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Invasion status of the common carp *Cyprinus carpio* in inland waters of Argentina

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This study documents the presence of *Cyprinus carpio* in 119 natural environments and 49 artificial habitats in Argentina, showing an exponential increment of invaded locations over time since it was introduced in the nineteenth century. Geographic expansion patterns revealed that since its initial introduction, species records demonstrate an increment in the central portion of the country only after 1970 and subsequent expansion after 1990 to the north, west and south. Using an environmental similarity index it was determined that more than half the country offers good conditions for *C. carpio* establishment. Environmental factors and anthropogenic impacts are relevant drivers that can account for the current and future distribution of *C. carpio* in Argentina.

Key words: environmental similarity index; geographic expansion; invasive fish; lakes and reservoirs.

INTRODUCTION

Biological invasion is a process that involves the arrival of an organism into an environment in which it did not previously exist (Williamson, 1996). The consequences of this process are reflected in the interactions between the invading life form and the native members of the ecosystem (Lodge, 1993; Williamson, 1996). The introduction of a non-native species to an ecosystem exhibits a potential ecological risk if the species is able to establish a self-sustaining population in the new habitat (Gozlan & Newton, 2009), resulting in possible detrimental interactions (Gozlan *et al.*, 2010). Although some successful introductions have not caused negative impacts (Moyle & Light, 1996; Gozlan, 2008), introductions of alien species have often resulted in deleterious ecological effects on the ecosystem (Crivelli, 1983; Zambrano *et al.*, 1999; Parkos *et al.*, 2003; Kloskowski, 2011).

A notable example of this sort of introduction is the global introduction of the common carp *Cyprinus carpio* L. 1758. This invasive species is considered to be one

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of the most ecologically harmful freshwater fish (Koehn, 2004; Britton *et al.*, 2010; Kloskowski, 2011) and worldwide it accounts for most of the records of successful establishments (Casal, 2006; Kulhanek *et al.*, 2011). *Cyprinus carpio* exhibits high physiological tolerance to environmental stress, allowing it to survive in a wide range of abiotic conditions (*i.e.* temperature, dissolved oxygen, pH and turbidity) (Crivelli, 1983; Koehn, 2004; Zambrano *et al.*, 2006). In addition, *C. carpio* employs a generalist feeding strategy, capable of exploiting a wide range of food resources such as detritus, macroinvertebrates, zooplankton and plant material (Sibbing, 1988; García-Berthou, 2001). These adaptive life-history traits, together with rapid growth, early maturation and high fecundity (Colautti, 1997; Sivakumaran *et al.*, 2003; Winker *et al.*, 2011) make *C. carpio* not only a highly successful invader, but also a target species for commercial and aquaculture purposes. For these reasons, *C. carpio* is one of the most extensively translocated and domesticated species worldwide (Welcomme, 1988; Sivakumaran *et al.*, 2003; Casal, 2006; FAO, 2010).

The native distribution of *C. carpio* covers a wide area ranging from eastern Europe, eastward across Russia and China (Balon, 1995; Zambrano *et al.*, 2006). Due to introductions associated with human activities, however, the species is currently established on every continent, making it the most widely distributed freshwater fish (Sivakumaran *et al.*, 2003; Kloskowski, 2011). Although the worldwide *C. carpio* distribution has been modelled and predicted by global climatic conditions (Zambrano *et al.*, 2006), local factors based on environmental conditions, catchment morphology and anthropogenic effects can also be important and responsible for this species distribution at a local scale. According to Zambrano *et al.* (2006), the areas climatically suitable for *C. carpio* colonization in South America encompasses mainly Argentina, southern Brazil and southern Chile, but information about its current distribution and invasion status are still scarce.

