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Species substitutions driven by anthropogenic positive feedbacks: Spanish crayfish species as a case study

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ABSTRACT

Human preferences may generate purely anthropogenic positive feedback loops reinforcing either declines of overexploited populations or expansions of prized introduced species, potentially leading to species substitutions. I illustrate this process based on a content analysis of 20th century Spanish newspapers that document a rapid, country-wide substitution of an originally exploited crayfish (*Austropotamobius italicus*) by two North American species (*Procambarus clarkii* and *Pacifastacus leniusculus*). The substitution was driven by anthropogenic positive feedbacks acting over a short period, coinciding with an exponential increase of crayfish market value, high numbers of crayfish-related articles and a rapid change in the thematic content of those articles. Similar substitutions involving economic or socially valued organisms occur in other regions and concerning other taxa. Human preferences and choices may constitute relevant drivers of several species declines and invasions, which can be very quick due to positive feedback loops. Conservation biology in general and invasion biology in particular have been traditionally focused on biological aspects, but, as shown here, would largely benefit from social perspectives dealing with human motivations and preferences.

1. Introduction

The stability of natural systems is maintained through deviation-counteracting forces known as negative feedback loops. However, positive feedback loops are also frequent in nature, constituting deviation-amplifying forces that may change system modes or states (DeAngelis et al., 1980). Positive feedbacks may act on small and declining populations, driving further declines and thus establishing a self-reinforcing process known as the extinction vortex (Fagan and Holmes, 2006). Courchamp et al. (2006) pointed out that positive feedbacks acting on declining populations could arise due to human preferences whenever the socioeconomic value of an exploited species increased with declining population size. The density-dependent value of species is related to human attraction for rare items, which seems to be a widespread, cross-cultural human characteristic (e.g., Koford and Tschoegl, 1998; Angulo et al., 2009; Booth et al., 2011; Wu et al., 2012). This lure for the few, as termed by Brook and Sodhi (2006), has already fuelled the overexploitation of wild populations of several endangered species (Gault et al., 2008; Collette et al., 2011; Biggs et al., 2013).

Human preferences and choices could also generate positive feedbacks in invasion processes, because large incentives can be associated with the introduction and spread of economically and/or socially valued species (Brunet et al., 2013). The success of the introduction of a prized species would arguably increase both awareness and interest, potentially fuelling its spread through new introductions in a self-reinforcing process. Eventually, when the new species becomes widespread and/or has low value, the positive character of these feedbacks would be lost and the invasion process would end up driven by biological controls. Positive feedbacks involved in invasion processes have been previously reported, but mainly as biological processes (Simberloff and Von Holle, 1999), while the role of human preferences has received relatively little attention (García-Llorente et al., 2008).

Positive feedbacks driven by human preferences and leading to overexploitation of wild populations and biological invasions could interact to generate rapid processes of species substitution. Since species involved in anthropogenic extinction vortices have by definition high socioeconomic value (e.g. Gault et al., 2008), there always will be important incentives to find substitute taxa for the depleted populations, given this is at all possible (e.g. Gentner and Sutton, 2008). The driver role of anthropogenic positive feedbacks in such species substitution processes could arguably be identified if four temporally consecutive processes take place, these being: 1) there is an exploitation-driven decline of species A; 2) the value of species A increases with increasing rarity, further fuelling overexploitation; 3) the rarity and high value attained by species A induce the introduction of species B as a substitute; and 4) species B becomes a valued resource and spreads rapidly due to successive secondary introductions. Here I explore the occurrence of such hypothesized anthropogenically-driven species substitution processes, using crayfish species in Spain as a study case.

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Europe has centuries-old traditions and cultural heritage related to crayfish (Swahn, 2004), which have motivated the artificial spread of all native European crayfish species beyond their original distribution ranges (Kouba et al., 2014). The white-clawed crayfish (*Austropotamobius italicus*) was introduced in Spain from Italy in the late 16th century (Clavero et al., 2015) and became an abundant and highly appreciated species (see Fig. 1A) until its collapse in the 1970s. Its sudden decline is attributed to the irruption of the crayfish plague, a fungal disease caused by the oomycete *Aphanomyces astaci* and linked in Spain to the introduction and expansion of two North American crayfish species, the red swamp (*Procambarus clarkii*) and signal (*Pacifastacus leniusculus*) crayfish (Diéguez-Uribeondo et al., 1997). Nowadays the surviving *A. italicus* populations in Spain are highly fragmented and largely restricted to mountain areas while both North American crayfish species are widely distributed throughout the country.

