Historical Ecology and Invasion Biology: Long-Term Distribution Changes of Introduced Freshwater Species

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*We used historical written accounts from Spain to describe the long-term dynamics in the distributions of tench (*Tinca tinca*), common carp (*Cyprinus carpio*), and white-clawed crayfish (*Austropotamobius italicus*) from the sixteenth century to the present. The results show the widespread, human-mediated expansion of the three species and support their introduced status, which has been controversial for tench and crayfish. The temporal patterns of spread of the three species differ dramatically. Although tench and crayfish expanded rapidly, carp spread mainly during the twentieth century, probably because of hydrologic alterations to Spanish streams. This prolonged time lag in the expansion of an introduced species calls for precaution when judging species invasiveness.* Austropotamobius italicus *is the focus of several conservation actions in Spain, a strategy that should be questioned in the view of the crayfish's probable introduced status. This work provides an example of how historical ecology analyses may have implications for present-day environmental management.*

Keywords: historical distributions, Iberian Peninsula, Austropotamobius, Tinca tinca, Cyprinus carpio*, invasion time lags*

Ecological studies are most often conducted over short periods, spanning at most a few decades, but systems that have been affected by human activities for centuries or millennia are often their subject. Historical ecology may provide a proper context to better understand the structure and function of contemporary ecosystems and landscapes (Szabó 2010, Rick and Lockwood 2012). Historical ecology is strongly interdisciplinary, is increasingly integrated into the ecological framework, and may become valuable to conservation practice. However, historical data have only rarely been used in the design of conservation strategies to date (Willis and Birks 2006).

Historical ecology can provide important insight into the understanding of biological invasions (Willis and Birks 2006). Human activities have promoted the transport of multiple species across previously insurmountable biogeographical barriers, a process that has occurred for centuries (e.g., Gippoliti and Amore 2006) but has exponentially accelerated since the beginning of the twentieth century (Olden 2008). Long-term analyses of the progression of these historical invasions are rare, although they can be relevant for understanding the invasion process. For example, historical information about species occurrences allows geographically explicit descriptions of changes in their distribution ranges (Josephson et al. 2008), which, in the case of introduced species, would inform about the temporal and spatial patterns of their establishment and expansion. Historical ecology analyses can also be used to discern the status of cryptogenic species, which are those whose status (i.e., native or introduced) is uncertain in a given area (Carlton 1996) and can therefore be useful in setting conservation priorities.

In the present article, we analyze the changes in the distributions of the tench (*Tinca tinca*), the common carp (*Cyprinus carpio*), and the white-clawed crayfish (*Austropotamobius italicus*) in Spain since the sixteenth century. These three species are probably the first human-mediated aquatic species introduced into the Iberian Peninsula, although both *A. italicus* and the tench have been considered cryptogenic species there (García-Berthou et al. 2007). Establishing whether these two species are native to the Iberian Peninsula is important for setting conservation priorities, especially in the case of *A. italicus*, because it is a threatened species and the focus of several conservation actions. This species is commonly known as the *autochthonous crayfish* in Spain, where all other crayfish species are recent (i.e., the second half of the twentieth century) introductions with