In Argentina, *C. carpio* was first introduced in the mid-nineteenth century for ornamental and aquaculture purposes, and this represents the first recorded introduction of an alien fish in the country (Baigún & Quirós, 1985). In the early and middle 20th century, *C. carpio* was also stocked for commercial harvest and sport fishing into several reservoirs of central and northern Argentina (Baigún & Quirós, 1985). The first record of the species in the wild was in 1945 from the Río de la Plata estuary (Mac Donagh, 1945), and the second in 1967 from the same area (Candia *et al.*, 1967). Baigún & Quirós (1985) developed the first *C. carpio* distribution map, identifying the Colorado River system as the southern boundary of the species distribution (39° S). Since then, the number of new reports in Argentina has increased (Liotta, 2005) probably not only as a result of the invasive traits of this species (Koehn, 2004), but also due to multiple direct stocking across the country. For this reason an update of the invasion status of *C. carpio* is urgently required. The aims of the current study were to update the invasion status of *C. carpio* in Argentina by describing the patterns of occupation over time and to discuss future expansion scenarios based on an assessment of environmental suitability.

MATERIALS AND METHODS

STUDY AREA

Argentina is the second largest country in South America, and the eighth largest in the world, extending its American continental surface from subtropical (21° S) to subantarctic (55° S)

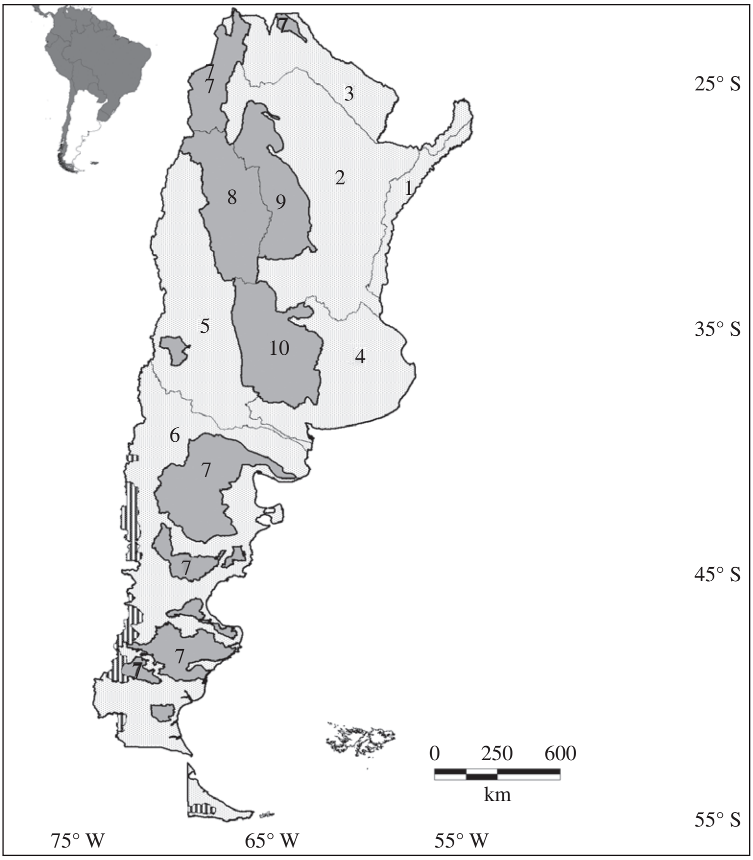

FIG. 1. Hydrographic regions of Argentina (Subsecretaría de Recursos Hídricos, 2010). ▭, Atlantic drainage: 1, Uruguay River system; 2, Paraná River system; 3, Paraguay River system; 4, Río de la Plata River system; 5, Colorado River system; 6, Patagonic River system; ▬, Endorheic catchments: 7, Independent systems; 8, Serrano systems; 9, Mar Chiquita systems; 10, Pampeano systems; ▥, Pacific drainage.

regions, encompassing wide ranges in both latitude and altitude. The Andes Mountains along the western border of the country are responsible for remarkable orographic effects over precipitation on a west to east gradient, particularly in the southern area (Patagonia). Climatic variability, in addition to topographic differences, has created a diverse mixture of ecoregions, ranging from regions of high to low rainfall (Burkart *et al.*, 1999; Morello *et al.*, 2012). This gradient promotes the existence of different natural and artificial aquatic systems portrayed by a wide array of lake types that differ according to their origin, size, shape, chemistry and edaphic characteristics (Drago & Quirós, 1996).

