant changes in suitable climate conditions. These projections showed expansion areas for *C. largillierti* (i.e. areas with high suitability values only in future predictions) located in southeast North America, southern and central South America, central and northern Europe, central and eastern Asia, southern Africa, south-eastern Australia and central Madagascar (Fig. 2(a)). *C. fluminalis* showed increasing areas in north-eastern North America, South America, Australia, north-eastern Europe, western Asia and northern Africa (Fig. 2(b)). *C. fluminea* showed increases in climate suitability in Central America and in a band along North America, toward central and north-eastern Europe, southern South America as well as central and eastern Asia (Fig. 2(c)). On the other hand, 'retraction' areas (i.e. areas with high suitability values only with current predictions, not in the future) for *C. largillierti* were mainly located in central and northern South America, southern North America, southern Africa, north-eastern and southern Australia, Central America and in central and east Asia (Fig. 2(a)). For *C. fluminalis*, these areas were southern South America, small areas of south-eastern Asia, North America, Australia and in some parts of Europe (Fig. 2(b)). For *C. fluminea*, they were located in southern and north-western South America, northern Central America and southern North America. Other 'retraction' areas for the same species were identified in an area corresponding to Europe and south-eastern Asia, Australia and northern and southern Africa (Fig. 2(c)).

The niche overlap results showed values of 0.17 between *C. largillierti* and *C. fluminalis*; of 0.42 between *C. largillierti* and *C. fluminea*; and of 0.46 between *C. fluminalis* and *C. fluminea*. The equivalency test showed that the three niches were not equivalent. The similarity test showed the niches of *C. largillierti* and *C. fluminea* and of *C. fluminalis* and *C. fluminea* to be more similar than was expected at random ($p < 0.05$; Fig. 3).

DISCUSSION

Our assessment for the first time of the invasive potential of *C. largillierti* and *C. fluminalis* also provided additional evidence of the great invasive potential of *C. fluminea*. Despite the narrower global (i.e. native plus invasive) distribution of *C.*

Figure 1 Maps of global invasion risk of (a) *Corbicula largillierti*, (b) *Corbicula fluminalis* and (c) *Corbicula fluminea*.



largillierti and *C. fluminalis* compared to *C. fluminea*, their invasive potential should not be neglected. Both species share close biological characteristics with *C. fluminea*, such as a high fertility rate, short lifespan and fast growth, characteristics that give the latter species its high invasive aptitude (Ituarte 1994; Martins *et al.* 2006). In the light of our models, we pinpoint a potential shift in distribution as a consequence of future changes in climate.

Current distribution

At a global scale, climatic environmental limits can accurately predict the areas prone to colonization by freshwater invaders (Karatayev *et al.* 2007). This approach has been recently validated for *C. fluminea* (McDowell *et al.* 2014; Crespo *et al.* 2015; Gama *et al.* 2016). Our models predicted suitable

conditions and zones prone to invasion of *Corbicula* spp. and indicated areas of invasion where *C. largillierti* and *C. fluminalis* have not yet been reported.

In particular, we point out wide areas in which the potential distributions of the three invasive species overlap, highlighting areas with high suitability for them, such as central and southern South America, southern North America, south-eastern Asia, south-eastern Australia and Europe. A sympatric distribution of these species is very likely in those areas. This phenomenon was reported in areas of South America where they coexist (Callil & Mansur 2002; Martins *et al.* 2004). *C. fluminea* and *C. fluminalis* are also sympatric in Europe (Ciutti & Cappelletti 2009; Marescaux *et al.* 2010). In areas where the presence of more than one *Corbicula* species is possible, interaction between them could magnify the negative effect on native species and ecosystems (Jackson 2015).

Figure 2 Maps of shifts of future distributions of *Corbicula* spp. showing differences between current and future scenarios. Colour scale indicates expansion (black), stable distribution (grey) and retraction (white). (a) *Corbicula largillierti*, (b) *Corbicula fluminalis* and (c) *Corbicula fluminea*.

