

# Distribution of *Corbicula fluminea* (Müller, 1774) in the invaded range: a geographic approach with notes on species traits variability

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**Abstract** *Corbicula fluminea* is considered one of the most important non-native invasive species (NIS) in aquatic systems mainly due to its widespread distribution and ecological and economic impacts. This species is known to negatively affect native bivalves, also with severe effects on biodiversity and ecosystem functioning. Throughout an exhaustive bibliographic survey and with the aid of Geographic Information Systems tools, this study tracks the species dispersion from its native range, including the description of important physical and environmental barriers. Additional analyses were conducted to examine possible influences of latitudinal/temperature gradients on important traits (e.g. life span, maximum and mean body length, growth at the end of first year). Altitude and winter minimum temperature appear to be delaying the invasion worldwide, but it seems inevitable that the species will spread across the

globe. Latitude and summer temperature show a relationship with growth and life span. Overall, the information gathered in this review may be relevant to forecast future distribution patterns of this NIS, and to anticipate the possible implementation of effective management measures. Moreover, it may constitute a valuable tool in the prediction of population responses to an increasingly changing environment.

**Keywords** *Corbicula fluminea* · Invasive species · Vectors of dispersion · Geographic gradients · Invasion history · Species traits

## Introduction

In the last decades, globalization has been dissolving natural biogeographic barriers and allowing the

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transport (either inadvertently or not) of many species (Simberloff et al. 2013; Gutiérrez et al. 2014). These transported species, usually defined as non-indigenous, non-native or alien, could become invasive. By definition, a non-native invasive species (NIS) needs to expand its geographical range into an area not previously occupied, marked by successive stages of arrival, establishment and integration (Vermeij 1996). In introduced areas some of these NIS find niches with similar conditions to those available in the native range, but without their natural predators, parasites or competitors (Sakai et al. 2001; Torchin et al. 2003). Not surprisingly, NIS have been causing disruptions in native communities, and ultimately, a global biodiversity reduction due to, for example, predation, introduction of diseases and parasites, competition and altered abiotic conditions (Ruiz et al. 1997; Dukes and Mooney 1999; Revenga and Kura 2003; Sousa et al. 2008b; Butchart et al. 2010).

The traits that define the invading potential of a species have not yet been consistently tested, especially in animals. Anyway, high reproductive rate, single parent or vegetative reproduction, eurytopy, polyphagy, early maturation and small body size have been considered important (Kolar and Lodge 2001). Usually, these species show *r*-strategies (opportunistic behaviour), with several generations per year, short periods between spawning activity and spend a great effort in reproduction and recruitment (Den Hartog et al. 1992; Lavoie et al. 1999). However, the characteristics of NIS *per se* may be a highly reductionist view to define the invading potential because the characteristics of the invaded habitat (Byers 2002) and propagule pressure (Simberloff 2009), at least, may also play a fundamental role.

NIS are amongst the most serious threats that aquatic systems are currently facing, and their impacts are not always easy to follow (Strayer 2010). One faunal group responsible for high ecological and economic impacts in aquatic ecosystems comprises bivalves (Sousa et al. 2014). Within this group, *Corbicula* has become a threat during the last century due to its invasive potential (Nguyen and De Pauw 2002; Elliott 2008; Sousa et al. 2008a, b; Pigneur et al. 2011). With its origins in Asia, Australia and Africa, species belonging to this genus have spread worldwide during the twentieth century (Araujo et al. 1993; Sousa et al. 2007, 2008a) with *Corbicula fluminea* (Müller 1774) being considered one of the most important NIS in aquatic systems (Sousa et al. 2008a; Morais et al. 2009; Ilari and Sousa 2012). This species first established in the United States of America

(USA) during the first half of the twentieth century, entered the South American systems in the late 1960s/ beginning of the 1970s and reached Europe probably during the 1980s (Araujo et al. 1993; Mouthon 2001; Darrigran 2002; Morais et al. 2009). Human activities (e.g. ballast water transport, use as bait or as food resource, aquarium hobbyists releases, tourist curiosity) are considered the primary introducing vectors for this species (McMahon 1983; Vermeij 1996; Ruiz et al. 1997; Rigby et al. 1999; Lavoie et al. 1999; McMahon 2000; Bódis 2007; Sousa et al. 2008a). Also, pediveligers or juveniles can be dispersed by natural means, that include fluvial or tidal currents (Den Hartog et al. 1992; Rosa et al. 2012), or adhered with a byssal attachment to mobile animals such as birds and mammals (Prezant and Chalermwat 1984; McMahon 2000; Sousa et al. 2008a). As an opportunistic species, it is well adapted to colonize lotic and lentic ecosystems, with a very plastic feeding behaviour that includes both filter- and deposit-feeding (McMahon 1983; Sousa et al. 2008a; Dias et al. 2014).

Populations of *C. fluminea* seem to be negatively affected by the combination of hypoxia and high temperatures. The species show a clear preference for well oxygenated sandy substrates (Belanger et al. 1985). Mattice and Dye (1976) determined the lower and upper lethal temperatures as 2 and 34.8 °C, respectively. In the USA, the populations further north have been associated with the water outlets of steam electric power plants, which increase the temperature in adjacent areas and allow the survival during colder winters (McMahon 1983; Den Hartog et al. 1992). In addition, despite being usually described as a freshwater bivalve, it can tolerate salinities of 10–14 (McMahon 1983, 2000), allowing the species to colonize the upstream areas of estuaries (Sousa et al. 2006; Franco et al. 2012; Modesto et al. 2013).

As for reproduction, it usually presents two major spawning periods per year (McMahon 1983; Rajagopal et al. 2000; Sousa et al. 2008a). *Corbicula fluminea* is usually described as a simultaneous hermaphrodite, which incubates fertilised eggs within its inner demibranchs and releases pediveligers with reduced mobility to the water column that rapidly settle into the sediments (McMahon 1983; Rajagopal et al. 2000; Sousa et al. 2008a). This species is capable of androgenetic self-fertilization, which may increase its invasive potential: a single individual in the proper environmental conditions has enough potential to start a new population (Pigneur et al. 2011).