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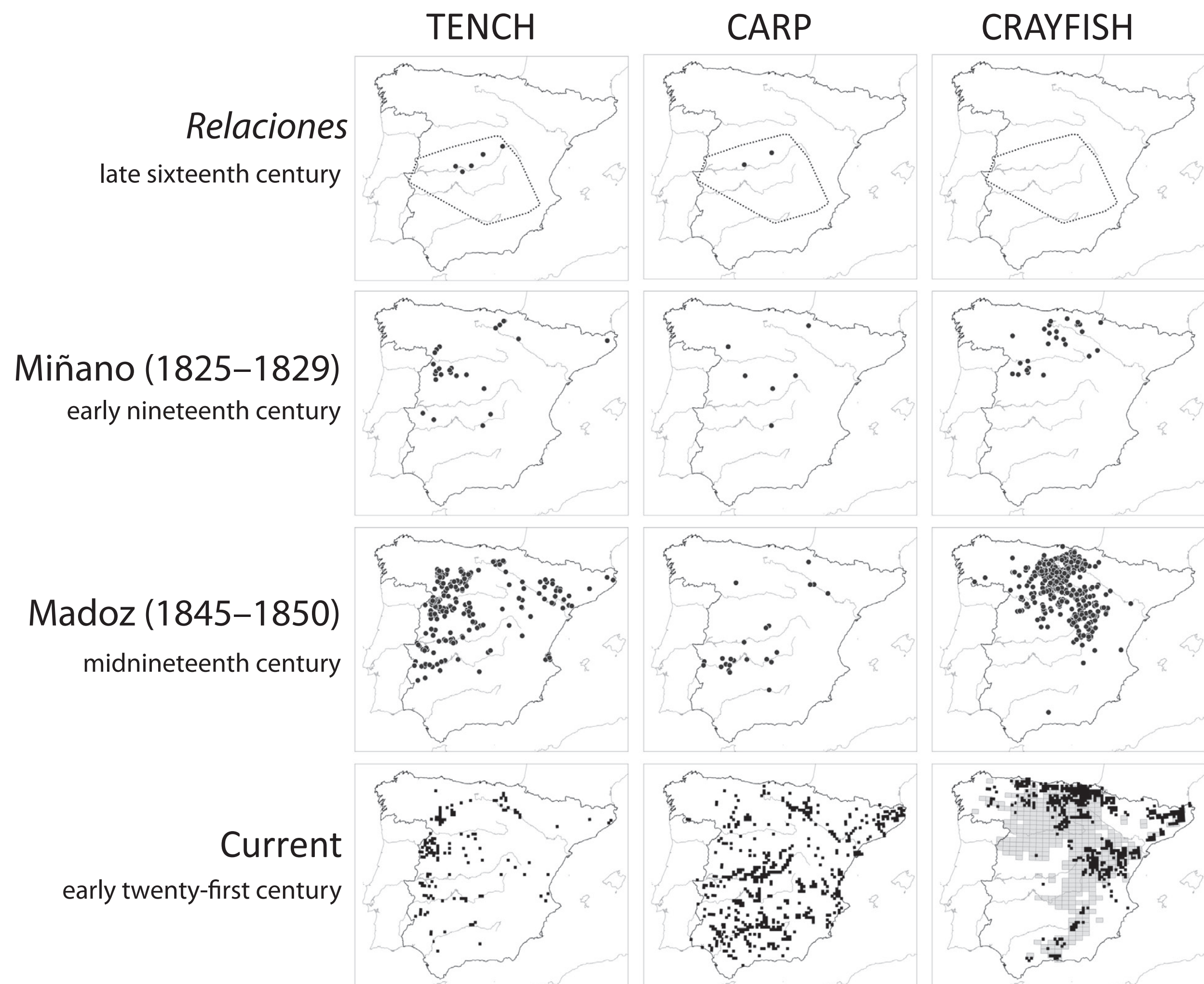

Figure 1. Distributions of the tench (**Tinca tinca*****), the common carp (*****Cyprinus carpio*****), and the white-clawed crayfish (*****Austropotamobius italicus*****) in Spain from the sixteenth century to the present. The maps from the sixteenth and nineteenth centuries (the first three rows) represent specific locations in which the species had been cited, whereas the maps from the twenty-first century represent 10 × 10 kilometer Universal Transverse Mercator squares. The gray rectangles in the bottom right map represent crayfish populations in the 1960s (according to Torre and Rodríguez 1964, Alonso et al. 2000). The polygons in the sixteenth century maps (the upper row) delimit the areas enclosing the 601 accounts (*****relaciones topográphicas*****) reviewed for this work.***

non-European origins. We assessed species distributions in three different periods—the late-sixteenth century, the early to midnineteenth century, and the present—on the basis of the available systematic descriptions of the Spanish territory or parts of it and on contemporary biodiversity databases. The specific goals of this study are to describe long-term patterns and mechanisms involved in the arrival and spread of introduced species and to complement other studies to discern the native or introduced origin of the tench and *A. italicus*.

Data sources and collection

Although we used mainly Spanish sources, throughout the manuscript, we often refer to the Iberian Peninsula, including Portugal, since the whole peninsula is the truly meaningful biogeographical entity (Ribeiro et al. 2008). This is unlikely to have a large effect on our results, because it has been previously shown that many invasive species—and, particularly, most freshwater ones—enter Portugal via Spain (García-Berthou et al. 2005).