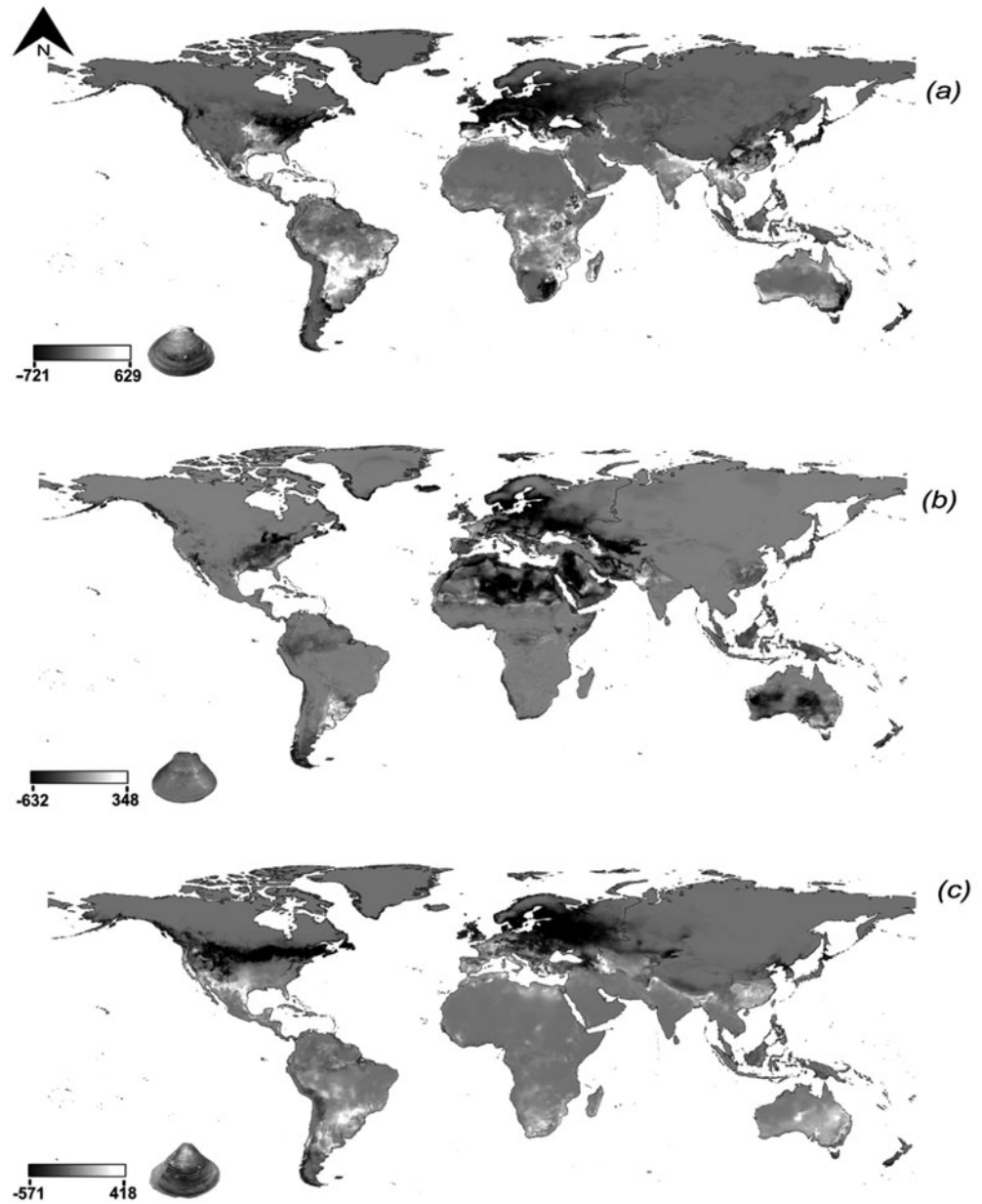
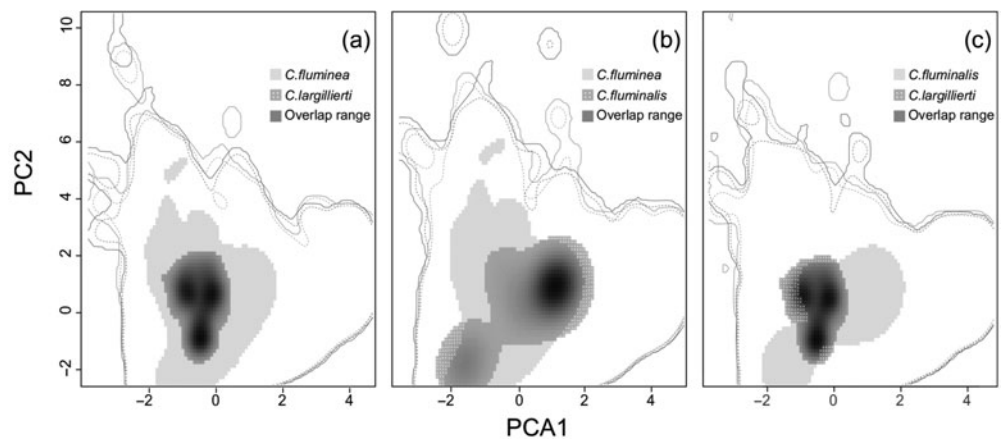


Figure 3 PCA-env niche overlap between *Corbicula* spp. (a) *Corbicula largillierti* and *Corbicula fluminea*, (b) *C. fluminea* and *Corbicula fluminalis* and (c) *C. largillierti* and *C. fluminalis*. The solid and the dashed lines correspond to 100% and 50%, respectively, of the available environment for each range of *Corbicula* spp. considered in the analysis.