*Corbicula fluminea* can affect hydrology, biogeochemical cycling and biotic interactions via two general mechanisms: assimilatory-dissimilatory (uptake and release of energy and materials) and physical ecosystem engineering (physical environmental modification by organisms), with impacts ranging from individuals to ecosystems (Sousa et al. 2008a, 2009). This species alters community features, especially evenness, as it creates large monoculture patches on the invaded systems. Those changes often affect other natural processes such as productivity, nutrient cycles and community stability, by using resources in a different way (Ilarri and Sousa 2012). Several impacts of the species are reported in the literature: —*C. fluminea* is responsible for the creation of a different habitat matrix for benthic fauna via bioturbation and shell production (Ilarri et al. 2012); —it has high filtration rates (Sousa et al. 2008a); —it is a highly productive species, which may cause disruption on food chains, either as food source for higher trophic levels mainly when massive die-offs occur (Sousa et al. 2008b, 2012) and as a consumer, by reducing phytoplankton availability for other species and; —it may be responsible for alterations in biogeochemical cycles due to their pedal feeding, with consequential alterations in the abiotic characteristics of the top layer of the sediments and high rates of nitrogen excretion (Sousa et al. 2008a, and references therein).

Taking into account the ecological importance of this species and its high invasive potential, the objective of this work is to evaluate, through an exhaustive bibliographic survey, the effect of geographic gradients relating to environmental variables on the most descriptive population traits, such as the life span, maximum and mean body length and growth at first year. Simultaneously, we look upon those gradients in order to detect possible pathways of dispersion and areas of potential future introduction and establishment of the species. This information may help us anticipate future distribution patterns of this NIS and also to aid in the implementation of management measures. Moreover, this information may be used in the prediction of population responses to an increasingly changing environment.

## Materials and methods

For this review, a wide bibliographic survey was conducted on scientific publications, technical reports,

theses and web sites devoted to the NIS *C. fluminea*. The present work focused on population traits such as the number of reproductive periods, life cycle duration, first year growth, number of simultaneous cohorts, density, biomass, mean and maximum body length. Nevertheless, literature was very sparse with respect to some of those data and therefore it was not possible to use all of those population traits. The traits with more extensive and useful data were life span, maximum body length, mean body length and length at the end of the first year. Another metric that was looked at was the year of invasion. For each population, the geographic position was identified, either using the precise coordinates, whenever they were reported, or searching by their toponym with the Google Earth® search engine. In the case of wide areas and/or unspecified geographic coordinates, the central point of the system was chosen. The geographic data were loaded in the open-source software Quantum GIS (QGIS) Desktop 2.2.0-Valmiera together with all population traits associated with their respective coordinates. Data were transformed to raster layer using the Data Interpolation tool. The method used was the Inverse Distance Weight (IDW). The river basin shape files were obtained in the Water Base project site (<http://www.waterbase.org/home.html>) (George and Leon 2007). The invaded basins were selected and for better visualization, a fixed distance (1 map units) buffer was created. These shapes were used to cut the interpolation surfaces. The grids for temperature and altitude were obtained in the WorldClim site (<http://www.worldclim.org/>) (Hijmans et al. 2005), with a 2.5 arc-minutes resolution.

Information on the population traits was plotted against temperature and latitude classes (boxplots). These data were tested with an ANOVA being each population trait the dependent variable and temperature and latitude the explanatory variables. Prior to the analyses, we checked for collinearity among explanatory variables with variation inflations factors (VIF, Zuur et al. 2009). The assumptions of the linear regression were verified with graphical validation tools (Zuur et al. 2009). For the non-parametric data, Kruskal–Wallis tests were used. Also, the sighting sites were grouped and characterized according to geographic and temperature classes and their relation assessed. All analyses were performed with R software (R Development Core team 2012).

## Results

In the bibliographic survey we retrieved 1058 sites with sightings, based in 96 studies with data about *C. fluminea*: 74 scientific papers, 8 conference proceedings, 5 reports, 2 bulletins, 2 books, 2 book chapters and 1 MSc thesis.

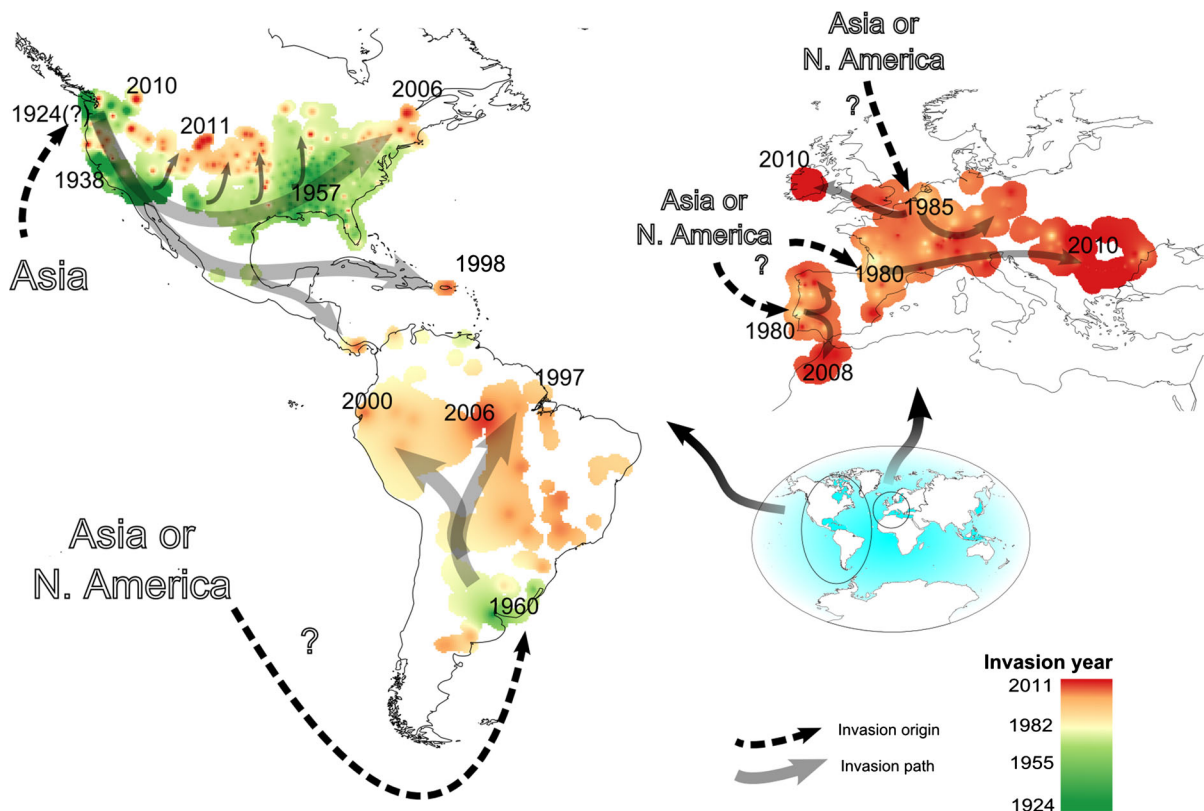
The first occurrence of *C. fluminea* outside its native range was recorded in North America in 1924 at Vancouver Island, British Columbia (Fig. 1). That occurrence refers to an empty shell found in a natural system. From the Vancouver Island, the species spread across the USA, apparently from Northwest along the coastal states, then crossing the southern states. The south-eastern states were reached during the 1950s. The most recent invasions of water basins by *C. fluminea* occurred in the twenty-first century, on the North and Northeast USA. Besides the 1924 event in the Vancouver Island, the species only appeared again in Canada in 2006 (Simard et al. 2012). Nowadays a high percentage of North and Northeast USA has been