A complete list of historical sources and related Internet resources can be found in supplemental appendix S1. Supplemental appendix S2 lists all historical records of the three species analyzed (i.e., those presented in figure 1).

***Relaciones topográficas* (1574–1582).** The *relaciones topográficas* (topographic accounts; henceforth, *relaciones*) are the result of a statistical survey developed in Spain during the reign of Felipe II, which lasted from 1556 to 1598. The survey took the form of questionnaires (*interrogatorios*), which were sent to villages and had three different versions, delivered in 1574 (24 questions), 1575 (57 questions), and 1578 (45 questions). The instructions of the *relaciones* stated that the questions should be answered by at least two inhabitants of the village, who should be "intelligent and inquisitive." The requested information included questions about history, geography, population, social organization, religion, health, crops, livestock, forests, and game animals. There were also specific questions about aquatic systems and the fish and fisheries that they contained. The *relaciones* were scheduled to be sent to all villages of the Iberian part of Felipe II's kingdom, which, at that time, largely corresponded to present-day Spain (after 1580, it also included present-day Portugal). However, the plan largely failed, and the compiled information was limited to some 630 villages, mainly from central eastern Spain. In spite of this failure, the *relaciones* constitute the most important standardized geographic account developed in the sixteenth century anywhere in the world. The *relaciones* have been an important source for several historical studies (e.g., Campos y Fernández de Sevilla 2003), but, in spite of their potential, they have only rarely been used in biodiversity and landscape ecology studies. The records of components of the aquatic fauna found in the *relaciones* have not been analyzed before.

We collected information regarding wild plants and animals, with a focus on aquatic biota, contained in the *relaciones* from 601 villages (i.e., over 95% of the conserved documents), using the available published transcriptions (the transcriptions of some villages have not yet been published). The analyzed *relaciones* included citations of over 100 plant species and around 90 animal species, with more than 4500 individual records. The villages were geographically located using Google Earth. Whenever a given village had disappeared (47 cases), we estimated its original location using the answers to the questions of the *relaciones* in which the names of and distances to the nearest villages were ascertained.

Nineteenth century dictionaries. In the dictionary edited by Pascual Madoz (1846–1850), systematic geographic, historical, and statistical information was compiled for Spanish villages, territories, rivers, and mountains (appendix S1). It was a vast work of 16 volumes edited between 1846 and 1850 that involved the participation of over 1000 collaborators over a period of more than 15 years. The information about villages and cities was structured in a fixed manner across the text, although the length of the articles varied greatly in relation to the perceived importance of each population center. Under the heading "Productions," Madoz (1846–1850) listed the most important crops and livestock held in the village and often also included information on wildlife and fisheries. Madoz (1846–1850) has been used as a data source for many scientific studies in various areas, including analyses of the distribution of different animal species (e.g., Wiegand et al. 2008). The dictionary compiled by Sebastián Miñano (1826–1829), edited in 11 volumes between 1826 and 1829, was a predecessor of Madoz (1846–1850), although it was less complete. In spite of that, Madoz (1846–1850) used the information contained in Miñano (1826–1829) for several articles.

We searched the tench, carp, and *A. italicus* records included in the Madoz (1846–1850) and the Miñano (1826–1829) dictionaries, which allowed us to depict the distribution of the three species across Spain during the first half of the nineteenth century. The search was focused on the Spanish names of the three species (*tenca*, *carpa*, and *cangrejo*, respectively), which seem to be very stable, both spatially and temporally, and which referred univocally to the species of interest. We located population centers, administrative territories, or geographical features using Google Earth, estimating the central locations in the two latter cases.

Current distributions. The present-day distributions were compiled in terms of 10 × 10 kilometer Universal Transverse Mercator squares. The distributions of the tench and the carp were obtained from the Spanish national biodiversity inventory, available at the Web page of the Spanish Ministry of Agriculture, Food, and Environment (see appendix S2). The contemporary *A. italicus* distribution was obtained from Alonso (2011). We also compiled the *A. italicus* distribution in the 1960s on the basis of the map presented by Alonso and colleagues (2000), with some modifications following the information contained in the original review made by Torre and Rodríguez (1964).