In this work I study the evolution of human-crayfish relationships in Spain along the 20th century in order to describe the possible occurrence of anthropogenic positive feedbacks driving crayfish species substitutions. To this aim I analysed the information about crayfish published by Spanish newspapers between 1900 and 2000. Historical newspapers may provide relevant information about human perception and uses of wildlife as well as about long-term variation of biological communities (Vuorisalo et al., 2001; Muter et al., 2013). This information is mainly focused on the social dimension of the species concerned and provides an opportunity to analyse anthropogenic processes of ecological change, such as the hypothesized anthropogenic positive feedbacks, which may be difficult to assess based on purely biological data. Newspapers and alternative historical sources (e.g. historical photographs) may be equally useful to describe ecological processes when original biological data are lacking (McClenachan, 2009). This is the case of the substitution of crayfish species in Spain, which took place before field surveys and monitoring schemes widely implemented.

2. Methods

Articles focused on crayfish and published in the 20th century in Spanish newspapers were compiled using the four most comprehensive digital libraries available to the date. Two of the libraries included articles published by specific diaries, *La Vanguardia* and *ABC*, which have produced and published fully searchable databases of contents covering the whole 20th century (e.g. Bernal-Triviño, 2014). *La Vanguardia* (http://www.lavanguardia.com/hemeroteca) has been published since 1881 in Barcelona, while *ABC* (http://hemeroteca.abc.es/) started being published in 1903 in Madrid and since 1929 has had a semi-independent edition in Seville. Both diaries have been published interruptedly since their creation and are still among the most widely distributed Spanish diaries. The other two digital libraries include several publications and are hosted, respectively, by the Spanish National

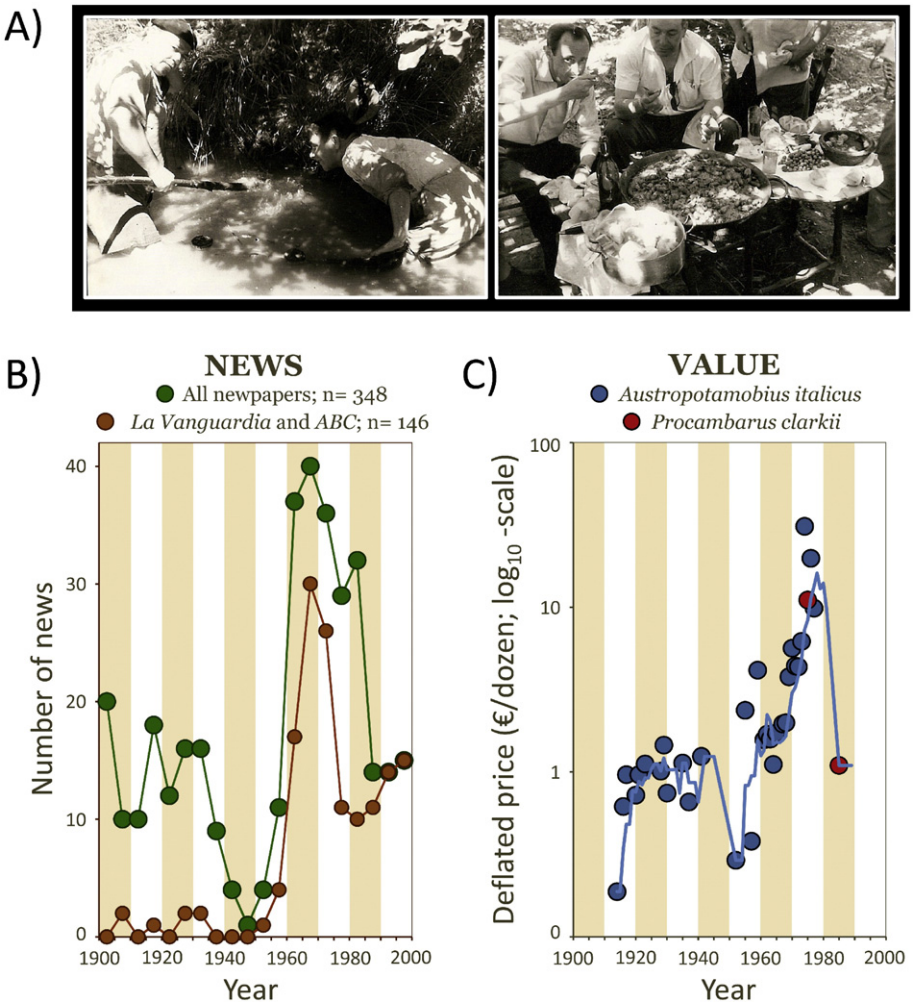

Fig. 1. A) A typical *cangrejada* (crayfish day) in southern Spain in the early 1960s (photos: JM Pineda). B) Temporal patterns in the publication of crayfish-related articles in Spanish newspapers along the 20th century, showing total numbers and those corresponding to *La Vanguardia* and *ABC*, pooled in 5-year periods. C) Deflated prize of a dozen crayfish, averaged in a yearly basis and using 1 euro in 2000 as reference value (note the logarithmic scale). Temporal trend is represented by a weighted average line with a 5-year period. In B and C the yellowish background bars separate decades.