Within this heterogeneous landscape, three main hydrographic drainages encompassing different river systems can be identified (Subsecretaría de Recursos Hídricos, 2010) (Fig. 1): (1) The Atlantic Drainage, which at its upper portion encompasses the Uruguay River system, two large floodplain rivers, the Paraná and Paraguay River systems, and the Río de la Plata River system. Its southern portion contains extended rivers that drain the Andes Mountains, crossing the Patagonic plateau and flowing into the ocean, including the Colorado and the Patagonic River systems, (2) The endorheic catchments, comprising the Independent Systems, spread along the country, and the Serrano, the Mar Chiquita and the Pampeano systems in the central portion of Argentina and (3) The Pacific Drainage, including short rivers draining from Andean Mountain lakes located in the west Patagonic border (Fig. 1).

DATA COLLECTION AND HISTORICAL ANALYSIS

A review of literature encompassing around 450 documents, including scientific publications, PhD theses, books, official reports and conference presentations was used to determine *C. carpio* occurrences across the country. Also, local fishery management authorities and stakeholders were consulted on the presence of *C. carpio*. In addition, to find more records of water bodies invaded by the species an internet search was made.

Cyprinus carpio records were numbered and their location, geographic position, data source and year of publication were also identified. Environments with *C. carpio* records were classified as natural (lakes and rivers) or artificial (reservoirs and canals). In those environments with multiple records of *C. carpio* presence, only the oldest citation for each location was considered for the study. The cumulative number of invaded locations through decades was calculated and a regression model was fitted to the data-set to determine invasion rate.

The cumulative records of *C. carpio* were mapped for the Argentine territory, considering hydrographic systems and natural or artificial environments for three different time periods since the first citation until present, to elucidate both temporal and geographical invasion patterns. Record mapping was accomplished using Mapinfo Professional 6.5 GIS software (www.mapinfo.com).

ENVIRONMENTAL MODELLING

A niche distribution model was developed based on the environmental conditions corresponding to species records in the natural habitats. This approach represents a scenopoetic and Grinnellian niche (Soberón, 2007), as it only takes into account physical environmental factors in the landscape at regional scales and the choice of predictor variables is of particular importance when developing niche models (Araujo & Guisan, 2006). The following variables $X_{\rm i}$ were selected for modelling: (1) temperature: annual mean X_1, minimum of the coldest month X_2 and maximum of the hottest month X_3; (2) annual precipitation X_4, which was used as proxy for freshwater availability and permanence in water bodies; (3) elevation X_5; (4) slope X_6. The last two variables were also included because they have been historically used to describe the distribution of freshwater fishes as they relate to river's order, flow, water velocity and habitat availability (Huet, 1959; Illies & Botosaneanu, 1963; Lasne *et al.*, 2007).

Temperature (° C) and precipitation (mm) were obtained from WorldClim 1 km cell size current climate grid databases (Hijmans *et al.*, 2005). Elevation (m a.s.l.; Shuttle Radar Topographic Mission (SRTM) grids 90 m cell size) was obtained from International Centre for Tropical Agriculture (CIAT) (Jarvis *et al.*, 2008). Slope (degrees $\times 10^4$) was derived from the SRTM elevation grids, and median elevation and slope grids were calculated to match the 1 km cell size of climate grids. All geographic data were processed with ArcGIS Desktop 10.1 (www.esri.com).

Taking into account the entire environmental data set from those locations already invaded by *C. carpio*, the distribution of values for each variable (X) was divided according to 20, 40, 60, 80 and 100th percentiles ($Q_i^{(\rm X)}$ for i = 1, 2, 3, 4, 5). Given that the number of locations within each $Q_i^{(\rm X)}$ is the same, but the range of values within each percentile is different as it depends on the distribution of the focal variable, the number of *C. carpio* locations at each quantile (N) were divided by the range of the corresponding quantile ($R_i^{(\rm X)}$) to obtain a score $V_i^{(\rm X)}$: $V_i^{(\rm X)} = NR_i^{-1}$. The $V_i^{(\rm X)}$ scores where then expressed relative to the maximum $S_i^{(\rm X)}$, ranging from 0 to 1. To assess the similarity of the different areas of the entire country with the ones invaded by *C. carpio*, the values of each environmental variable considered were obtained for the whole Argentina territory on a cell by cell basis, following the procedures described for the invaded locations. Each cell was qualified according to the S matrix or considering $S^{(\rm X)} = 0$ if the environmental variable for the cell fell out of the range of values where *C. carpio* is present in natural environments.