invaded, especially in low altitude regions (Fig. 2a) and above  $-10\text{ }^{\circ}\text{C}$  winter air temperature (Fig. 2b).

Central America shows a more recent invasion that started around 1998 (Fig. 1). The number of sites for Central America is low (Fig. 2). Nevertheless, is possible to track an invasion pathway that crosses Mexico and reaches some Caribbean islands, in particular Puerto Rico (Williams et al. 2001).

The first reference in South America is in Rio de la Plata estuary (Ituarte 1981) by the end of the 1960s (Fig. 1). The number of invaded sites was lower than in North America (Figs. 2, 3). Still, invaded sites are mostly at low altitude, although the species can also be present at high altitude (Fig. 3a), and in considerably high temperature regions (around  $30\text{ }^{\circ}\text{C}$ , Fig. 3b). The progression from Argentina towards the Northeast of Brazil took nearly 40 years.

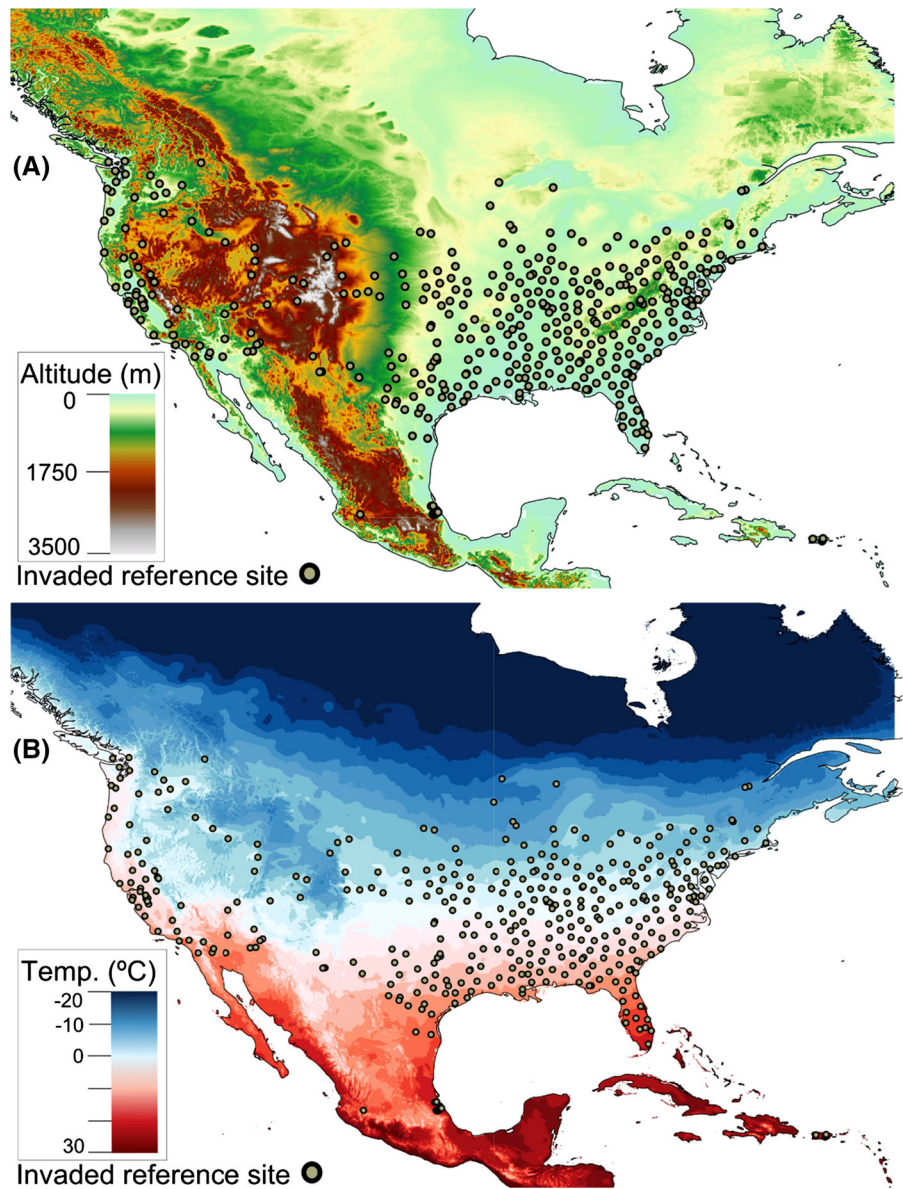
In Europe, the first records were described in the Tagus Estuary in Portugal and the Garrone Estuary in France in 1980 (Mouthon 1981), followed by the River Rhine, near Rotterdam (Holland) in 1985 (Fig. 1). The