Tench

In the sixteenth century, the range of the tench was limited to the northern part of the area covered by the *relaciones*, but the species was widespread in Spain by the middle of the nineteenth century, especially in its western part (figure 1). This distribution pattern has been largely conserved to the present, although the species seems to have disappeared from historically occupied areas. For example, since the nineteenth century, tench have become much rarer in the plain areas of the northern plateau and the lower Ebro River valley, where it had apparently been common (figure 1).

Out of the five tench citations in the *relaciones*, four of them referred to its presence in lagoons or ponds, and one of them mentioned "a lagoon for keeping tench." This suggests that the species was already linked to managed systems in the sixteenth century. Madoz (1846–1850) reported the presence of tench in lagoons or ponds (whether natural or humanmade) in 68 of the 219 tench citations (i.e., 31%). Around that time, Graells (1864) noted that the tench lived in stagnant, muddy waters and could be easily bred in orchard ponds. Tench cultivation continued in both Spain and Portugal during the twentieth century (Lozano Rey 1935, Almaça 1995, Doadrio 2002); they were intensively bred in aquaculture centers and were frequently stocked.

Figure 2. The locations of geographic features cited throughout the text. The white dots mark villages, whereas the larger territories (mountain ranges or large political entities) are named using bold characters. The main Iberian rivers are marked with italics. The star marks the position of the Castellón Alto archaeological site, where remains attributed to the tench (*Tinca tinca*) were reported by Milz (1986). The background gray shading denotes elevation, with higher areas being represented by darker tones.

The status of the tench in the Iberian Peninsula has been controversial for a long time (García-Berthou et al. 2007). Some authors (e.g., Doadrio 2002) consider it a native species on the basis of the occurrence of bone remains attributed to tench in a single archeological site from the Bronze Age, located in southeastern Spain (Milz 1986). However, these archaeological remains come from an area in which the tench has been absent—or, at best, rare—in historical times (see figures 1 and 2). They should therefore be reassessed, and any possible confusion with southern straight-mouth nase (*Pseudochondrostoma willkommii*) remains, a common species in the area that was not identified in the original work (Milz 1986), should be taken into account. The analyses on tench genetic structure in Europe strongly suggest that the species was introduced into the Iberian Peninsula, because Spanish samples clustered together with Eastern European populations (Lajbner et al. 2011). Our results reinforce the idea of the introduced status of the tench by showing that the species has been closely related to human-modified habitats and has been artificially stocked for centuries.

It has been suggested that the tench could have been introduced into the Iberian Peninsula by monks during the Middle Ages (Almaça 1995). These statements are probably based on the generalized existence of fish ponds that often held tench in monasteries, but there is no direct evidence of tench being bred in these ponds in Spain or Portugal in the sixteenth century or earlier. The first evidence of the presence of tench in Spain (figure 1) could alternatively be linked to the Habsburg dynasty, which reigned from 1517 to 1700. This dynasty had strong Central European roots and also ruled large areas of the Italian Peninsula. King Carlos I (Felipe II's father) was born in Ghent (currently in Belgium) and arrived for the first time to Spain in 1517 (at age 17) only to be sworn in as king (one of the first exigencies of the Castilian courts was that he must learn Spanish, which he apparently never fully accomplished). It is known that, in his retirement in the Yuste monastery in Extremadura (from 1557 to his death in 1558), the king had a fish pond, where he fished tench. It is therefore possible that the links established at the beginning of the sixteenth century between Iberian and Central European noble families facilitated the arrival of the tench.

Carp

The *relaciones* include only two records of carp, both of them from ponds and both of them in cooccurrence with tench. The Miñano (1826–1829) dictionary includes 6 carp records, whereas the Madoz (1846–1850) dictionary contains 22 carp citations, half of them in coexistence with tench. The carp citations in the nineteenth century were scattered across Spain, although there seems to have been a concentration of occurrences in wetland areas of the Guadiana River basin. Current carp distribution is much more widespread than it has been in any previous period (figure 1). The carp occur in practically all Spanish basins and are often the dominant species in reservoirs, lower river stretches, and lowland wetlands (Doadrio 2002).