Finally, an environmental similarity index ($I_{\rm ES}$) was calculated for each cell (j) as the sum of all $S_i^{(\rm X)}$ on the corresponding cell and plotted for the whole country: $I_{{\rm ES}\,j} = {\rm n}^{-1}\,\Sigma S^{(\rm X)}$. $I_{\rm ES}$ ranges from 0 to 1, with high values being indicative of zones with better environmental conditions for *C. carpio* establishment in Argentina, due to their similarity with natural areas already invaded by the species.

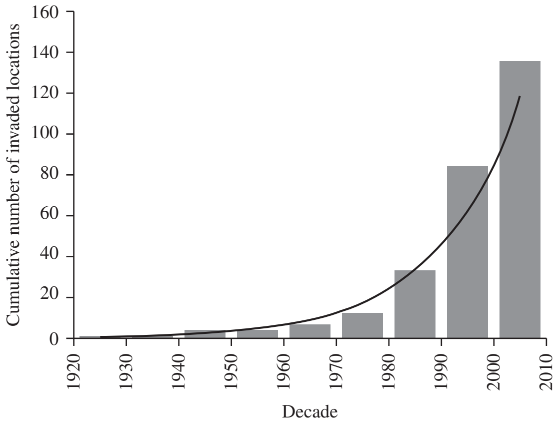

FIG. 2. Cumulative number of locations invaded by *Cyprinus carpio* across decades (■) and the exponential model fitted to dataset (——; $y = 0{\cdot}383e^{0{\cdot}6372x}$).

RESULTS

DATA COLLECTION AND HISTORICAL ANALYSIS

The total number of confirmed locations invaded by *C. carpio* was 168 (Table S1, Supporting Information), encompassing 119 natural environments (47·1% lakes and 52·9% rivers) and 49 artificial habitats (89·8% reservoirs and 10·2% canals). The *C. carpio* locality records, grouped by decade (*D*) since their first introduction grew exponentially according the following model: number of invaded records, $N_{IR} = 0{\cdot}383$ $e^{0{\cdot}6372D}$ ($r^2 = 0{\cdot}96$; Fig. 2).

Geographic distribution of *C. carpio* records over time shows that until 1970 [Fig. 3(a)], the species records were scarce and restricted mainly to the central portion of the country. From 1970 to 1990 [Fig. 3(b)], a noticeable increment occurred in the number of invaded locations, reflecting a geographic expansion. Finally, between 1990 and present, the number of occupied sites almost doubled, expanding the distribution even more to the north, west and south of Argentina. The records of invaded natural environments were located mainly in the central-east portion of the country, whereas the ones corresponding to artificial environments were mainly distributed in the west, central and north-west portions where *C. carpio* is almost absent in natural environments. Overall, these results indicated that *C. carpio* has occupied nearly all the river systems of Argentina with the exception of independent systems of the endorheic catchments and the Pacific drainage [Fig. 3(c)].

ENVIRONMENTAL MODELLING

The range of each variable values in each percentile and the variable scores required to build the I_{ES} model map are shown in Table I. The map indicates that more than half of the continental area of the country has environmental conditions similar to those natural environments already invaded by *C. carpio* (Fig. 4). The highest values of I_{ES} are located in the central-east area of the country, surrounded by intermediate values in all directions. In the north and central portions of these intermediate I_{ES} areas *C. carpio*