**Fig. 1** Dates and main paths for *Corbicula fluminea* in the invaded range



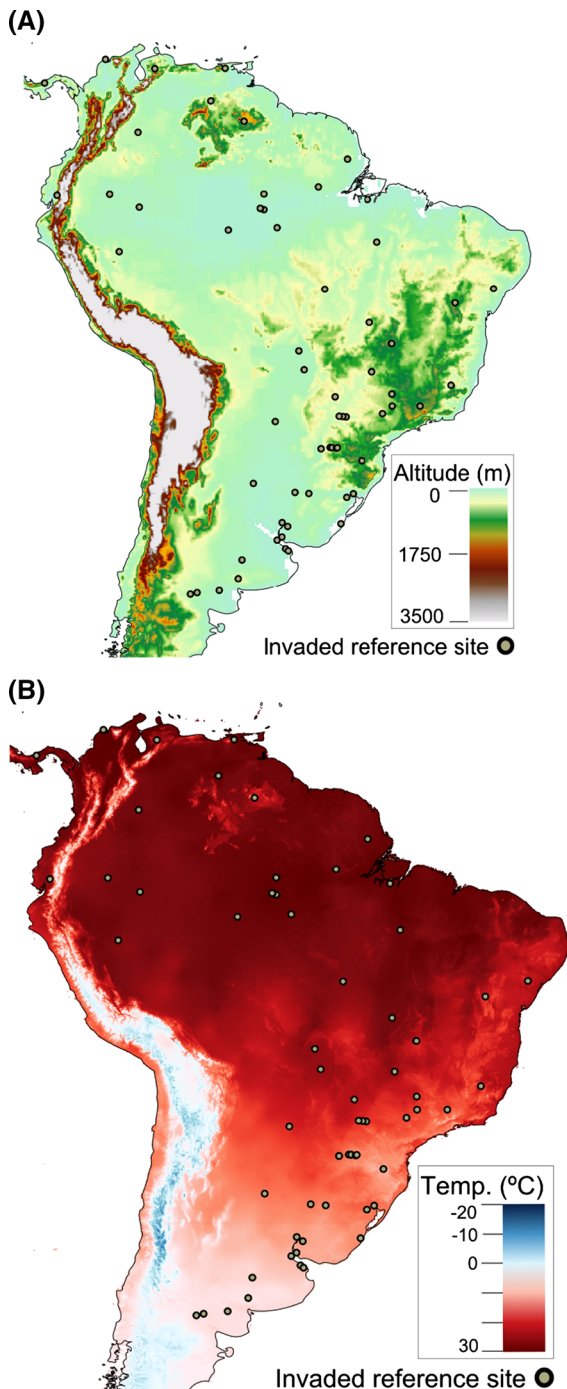
**Fig. 2** North and Central America digital elevation model (a), and average air temperature for January (1950–2000) (b). The invaded sites found in the bibliography are represented by dots



most recent invasions in Europe were recorded in Ireland (Caffrey et al. 2011), in some central European systems (Schmidlin et al. 2012) and in an Italian lake on the Alps (Kamburska et al. 2013). Almost all rivers and oligohaline estuarine areas in Portugal have been invaded by the species (Fig. 4). In remaining European countries, *C. fluminea* distribution appears sparser, with exception of France. Again, its distribution seems preferentially associated to low-altitude areas (Fig. 4a) and to regions with winter temperature higher than  $-5^{\circ}\text{C}$  (Fig. 4b).

Africa recorded its first invasion in Morocco in 2008 (Fig. 1) (Clavero et al. 2012).

The invaded sites exhibited some similar characteristics in terms of geography and temperature (Fig. 5). 88 % of invaded sites were below 500 m altitude (Fig. 5a) and more than 90 % were between latitudes  $30^{\circ}$  and  $55^{\circ}$  (Fig. 5b). In fact, no records or only recent records were reported in high altitudes such as Rocky Mountains (USA, Fig. 2a), the Andes (South America, Fig. 3a) or Alps and Pyrenees (Europe, Fig. 4a), although the species appeared in



**Fig. 3** South America digital elevation model (a), and average air temperature for June (1950–2000) (b). The invaded sites found in the bibliography are represented by *dots*

surrounding areas. More than 75 % of the sites were characterized by winter air temperatures between  $-5$  to  $10$  °C (Fig. 5c). In fact, for all continents only one

record was found below  $-10$  °C, and only occasional occurrences were registered around  $-5$  °C (Figs. 2, 3 and 4a). For summer temperatures, almost 97 % of the sites fall in the  $15$ – $30$  °C range (Fig. 5d). For annual average temperature, almost 90 % of the invaded sites were within  $5$ – $20$  °C, and from this range 40 % were located in the  $10$ – $15$  °C interval (Fig. 5e).

*Corbicula fluminea* population traits were plotted against geographic and environmental gradients to identify trends in those relationships (Figs. 6, 7, 8 and 9). The data used included all available information related to the traits more frequently found in the bibliographic survey. No statistical differences were found between the classes of life span, growth at the 1st year and mean body mass (ANOVA Life span: F-statistic = 1.528,  $p = 0.2168$ ; 1st year growth: F-statistic = 1.251,  $p > 0.05$ ; mean body length F-statistic = 2.487,  $p$  value: 0.0793). Yet, some trends could be identified: longer life span and higher mean body mass were found in higher altitude regions (apparent positive relation), while the growth in the first year generally decreased with increasing altitude (Fig. 6). In addition, a negative relationship between latitude and growth at the end of the 1st year and mean body mass seemed to occur. Temperature (summer and winter) showed a positive effect on 1st year growth and mean body length (Figs. 8, 9).