Elvira and Almodóvar (2001) reported the seventeenth century as the introduction date of the carp into Spain, and this date has been repeated in subsequent works. The original information probably comes from Lozano Rey (1935), who, in general terms, reported that the species was introduced during the Habsburg dynasty. The sixteenth century citations reported here therefore constitute the oldest explicit carp records for the Iberian Peninsula. The arrival of the carp could also be related to the European connections of the Habsburg monarchs, as was discussed above in the case of the tench.

The secondary spread of the carp across the Iberian Peninsula was much slower than that of the tench, maybe because of the culinary preferences of the area's inhabitants. As in Portugal (Almaça 1995), carp meat has not been traditionally appreciated in Spain. Tench were often referred to as *excellent* or *good* as food in nineteenth century dictionaries, adjectives that were never used for the carp. In spite of that, the carp's productivity impressed the Spanish people and probably promoted its expansion. In a lagoon in Daimiel, a village within a wetland complex along the upper Guadiana River (figure 2), Madoz (1846–1850) reported that "there are fishes called carps that multiply prodigiously" (vol. 1, p. 341). The use of the expression *fishes called* instead of its direct naming (as was done for other fish species) and the apparent surprise regarding the carp's reproduction potential suggest a recent arrival of the species to the area. The carp was cited in the eighteenth century from stagnant waters near Zaragoza, in northeastern Spain (de Asso y del Río 1784), but it was not included in accounts of fish fauna from that century in Portugal (Almaça 1995). Graells (1864) mentioned Spanish fishermen taking carp and gave information on how to stock the species into new waters. However, Steindachner (1865) noted that the carp was rare in the Iberian Peninsula at that time. Lozano Rey (1935) does not apply the adjective *common* to the carp (although he does for the tench) and lists only about five specific localities inhabited by the species (at least three of which were also cited by Madoz 1846–1850, almost one century earlier). Therefore, although the carp has been present in the Iberian Peninsula for at least the last five centuries, its current status as a widespread invader seems much more recent, originating during the twentieth century. Arguably, the carp has become a successful invader in the Iberian Peninsula, favored by the massive construction of dams since 1900 and the associated alterations of flow regimes (Clavero et al. 2004).

Crayfish

The *relaciones* did not include any *A. italicus* record, although several accounts were made in areas assumed to fall within the historical range of the species (figure 1). For example, Torre and Rodríguez (1964) described a productive crayfish fishery in the upper Guadiana River (see figure 2), which involved the direct work of up to 200 families. The *relaciones* did cite in that area the presence of freshwater shrimp (*Atyaephyra desmaresti*) that were described as being "smallish, like crickets," which makes it clear that the text was not referring to crayfish. Diéguez-Uribeondo and colleagues (2008) interpreted citations of shrimps in Iberian Arabic texts as possible references to *A. italicus*, even though they came from localities where the species has never been reported (Seville, southwestern Spain). The *relaciones* also included several records of very small fish species, such as the southern Iberian spined loach (*Cobitis paludica*) and the bermejuela (*Achondrostoma arcasii*). This reinforces the idea that if an important and abundant resource such as *A. italicus* were present in the area, it would have been cited in at least a few *relaciones*.

Austropotamobius italicus's distribution was concentrated in the calcareous areas of the northern plateau up to the middle of the nineteenth century, as was shown by the records included in Miñano (1826–1829; n = 29) and Madoz (1846–1850; n = 501) (figure 1). Previous crayfish records were even more concentrated to the north (supplemental appendix S3). The nineteenth century data suggest that, during the first half of that century, there was a southward and eastward expansion of the species. For example, *A. italicus* populations in the upper sectors of the Tagus and the Júcar basins could have been introduced in that period, because they were not cited in Miñano (1826–1829). *Austropotamobius italicus* expansion toward the south and the east continued and shaped the current crayfish distribution (figure 1). Populations south of the Júcar and Tagus basins and along the Mediterranean coast seem to have originated after 1850.

Human-mediated transportation has been changing the distributions of native European crayfishes for centuries (Swahn 2004), which has led to important expansions of the ranges of the noble crayfish (*Astacus astacus*) and the narrow-clawed crayfish (*Astacus leptodactylus*) (Holdich et al. 2009). Although *Austropotamobius* crayfishes may stir up less interest than *Astacus* do, because of their smaller size, *Austropotamobius* species have also been introduced into several areas (Machino et al. 2004). Albrecht (1983) was the first to suggest that Spanish *Austropotamobius* populations could have been introduced from Italy (an idea that was latter supported by genetic studies; see below), noting that *A. italicus* seemed to be absent in Spain in the middle of the seventeenth century.