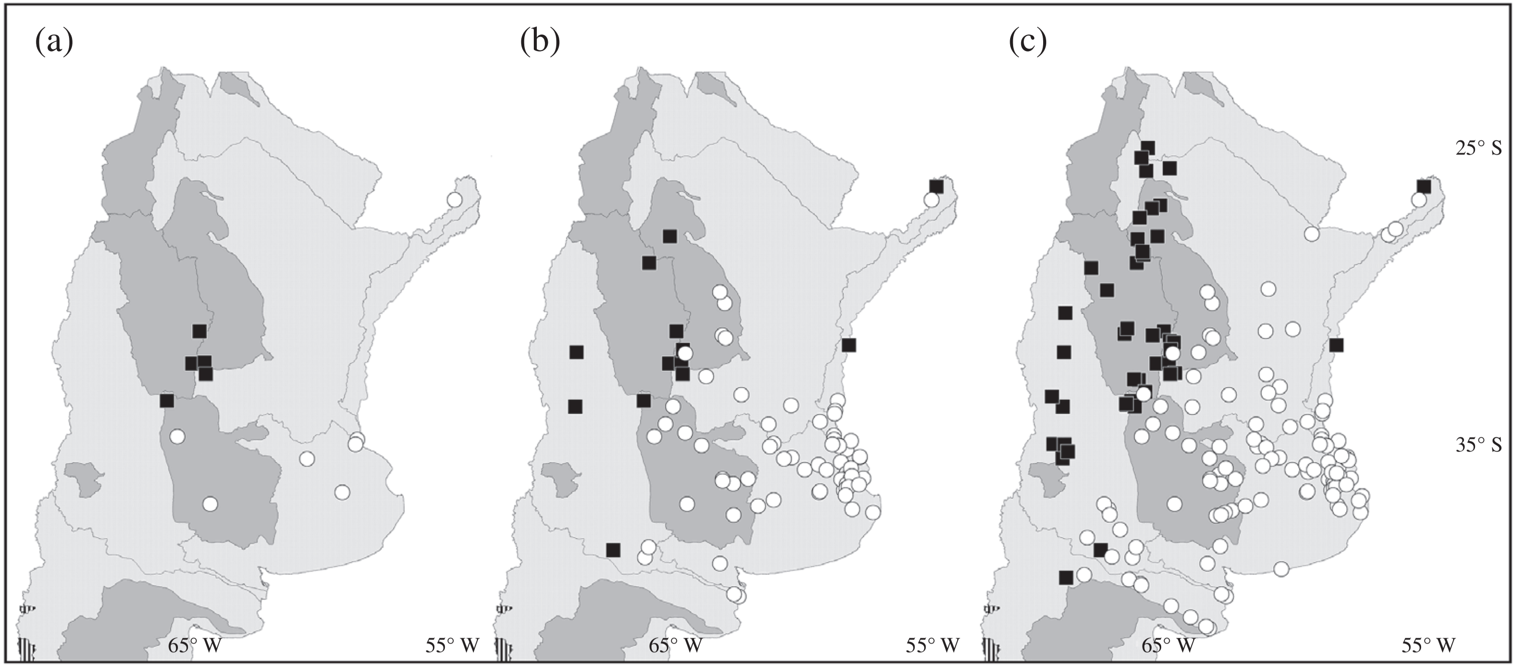

FIG. 3. Cumulative number of locations invaded by *Cyprinus carpio*: (a) before 1970, (b) until 1990 and (c) until 2014. ■, artificial water bodies; ○, natural water bodies.

TABLE I. Range of values for each variable (X) where *Cyprinus carpio* is present in natural environments, by percentile ($R_i^{(X)}$); score of each variable for each percentile ($V_i^{(X)}$) and their relatives values to the maximum value ($S_i^{(X)}$)