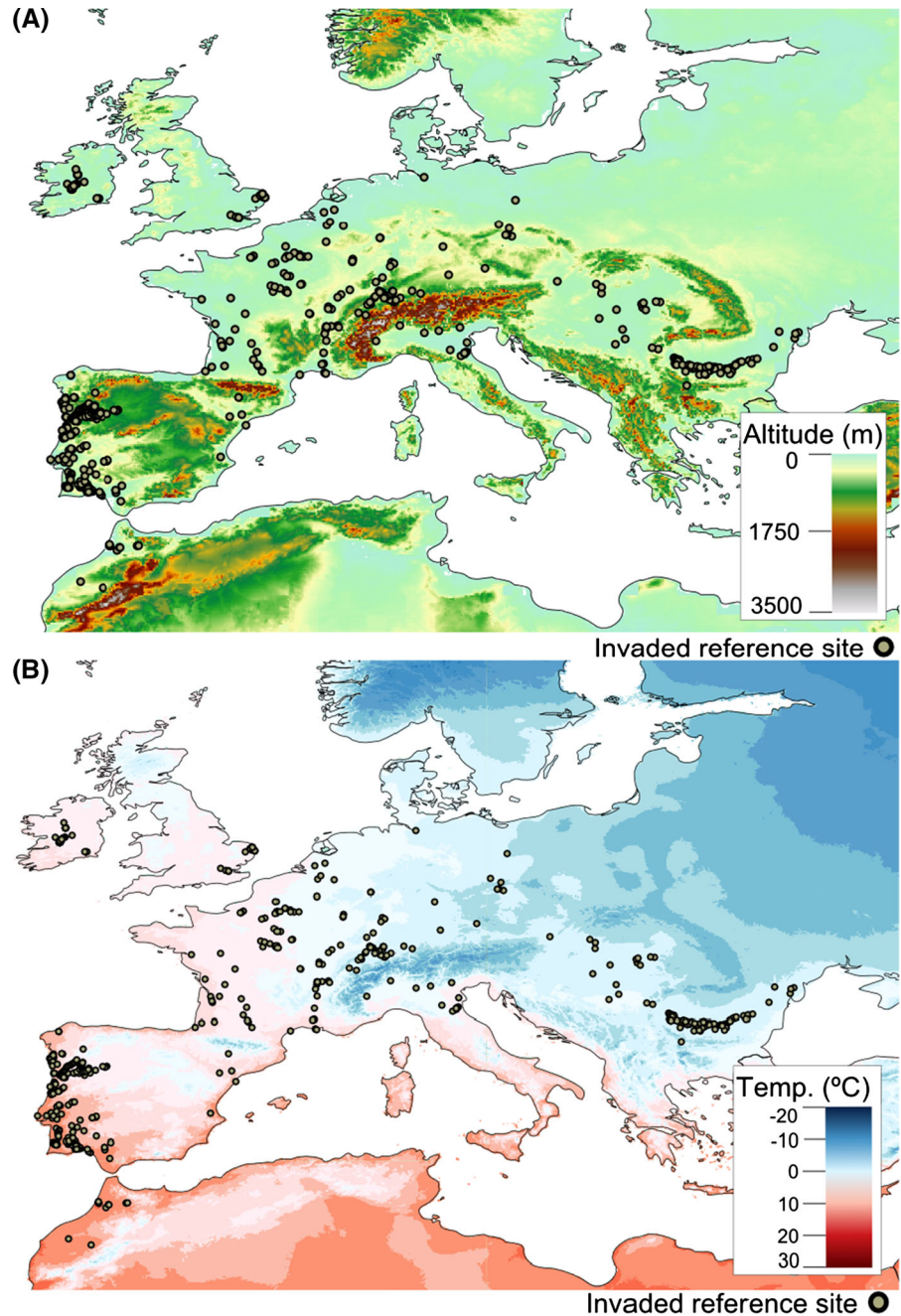
With regard to maximum body length alone, higher maximum body mass was associated with higher altitude (Kruskal–Wallis Chi squared—KW = 17.9156,  $p$  value  $< 0.001$ ), with higher temperatures (Summer temperature KW = 59.6941,  $p$  value  $< 0.001$ ; Winter temperature KW = 66.4444,  $p$  value  $< 0.001$ ) and lower latitude (KW = 52.8702,  $p$  value  $< 0.001$ ).

## Discussion

### Invasion history, paths and current record of *C. fluminea*

The dispersion in North America could be described as an arch, avoiding the central states of the USA until very recent years (Fig. 1). This may be related with the Rocky Mountains, crossing the continent from north to south, which acts as a barrier to the invasion of eastern areas. Indeed, many examples confirm the Rocky Mountains as a biogeographic barrier for fishes (e.g.

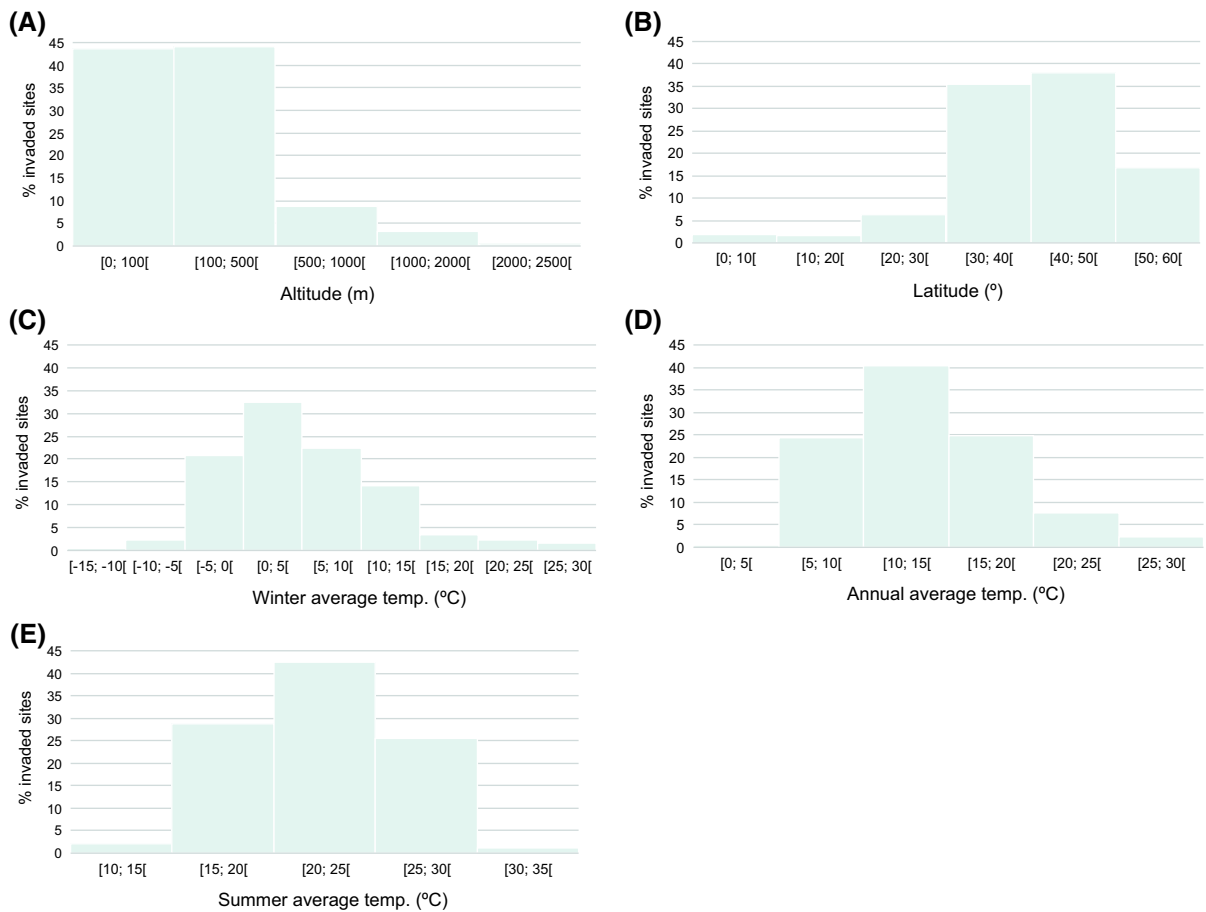
**Fig. 4** Europe and North Africa digital elevation model (a), and average air temperature for January (1950–2000) (b). The invaded sites found in the bibliography are represented by dots