The analysis of the historical references to *A. italicus* in Spain and the temporal dynamics of its range highlight the role of human transport in shaping the species's distribution and support the idea of its introduced status. Aldrovandi (1606), who was already aware of the presence of crayfishes in North America, wrote that crayfishes were absent from Spain, although they were common in other European territories, including France. The first written *A. italicus* accounts were reported in the late eighteenth century by Bowles (1775) and de Asso y del Río (1784) (appendix S3). This led Machino and colleagues (2004) to date the introduction of *A. italicus* into Spain between the seventeenth and eighteenth centuries. In the middle of the nineteenth century, *A. italicus* was introduced into the upper Guadiana River (Álvarez-Cobela et al. 2010). Shortly thereafter, Graells (1864) was enthusiastic about the artificial propagation of the crayfish, which was "within the reach of everyone." *Austropotamobius italicus* distribution has been highly dynamic since the beginning of the nineteenth century (figure 1). The spread of the species had dominant southward and eastward directions but also involved the colonization of different areas to the northwest, such as the Cantabrian Mountains and Galicia. Torre and Rodríguez (1964) cited numerous examples of successful *A. italicus* introductions across Spain. *Austropotamobius italicus* arrived in Portugal around 1880 (Machino et al. 2004) and was artificially stocked there during the twentieth century by governmental agencies (Almaça 1990). Its distribution range in Spain reached a maximum extent between the 1960s and the 1970s (Torre and Rodriguez 1964), but then its populations crashed because of the arrival of the crayfish plague, which was produced by the oomycete *Aphanomyces astaci*. Since that moment, there has been a continuous loss of *A. italicus* populations, favored by the spread of two American crayfish species (*Procambarus clarkii* and *Pacifastacus leniusculus*) that are carriers of the crayfish plague but immune to its effects (Alonso et al. 2000). As a result, *A. italicus*'s range in Spain is currently restricted to mountain areas and has been reduced by over 90% from its maximum—its assumed historical extent (Alonso et al. 2000).

Early genetic studies made on Iberian *A. italicus* populations showed that they had very little genetic diversity and that they were very similar to Italian populations, which supports the human-mediated introduction from Italy (Trontelj et al. 2005). In more recent studies (Diéguez-Uribeondo et al. 2008, Pedraza-Lara et al. 2010), relatively more genetic diversity has been found. However, a weak geographic structure of Spanish *A. italicus* genetic diversity is described in these studies, much lower than that observed for freshwater crayfishes in other areas of the world (Koizumi et al. 2012, Larson et al. 2012). Pedraza-Lara and colleagues (2010) argued that this lack of geographic structure could be explained by complex biogeographical scenarios, involving several bottlenecks and colonization processes. Nevertheless, Pedraza-Lara and colleagues (2010) and others did not rule out the possibility of a human-mediated introduction of *A. italicus* into Spain and even assume strong human-mediated modifications of its range (although they restricted introductions to those performed within Spanish political borders). Other crayfish geneticists assume the nonnative status of Iberian crayfishes, such as Chiesa and colleagues (2011), who discussed the "well-known translocation to the Iberian Peninsula from northwestern Italy" (p. 9).

Future genetic studies that include a good coverage of the different lineages of *A. italicus* could be useful to clarify the origin of this taxon. However, the understanding of the genetic structure of *A. italicus* will probably be hindered by recent population declines and complex human influences. European crayfish species, including all *Austropotamobius*, have experienced a generalized recent (i.e., since the early twentieth century) collapse, with several local extinctions, mainly because of the crayfish plague. This decline should have resulted in the loss of part of the original genetic diversity (although the magnitude of that loss is unknown), which would hamper the reconstruction of the historical processes leading to the contemporary genetic structure (see Koizumi et al. 2012). Moreover, *A. italicus* could have been introduced by humans several times across its range, including multiple introductions into the Iberian Peninsula. Multiple-introduction scenarios can avoid the loss of genetic diversity of introduced populations (Roman and Darling 2007). Pedraza-Lara and colleagues (2010) doubted the feasibility of two independent introduction events into the Iberian Peninsula. However, the records shown in figure 1 suggest the existence of hundreds of such independent introduction events, many of which are explicitly documented (Torre and Rodríguez 1964, Álvarez-Cobela et al. 2010). Historical analyses of species distribution dynamics, such as those presented here, can be a very useful complement to genetic studies, especially when, as in the case of *A. italicus*, genetic results could be affected by the uncertainties mentioned above.