Variable X	*R*, *V* and *S*	Q_1	Q_2	Q_3	Q_4	Q_5
X_1: Annual mean temperature (° C)	*R*	13·80–15·19	**15·20–15·59**	15·60–16·09	16·10–16·89	16·90–21·60
	V	2·40	**8·40**	6·72	4·20	0·71
	S	0·29	**1·00**	0·80	0·50	0·09
X_2: Minimum of the coldest month (° C)	*R*	−10·00–2·09	2·10–3·79	**3·80–4·39**	4·40–5·73	5·74–10·80
	V	1·08	1·98	**5·60**	2·51	0·66
	S	0·19	0·35	**1·00**	0·45	0·12
X_3: Maximum of the hottest month (° C)	*R*	27·20–29·19	29·20–30·39	30·40–31·27	**31·28–32·07**	32·08–34·30
	V	1·68	2·80	3·81	**4·20**	1·51
	S	0·40	0·67	0·91	**1·00**	0·36
X_4: Annual precipitation (mm)	*R*	176·00–688·50	688·60–832·30	832·40–938·70	**938·40–978·30**	978·40–1730·00
	V	0·07	0·23	0·32	**0·85**	0·04
	S	0·08	0·28	0·37	**1·00**	0·12
X_5: Elevation (m a.s.l.)	*R*	−9·00–8·50	**8·60–12·90**	13·00–75·30	75·40–134·50	134·60–910·00
	V	1·91	**7·64**	0·54	0·57	0·04
	S	0·25	**1·00**	0·07	0·07	0·01
X_6: Slope (degrees × 10^4)	*R*	0–11·50	**11·60–19·90**	20·00–31·70	31·80–80·90	81·00–554·00
	V	2·90	**4·00**	2·85	0·68	0·07
	S	0·72	**1·00**	0·71	0·17	0·02

The range of X_i values corresponding to the highest scores are indicated in bold.

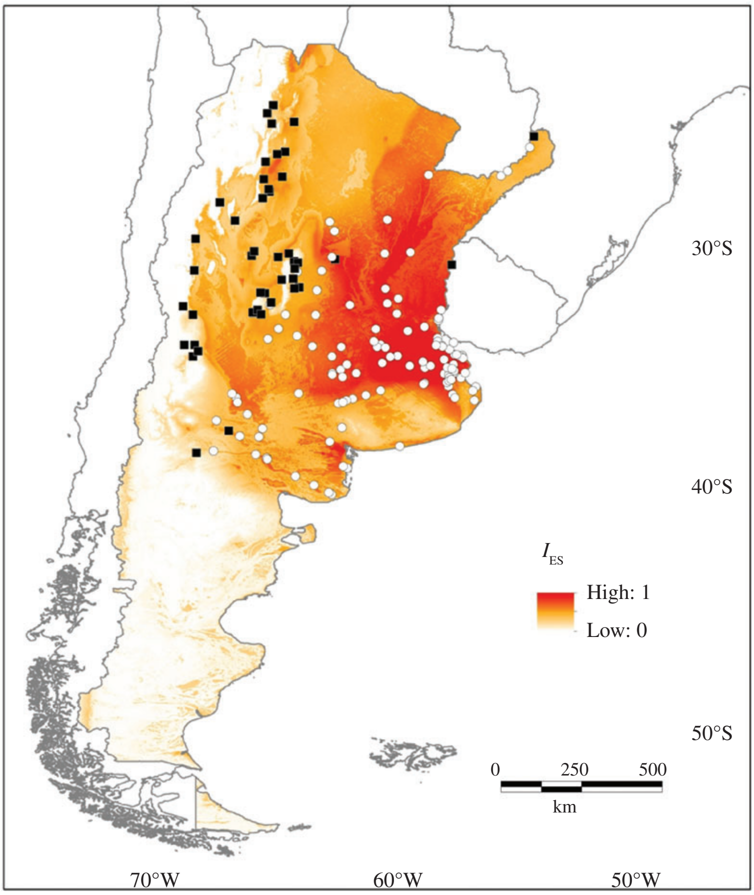

FIG. 4. Environmental similarity index (I_{ES}) model map for *Cyprinus carpio* based on occurrences in natural water bodies. ■, artificial water bodies; ○, natural water bodies.

has occupied mostly impoundments, meanwhile in the southern portion of this area the species has mainly invaded natural water bodies. On the other hand, the lowest or null I_{ES} scores, ergo the most environmentally dissimilar areas to those already invaded by *C. carpio*, cover an area that encompasses the north-west, the west (high mountainous landscape) and south (Patagonic River system) of Argentina.