Kruse et al. 1997; Adams et al. 2001; Rahel 2007; Smith et al. 2010) and invertebrates (e.g. Finn et al. 2006). The natural dispersion of *C. fluminea* seems to be limited by high slopes, characterized by low order streams. In the north, the limit is also defined by winter temperatures that fall below the lower lethal temperatures (2 °C, Mattice and Dye 1976). Apparently,

the invasion spread into new areas decreased with time for North America, taking about 82 years to spread from the Northwest to the Northeast coast. Still, there were some areas close to the oldest invasion sites with very recent introductions, probably related to human activities: (a) the building of new channels for water diversion, or channel widening can create new





**Fig. 5** Percentage of invasion sightings for **a** altitude; **b** latitude; **c** winter average temperature; **d** summer average temperature; **e** annual average temperature (n = 1058)

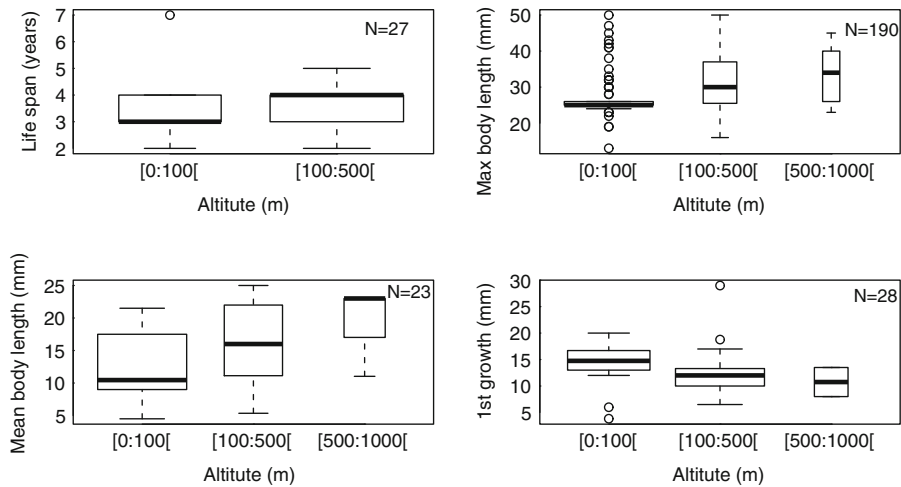
available niches for the species; (b) new industrial facilities that use water as cooling medium, create preferable conditions for new introductions, and therefore allowing for the species to appear in systems that, until that time, were protected against invasion; (c) the opening of water courses to recreational fisheries or other recreational activities could also be responsible for the introduction of the species in previously uninvaded areas.

The invasion in Central America probably resulted from a branch of the North American main invasive path. Some Caribbean isles were also invaded, probably following the main land invasion. This insular invasion was quite recent (1998) and, like similar island introductions, it was due to human activities since, as a freshwater species, *C. fluminea* is unable to survive an oceanic crossing (Verbrugge et al.

2011). Similarly to North America, Central America mountain ranges seemed untouched by this NIS.

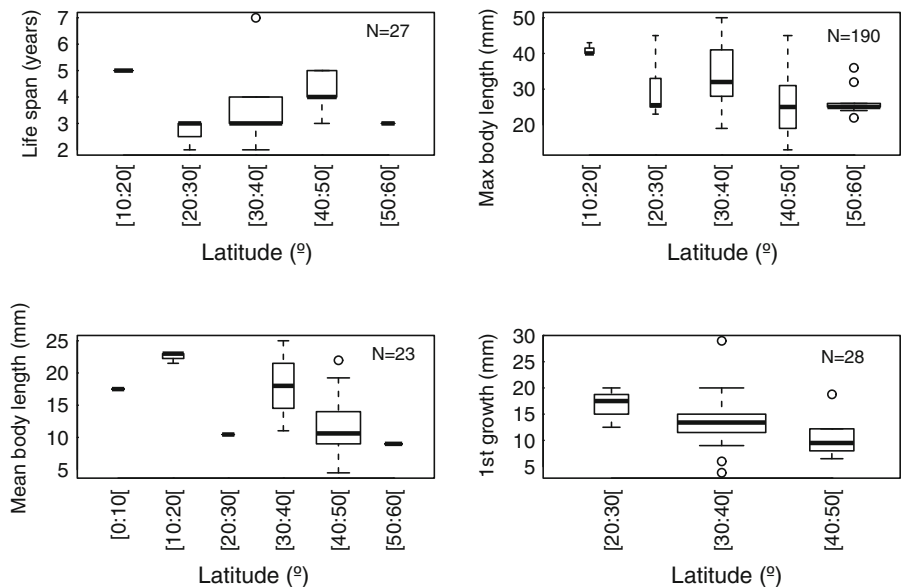
In South America, the origin of the introduction is still uncertain, although genetic studies suggest that south American populations shared some genetic similarities with North American populations (Lee et al. 2005). Therefore, hypotheses of a North American or Asian source are both viable. Apparently, the species has been kept away from the Amazonian Basin until recently. The high diversity that characterizes tropical habitats may be responsible for higher biological resistance (i.e. higher predation pressure, more parasites and diseases) and higher competition for resources, and therefore less susceptible to NIS establishment (Stachowicz and Byrnes 2006). Simultaneously, many of the water bodies in the Amazonian Basin are known to have anoxic waters (Scarpelli