Some of the old Iberian accounts suggest that *A. italicus* would have had negative impacts on native biota. De Asso y del Rio (1784) added the expression *truttis infestus* (which could be translated as "dangerous for trout") to the description of the crayfish, which suggests that *A. italicus* may have negative effects on trout populations. An interesting account comes from the Madoz (1846–1850) article about the Trabaque River, in Cuenca Province, at the southern edge of *A. italicus*'s distribution in the middle of the nineteenth century, in which it is suggested that the river "has abundant and nice trout and some fishes, but the many crayfish that there are have caused the decline of the cited fishery" (vol. 15, p. 126). The Madoz (1846–1850) article on Priego, also in Cuenca Province, suggests that the nearby stream had trout and eels "but only a few, because the infinity of crayfish destroy their spawn" (vol. 8, p. 221; there was an obvious mistake regarding eel spawn). Although these comments are scarce, they suggest that *A. italicus* could have had an important impact in Iberian streams, especially noticeable in areas into which it had been recently introduced.

Spread patterns and invasiveness

The patterns of expansion of the tench, the carp, and the crayfish across Spain differed dramatically (figure 3). The carp and the crayfish behaved as highly invasive species, although the timing of their spread was very different. The carp seems to have been initially introduced into central Spain, as was suggested by our results (figure 1) and as was previously noted by Lozano Rey (1935), subsequently spreading slowly from that area. Before becoming a widespread invader in the twentieth century, the carp had been rare in Spain, in spite of having established populations in the wild for hundreds of years. This represents an example of a very long time lag in the spread of an invasive species (Crooks and Soulé 1999). The retarded, massive spread of the species was most probably controlled by extrinsic factors (see Lelong et al. 2007), such as changes in the abiotic environment (e.g., through damming and flow regulation) or in human interests (e.g., the rise of sport fishing). Because population surges of introduced species can occur hundreds of years after the original introduction (see also Willis and Birk 2006), the short-term evaluation of species invasiveness should be judged with caution.

In contrast with the carp, *A. italicus* expanded rapidly, arguably through the creation of new populations that soon became self-sustained and abundant. The interest of the Spanish people in this new food resource favored its rapid spread, in a process resembling the one followed more than

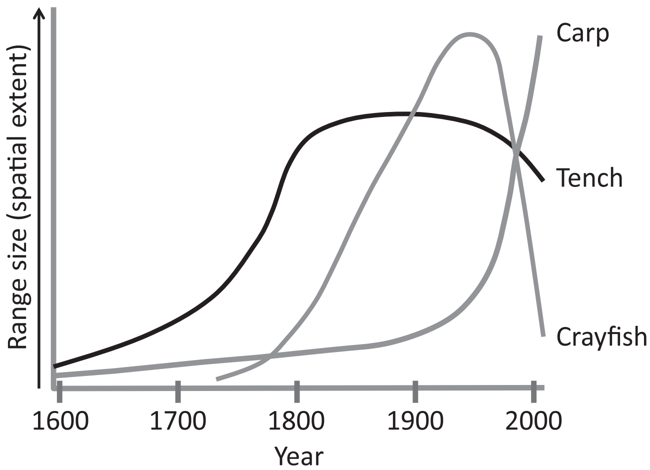

Figure 3. Hypothetical variation of the size of the distribution ranges of the tench, the common carp, and the white-clawed crayfish in Spain since 1600, inferred from the information contained in historical and contemporary sources.

a century later by the North American *P. clarkii* (Gherardi 2006). In both cases, crayfish transport and releases were massively and chaotically performed as individual initiatives (Alonso et al. 2000). Like *A. italicus*, the tench also became a favorite food item and spread across Spain before the nineteenth century. However, the tench does not seem to have behaved as a real invader, and, although there are self-sustained populations, the species has been constantly managed and frequently stocked (Lozano Rey 1935, Doadrio 2002). The tench is currently rarely recorded in large numbers in Iberian aquatic systems, and it has not been able to colonize reservoirs and other artificial systems as successfully as other introduced species have, including the carp (Fernández San Juan 1995).