DISCUSSION

This study is the first assessment of temporal and spatial expansion patterns of *C. carpio* in a South American country contributing to a better understanding of the factors explaining the successful colonization of the species in the south portion of this continent. Originally, after their first introduction, *C. carpio* exhibited a lag-phase in their spread, but since 1970 it has shown an exponential expansion which predicts an increase of up to 220 new locations by the end of the decade 2010–2020, as indicated by simple extrapolation. This trend was related to multiple stocking events together with the self-spread to new areas with suitable conditions.

In the last three decades, the spatial distribution of *C. carpio* has expanded significantly through Argentina, mainly to the west and south beyond the distribution boundaries described by Baigún & Quirós (1985). This remarkable expansion seems to be associated not only with a high dispersal capability (Jones & Stuart, 2009), but was probably also facilitated by human activities such as construction of impoundments and by direct stocking. In particular, habitat alterations generated by the building of structures for water management have been identified as facilitators of *C. carpio* recruitment in other countries (Bice & Zampatti, 2011), providing recruitment hot spots for non-native species (Sheehy & Vik, 2010). This situation is in agreement with reservoir development in the Iberian Peninsula, where the species was introduced more than five centuries ago but its expansion and establishment has increased in the last century because of an increase in the construction of dams that have facilitated its spread (Clavero & Villero, 2014). A similar scenario has been found in southern Africa where *C. carpio* is usually found in most impoundments (Ellender *et al.*, 2014) where they are often the dominant species (Ellender *et al.*, 2010). Dams and reservoirs in south-east Australia have also been shown to favour *C. carpio* (Koehn, 2014), reinforcing the relevance of reservoirs as key habitats for the species.

A possible driver for *C. carpio* invasions in impoundments may be the low biotic resistance in new impoundments, thereby making them particularly vulnerable to species invasions (Kolar & Lodge, 2000; Shea & Chesson, 2002; Havel & Medley, 2006). The conversion of free-flowing rivers to standing waters may therefore ultimately facilitate the development of invasive species populations (Fernando & Holcick, 1991; Johnson *et al.*, 2008; Butler & David, 2010; Clavero & Villero, 2014). This is supported by Gehrke (1997) who found that *C. carpio* abundance was related to the degree of river regulation.

In the case of Argentina, canalisation and weir construction in the Río de la Plata River system appears to have promoted *C. carpio* expansion, whereas stocking practices in reservoirs located in the Colorado, Serrano and Mar Chiquita systems could have been one of the main causes of *C. carpio* establishment in these areas. The high number of records in reservoirs in the central-west portion of Argentina reinforces their critical role in the expansion process, particularly in zones where slope and hydrological conditions could limit its self-propagation. Although this study is an update of *C. carpio* distribution based on the available information, the results could be biased due to unequal ichthyological study efforts across the country.

Zambrano *et al.* (2006) predicted the potential invasive range of *C. carpio* in South America based on large scale climatic variables and using ecological niche modelling based on the GARP algorithm. According to their model, practically all of Argentina was considered climatically suitable for *C. carpio* establishment, with the exception of the north-western area of the Paraguay and the central Patagonic River systems. The results obtained in this study, in terms of *C. carpio* occurrences, indicate that there are areas where the species has not been recorded despite being predicted as environmentally suitable by Zambrano *et al.* (2006). Such mismatch was particularly evident on the western fringe of the country and in the middle and south Patagonic River system, where the species has not been recorded.

When the I_{ES} map obtained in this study (I_{ES} model, Fig. 4) is compared to that of Zambrano *et al.* (2006), the results obtained are partially in agreement. The two models indicate that Paraguay River system and the northern portion of both Paraná and Uruguay River systems are suitable zones for *C. carpio* establishment, but the presence of the species is scarce. These basins have permanent connections with already invaded river systems of Argentina. Therefore, the limited establishment success of *C. carpio* suggests other environmental variables that have not been considered, could be affecting the species distribution in Argentina. Furthermore, biological variables such as species richness could also be playing an important role and should be incorporated in the I_{ES} model, but currently, such information is not available for most of the locations considered in the analysis. The vulnerability of non-saturated communities to *C. carpio* invasion was indicated by Hugueny & Paugy (1995). Therefore, the high species richness in the Paraguay, Paraná and Uruguay River systems (López *et al.*, 2002) may be an important factor limiting *C. carpio* presence when compared to the large number of *C. carpio* records in the central portion of the country (*i.e.* Río de la Plata and Pampeano River systems) where species richness is low. Such patterns were also found in Australia where *C. carpio* dispersion was slower in those rivers containing higher richness and particularly piscivorous species (Koehn, 2004).