**Fig. 6** Boxplots of the variation of life span, maximum and mean body length and length at the 1st year of growth per altitude. The *middle line* and extremities of the *box* are at the

25th, 50th, and 75th percentiles; the maximum length of each whisker represents the 5th and 95th percentiles



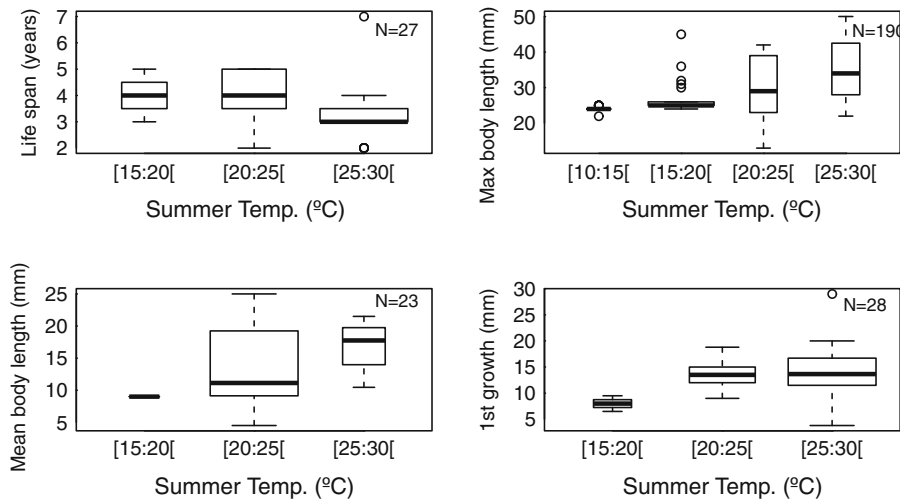
**Fig. 7** Boxplots of the variation of life span, maximum and mean body length and length at the 1st year of growth per latitude. The *middle line* and extremities of the *box* are at the

25th, 50th, and 75th percentiles; the maximum length of each whisker represents the 5th and 95th percentiles

2005; Bracho-Nunez et al. 2012; Junk et al. 2012), impairing the establishment of this species.

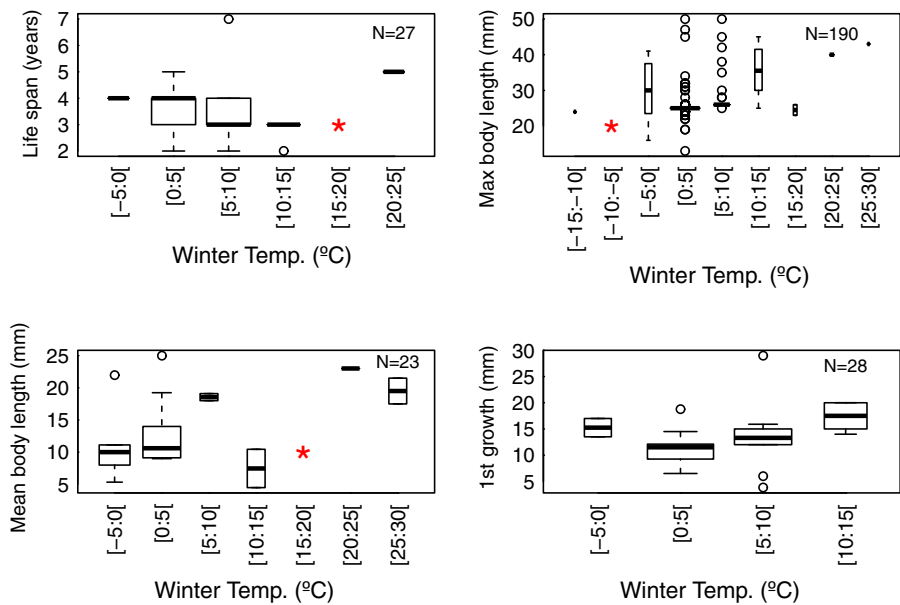
The species invasion did not occur in the higher mountain range of the Andes, where the high altitude probably acted as a barrier for invasion success. The winter temperatures, on average higher than those recorded in the North American continent, might have

also acted as a restrictive factor to the invasion, at least in the southernmost areas of the continent, where the average temperatures for June can be close to or below 0 °C. In addition, the oligotrophic conditions that characterize high mountain ranges act as an important limiting factor for the survival of many freshwater bivalves (Dillon 2004).



**Fig. 8** Boxplots of the variation of life span, maximum and mean body length and length at the 1st year of growth per classes of summer average temperature. The *middle line* and extremities

of the *box* are at the 25th, 50th, and 75th percentiles; the maximum length of each whisker represents the 5th and 95th percentiles



**Fig. 9** Boxplots of the variation of life span, maximum and mean body length and length at the 1st year of growth per classes of winter average temperature. The *middle line* and extremities

of the *box* are at the 25th, 50th, and 75th percentiles; the maximum length of each whisker represents the 5th and 95th percentiles. \*Classes with no occurrences

For Europe it was very hard to track a defined invasion path. The first records of the species were almost simultaneous and scattered across different geographic locations. This fact supports the theory that the introduction of the species across large scale distances is human mediated and connected with

maritime transportation (ballast water). Those introductions were responsible for the dispersal across Europe towards the Mediterranean and Eastern part of the continent. Britain and Ireland were recently invaded, probably, from already established populations in central and northern Europe. The Pyrenees

range might have acted as a physical barrier to the progression of *C. fluminea*, therefore, the central European populations could have origin on invasion episodes different of the Iberian ones (Fig. 1). In general, the invasion success was somewhat limited in the higher mountain ranges, low temperature regions and oligotrophic conditions.

For Africa, there are only recent records of the species in Morocco (Clavero et al. 2012). However, the species invasion in other African areas is possible, but going unnoticed due to the lack of environmental management and scientific awareness.

The data records presented in this study reflected the first invasive reference found in the literature, and the dates might present a slight delay relative to the real introduction dates. Nevertheless, Fig. 1 represents an accurate illustration of the main paths history of *C. fluminea* invasion. Even so, many uncertainties still exist about the global dispersion of this NIS and further biogeographic studies encompassing genetic data may be highly informative.