Management implications

The analysis of historical information dealing with the tench and *A. italicus* and the dynamics of their distribution ranges, together with the results of available genetic analyses, strongly suggest that both species were introduced into the Iberian Peninsula. Any other explanation of their presence in Spain and Portugal would be much less parsimonious with the currently available information. Even if the native status of the tench or *A. italicus* in the Iberian Peninsula could be demonstrated, it would still be clear that most of their Iberian distribution ranges are the result of human-mediated introductions. The nonnative status of these species has important management implications, because conservation efforts should be directed to native taxa in order to maximize the preservation of biodiversity (Gippoliti and Amore 2006).

This is especially relevant in the case of *A. italicus*. The species is listed as *vulnerable* in the Spanish Red Book of Invertebrates (Alonso 2011) and as *endangered* (as *Austropotamobius pallipes*) in the International Union for Conservation of Nature's Red List of Threatened Species, which considers the species native to the Iberian Peninsula. Four Spanish autonomous regions have approved *A. italicus* recovery plans, and there are different captive-breeding facilities that in 2009 produced up to 100,000 crayfish (Alonso 2011). These crayfish are used in numerous restocking reinforcements of existing populations and in the creation of new populations through introductions. *Austropotamobius italicus* is included (again, as *A. pallipes*) in Annex II of the European Commission's Habitats Directive, which implies that member countries, including Portugal and Spain, should design special areas of conservation for the species. It is therefore crucial to open a debate on whether conservation efforts should be devoted to an introduced species. The Iberian Peninsula has a highly threatened aquatic biodiversity with many endemic species, including native bivalve and fish species that are at the brink of extinction (Doadrio 2002, Araujo et al. 2009) and receive far less attention than does *A. italicus* from biodiversity managers. Moreover, different administrations have supported the stocking of American crayfish species, especially *P. leniusculus*, under the premise that the ecological role of "native" crayfish populations should be fulfilled wherever these have disappeared. Since this role most probably never existed before the eighteenth century in Iberian waters, there is no justification for trying to further promote it.

Finally, the carp is usually considered in Spain as a lifelong neighbor, treated differently from other invasive fish for having been part of the Iberian fauna for centuries. Although its centurieslong presence in Spain is a fact, our results also show that the invasiveness of the carp into Iberian waters is a recent phenomenon, more or less contemporaneous with the spread of other invasive species, such as the pike (*Esox lucius*) or the largemouth bass (*Micropterus salmoides*) (Ribeiro et al. 2008). It does not, therefore, seem reasonable to make exceptions regarding carp management when legislating about invasive species, as was done by the recent Spanish Catalogue of Invasive Alien Species (*www.boe.es/diario_boe/txt.php?id=BOE-A-2013-8565*), which does not list the carp.

Conclusions

Our results prove that historical ecology analyses may be valuable to the study of biological invasions with a long-term perspective, complementing short-term studies in the evaluation of the invasiveness of species and the invasibility of systems. For example, we have shown that the invasion process can remain stable at a certain stage for centuries, as was the case with the carp, which was for a long time a naturalized, range-restricted species before becoming a widespread invader in Spain. We were also able to use historical data to complement genetic and archaeological studies in discerning the status of species previously considered cryptogenic. Finally, these results have important implications for the management of biodiversity and the establishment of conservation goals, something that is especially relevant for threatened species, such as *A. italicus*.

Written accounts are not homogenously distributed across the world (Boakes et al. 2010), and, in some regions, they may be too scarce to allow the acquisition of useful data on invasive species or other biodiversity components. However, there are several regions in the world with important records of written biodiversity accounts that should be used, together with other historical ecology approaches, to enlarge the temporal perspective in the knowledge of biological invasions.

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Supplemental material

The supplemental material is available online at *www.bioscience.oxfordjournals.org*.

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