The I_{ES} model identified the central-east region of Argentina, characterized by the presence of numerous shallow lakes, as the most suitable for *C. carpio* establishment. The expansion of *C. carpio* in these environments represents an example of natural propagation of the species, a situation that has been taking place since the 1980s (Barla & Iriart, 1987), with this fish currently inhabiting almost all of them. These lakes provide ideal habitats for *C. carpio* because of optimal climatic and topographic conditions, and also because of their eutrophic condition which, according to Kulhanek *et al.* (2011), represents the most suitable trophic state for *C. carpio* population development. Furthermore, the existence of extraordinary rains and floods, together with canalisation for alleviating inundation problems, has led to the connection of most of the sub-basins within the Río de la Plata River system, representing another feature which facilitates fish movement among water bodies in this area (Colautti *et al.*, 2015). In addition, extraordinary flooding events, particularly in 1982 and 1997, could have improved *C. carpio* reproductive success by generating adequate environments for spawning activity. This assumption is in agreement with the results reported by Bajer & Sorensen (2010) who demonstrated that the success of this species in interconnected shallow freshwater environments is attributable, among other features, to their propensity to exploit peripheral unstable shallow areas as spawning/nursery habitats.

The Patagonic River system appears to be almost uncolonized by *C. carpio* with the exception of its northern portion, where the species was introduced in the mid 1980s and currently is a common component of the fish assemblage in main rivers (Colautti, 1997; Sidorkewicj *et al.*, 1998; López *et al.*, 2002; Pascual *et al.*, 2002; Alvear *et al.*, 2007). Several large dams lacking fishways, however, represent major barriers to the dispersal of this fish to western Patagonia. Moreover, the absence of *C. carpio* in the middle and southern catchments could be linked to the isolation of basins and, probably, to the lack of stocking events in the area. In addition, low lake temperatures (Baigún & Marinone, 1995) could be unsuitable for *C. carpio* spawning (Sivakumaran *et al.*, 2003). Despite the species never having been recorded in middle and south Patagonia (Baigún & Ferriz, 2003; Aigo *et al.*, 2008), it is documented that the species has been able to colonize cold-temperate lakes of Canada (McCrimmon, 1968; Scott &

Crossman, 1973; Chow-Fraser, 1998), located in a similar latitudinal range, but in the northern hemisphere.

Natural environments of the Serrano system, north of both the Mar Chiquita system and Colorado River system are almost unoccupied by *C. carpio* which, however, are present in impoundments mostly because of direct stocking (Baigún & Quirós, 1985; Colautti, 1997). Taking into account these observations, the natural environments of these river systems may not be suitable for *C. carpio* supported by low values of the I_{ES} model. Nevertheless, this condition can drastically change if any river in these regions is impounded, and may favour invasion by *C. carpio*.

In conclusion, the findings of this study support the idea that general climatic, topographic and hydrological factors, together with such anthropogenic impacts as habitat modification and stocking practices, were relevant drivers that can account for the current and future distribution of *C. carpio* in Argentina. Biological and ecological variables related to fish assemblage composition and trophic state of water bodies could also play an important role, and they need to be better understood for more accurate modelling of inland water vulnerability to *C. carpio* invasion. Since *C. carpio* has been identified as one of the world's worst invasive fish species (Lowe *et al.*, 2000) and its effects on natural environments have been reported in several parts of the world (Zambrano *et al.*, 1999; Koehn, 2004; Haas *et al.*, 2007; Weber & Brown, 2009; Kloskowski, 2011) further studies are needed to assess its economic and environmental impact in Argentina.

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Supporting Information

Supporting Information may be found in the online version of this paper:
TABLE S1. Records of *Cyprinus carpio* gathered in this study.

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