The USA showed a large record of invasion when compared with other countries. As the first country to be invaded by *C. fluminea* outside its native range, the awareness of the risk associated with the species has been raised very early on, as reflected, for example, on the US Geological Survey web site (<http://nas2.er.usgs.gov/viewer/omap.aspx?SpeciesID=92>), which displays a vast number of records of the species, with different levels of accuracy. Some regions across the globe may be less aware (e.g. South and Central America, Eastern Europe or Africa), and therefore the number of sightings might be underestimated. This could justify the difference on the number of sightings when comparing USA and the rest of the world.

In the worldwide invaded range, the southernmost reference is Negro River at Chimpay (Patagonia—Argentina) (Cazzaniga and Pérez 1999), with the latitude of  $-39.2034^\circ$  and longitude  $-66.159203^\circ$ . In the North Hemisphere, the most northern reference is the Shannon River at Carrick on Shannon (Ireland), with the latitude of  $53.9422^\circ$  and longitude of  $-8.087545542^\circ$  (Minchin 2014). The average winter air temperature in Chimpay falls to  $7.3^\circ\text{C}$  whereas at Carrick on Shannon it drops to  $4.3^\circ\text{C}$ . Nevertheless, there were other latitudes with more extreme negative winter temperatures: the coldest site in our database, with a winter average temperature of  $-13.8^\circ\text{C}$  is at St. Louis, USA (N  $47.02257876^\circ$ ; W  $92.21607517^\circ$ ). The

survival of the species in those locations was probably related to site-specificities: e.g. areas near industrial and residential water discharges that allow Asian clam populations to receive a constant input of warm water. These artificial conditions, in which the water temperature never goes under the vital limits of the species, allow the survival of *C. fluminea* in those geographic locations. Interestingly, in the northern hemisphere *C. fluminea* invaded further higher latitudes probably due to human activities that in one hand increased their dispersion rates and on the other hand enhanced the probabilities of establishment due to the thermal pollution associated with larger human agglomerates. In the southern hemisphere we have a less dense human population and thermal pollution is probably much less severe. Therefore, the thermal boundary is more effective in South America, only allowing the survival of *C. fluminea* at higher atmospheric temperature and lower absolute latitude.

According to this study, the preferable habitat for *C. fluminea* seems to be under 500 m of altitude, between the latitudes of  $30\text{--}50^\circ$  and annual mean temperature between  $5$  and  $20^\circ\text{C}$ , preferably  $10\text{--}15^\circ\text{C}$ . Higher altitudes and the oligotrophic conditions associated with the higher mountain slopes seem to limit the natural upstream dispersion of *C. fluminea*. A temperature of  $10\text{--}15^\circ\text{C}$  allows all vital biological activities of the species, including reproduction. In a scenario of predicted global warming, this may represent an increased challenge for management, because it widens an already extensive susceptible range for invasion (McDowell et al. 2014).

In the present study, the distinct distribution patterns across the invaded areas could be justified by three main reasons, gradually more relevant: (1) a differential biological resistance to invasion; (2) distinct amounts of human activities in the studied areas and; (3) an uneven research effort on the species.

#### Geographic and environmental gradients versus population traits responses

Despite the trends of lower 1st year growth and larger maximum and mean body mass with increasing latitude, winter temperatures do not seem to have such a clear influence on the body mass. This situation might be related to the thermal pollution in some of these low winter temperature areas (e.g. in  $-1^\circ\text{C}$  air temperature, Gollasch 2006). Summer temperature

seems to have a larger influence in the population traits, namely in the growth at the end of the 1st year and in the maximum body length. This could be related to more efficient metabolism during the growing season (Mattice and Dye 1976; Vidal et al. 2002).

Life span showed a positive relationship with the latitudinal gradient. Populations from higher latitudes have a slower growth, reflecting in general a slower metabolism and a longer life span. This type of relationship has been described for other mollusk species, including freshwater bivalves (e.g. Cardoso et al. 2002; Verdelhos et al. 2011; Varandas et al. 2013). On the contrary, populations at lower latitudes, with higher water temperatures, have higher growth rates and, consequently, shorter life spans. Also, the availability of food may be impaired at higher latitudes due to shorter sunlight periods. Colder environments reduce phytoplankton standing stocks on which *C. fluminea* mainly rely (although the species can also pedal feed and consume organic matter available in the sediments; Hakenkamp and Palmer 1999). Altitude may also play a role in this, because at higher altitudes nutrients availability is usually reduced.

We expected to have clearer patterns regarding the population traits and environmental gradient. Nevertheless, the species shows a high ecophenotypic plasticity (McMahon 2000) and local conditions may have a decisive role on the populations traits, which could confound the general latitudinal and geographic gradients.

The availability of calcium is also a fundamental issue for bivalves, as the shell is built on it. Organic matter is also fundamental for the growth of soft tissues as well as for the shell. Despite the lack of data on the hardness and nutrients for most of the sites where *C. fluminea* is present, it is expected that higher altitudes present lower calcium concentrations and oligotrophic conditions, thus contributing to the limiting of the species progression and populations growth in a synergistic effect with temperature.

## Conclusions

*Corbicula fluminea* invaded many ecosystems worldwide, being present from 39° South to 53° North latitude. In less than 100 years, it has invaded all continents, except Antarctica, making this clam one of

the most successful invasive species in aquatic ecosystems. This progression is human mediated and, apparently, only delayed by orographic constraints (e.g. high slope and oligotrophic conditions) and low temperature. However, the thermal pollution may help the species to establish beyond their current latitudinal and temperature limits.

It was possible to identify trends between latitude (and summer temperature) and some population traits such as growth in the first year and life span. Still, the highly ecophenotypic plasticity of the species makes those relationships less clear than expected. Simultaneously, the lack of a standard protocol for the study of the species population traits makes it harder to provide worldwide generalizations on the relationships between traits and invasion success.

Nevertheless, with the predicted climate change, one could expect that the species will go further beyond its current limits, invading freshwater and estuarine systems further north and south. Some of the high altitude systems have been already invaded. With the data gathered in this work, we hope to contribute to future models, where the susceptibility of certain geographical areas to invasion by *C. fluminea* may be predicted more accurately. Those models could be a precious help in order to detect the invasion in its earlier phases, eventually allowing successful eradication at lower ecologic and economic costs.

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