The current relatively narrow distribution of *C. largillierti* and *C. fluminalis* could be explained by different hypotheses: (i) misidentification: even assuming the hypothesis of the existence of lineages from a specific complex, instead of truly species (Pigneur *et al.* 2011), differences between morphotypes really exist (Mansur & Pereira 2006; Martins *et al.* 2006; Reyna *et al.* 2013). The presence of *C. fluminea* could be overestimated compared to its congeners. The dispersion and invasion success of *C. fluminea* are well known even by non-specialists, and the presence, for example, of *C. largillierti* is frequently ignored. (ii) Different capacity for spreading and colonization: since our study highlights large climatically suitable areas for both species, different biological factors, such as a low tolerance to high salt concentrations, could prevent their establishment. It is thus important to note that only *C. fluminea* is present in brackish zones (Sousa *et al.* 2006) and is therefore easily transported in ballast water. (iii) Competition: although *C. largillierti* and *C. fluminea* may be sympatric, it seems that *C. largillierti* is a less effective competitor than *C. fluminea*. In the Rio de la Plata Basin (where the former species was recorded before than the latter one), the density of *C. fluminea* has increased over that of *C. largillierti*. Different kinds of interspecific competition, such as space interference, food exploitation or interference from the adults to larval settlement, can occur (Darrigran 1991). This competition may act to filter or force a given species to shift their distribution. (iv) Time of dispersion: *C. fluminea* was the first species of the genus to spread out of its native range during the first half of the 20th century (Araujo *et al.* 1993), while *C. largillierti* and *C. fluminalis* spread later, at the end of the 1960s and 1980s (Haesloop 1922; Ituarte 1981).

Our projection model for *C. fluminea* in current climate conditions is quite similar to that recently proposed by Gama *et al.* (2016, 2017). Central and western South America are detected as risk areas for invasion of *C. fluminea*, but the species has not yet been reported there. It is suspected that *C. fluminea* is already invading most of this area (Darrigran 2002), and the gap in the records is probably due to the lack of studies for the species. There are other areas with risk of invasion where the species has not been detected yet, such as New Zealand, a portion of southern Africa, Madagascar and central Asia. Most of south-eastern Australia is highly suitable for the species. Some authors have recently recorded that central and south-eastern Australia are part of the native range of *C. fluminea* (e.g. Karatayev *et al.* 2007).

The comparison among climate niches of the species revealed a partial overlap among them, which suggests that some characteristics of the ancestral niche are conserved. Wiens *et al.* (2010) state that niches of sister species tend to be somewhat conserved, but rarely identical. *Corbicula* spp. are distributed in some areas within the same climate range, and hence it is expected that their niches will partially overlap. This is consistent with the potential distribution obtained by SMDs. As the climate niche of *C. largillierti* and *C. fluminalis* is similar to that of *C. fluminea*, they may have a higher invasive

potential than previously thought, in view of the invasiveness of the latter species.

Effect of climate change on future distribution ranges

It is known that climate change benefits the spread of some freshwater invasive species, particularly in terms of expanding their distribution range into regions where they were previously not able to survive and reproduce (Bellard *et al.* 2013). Although our results suggest that most of the suitable areas for *C. largillierti*, *C. fluminalis* and *C. fluminea* will remain stable, we detected wide zones of expansion of climatically suitable areas in the future, particularly in North America and Europe. For *C. fluminea*, our results are consistent with those of previous authors (McDowell *et al.* 2014; Gama *et al.* 2017). In addition, the present results suggest zones of retraction of suitable conditions in different parts of the world, such as Australia and southern North America for *C. fluminea* and *C. fluminalis*, as well as South America for *C. largillierti* and *C. fluminalis*. These areas will probably be stressful for the species in the near future due to changes in a combination of variables, such as drought and high temperatures (McDowell *et al.* 2017). Given the potential reduced competitiveness of the species in these areas (Bellard *et al.* 2013), they could be important sites to focus on for prevention and/or eradication activities.

Gallardo and Aldridge (2013) suggested that an increase in minimum winter temperature would allow the northward expansion of invasive species due to winter warming. Weitere *et al.* (2009) demonstrated that an increase in temperature in winter had a positive effect on the growth rate and reproduction of *C. fluminea*. Our results showed the minimum temperature of the coldest month was the most important variable in the models for the three species. Considering that climate change will have an effect on minimum temperatures mainly in cooler climates (IPCC 2014), it is very likely that this effect may produce a change in the worldwide distribution of *Corbicula* spp. On the other hand, climate change could have a negative effect on native species (Sorte *et al.* 2013), making them less competitive or leaving empty niches that could favour the invasion of *Corbicula* spp.

There is increasing evidence that invasive species may benefit from climate change, with strong ecological and economic implications (Kernan 2015). Thus, prevention policies are among the best and cheapest strategies to control biological invasions (Pyke *et al.* 2008; Gallardo & Aldridge 2013). We highly recommend the control of human activities that are main dispersal vectors. Prevention could focus on fishers that sometimes use *Corbicula* spp. as bait, as well as the control of sports boats that move from one basin to another and the ballast water of ships that arrive in ports. Environmental education is another way to prevent or to detect invasive species early. Our results indicate that *C. largillierti* and, to a lesser extent, *C. fluminalis* have great potential to invade new areas. It is imperative to generate additional (such as physiological or demographic) information for management

policies to control potential invasion pathways for these species. Finally, we strongly encourage the consideration of our findings in future eradication and control programmes.

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CONFLICT OF INTEREST

None.

ETHICAL STANDARDS

None.

Supplementary material

To view supplementary material for this article, please visit <https://doi.org/10.1017/S0376892918000139>

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