



The enemy release hypothesis and *Callosciurus erythraeus* in Argentina: combining community and biogeographical parasitological studies

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Received: 14 November 2019 / Accepted: 13 August 2020 / Published online: 25 August 2020
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Abstract The enemy release hypothesis (ERH) postulates that during the invasion process an introduced species is released from the natural enemies that regulate its populations, promoting its invasion success in the new environment. *Callosciurus erythraeus* is a sciurid native to Southeast Asia that has been successfully introduced into Argentina and other Asian and European countries. The aim of this study was to provide new parasitological data on this species and to compare it with studies in native and

other introduced ranges under the framework of the ERH. We proposed two working hypotheses: (1) an analysis at the community level to compare the prevalence, abundance and identity of parasites of *C. erythraeus* and sympatric native mammals in the main invasion focus of Argentina, and (2) an analysis at the biogeographical level to compare parasite richness in native and introduced ranges of *C. erythraeus* and parasite prevalence and richness among introduced regions with different invasion success (using population density and spread as proxy variables). The community analyses indicated that *C. erythraeus* has lost its specific parasites in Argentina and that it has a lower level of parasitism than other native mammals.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10530-020-02339-w>) contains supplementary material, which is available to authorized users.

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The biogeographical analyses indicated a lower macroparasite richness of *C. erythraeus* in introduced ranges compared to its native range. However, parasite richness in introduced ranges was not associated with population density and spread. The negative correlation between parasite prevalence and population parameters was mainly due to the low parasite prevalence of *C. erythraeus* in Argentina where this species shows high density and spread. The release of parasites of *C. erythraeus* in comparison to its native and other introduced ranges, the low acquisition of generalist parasites and the high population density and spread reached in Argentina are mostly in agreement with the expected outcomes based on the ERH. Further studies are needed to better understand the role of the ERH in the invasion success of this species.

Keywords Introduced squirrels · Invasion success · Parasite release · Invasion working hypotheses

Introduction

Biological invasions favour a scenario of new associations between parasites and hosts (Dunn 2009; Dunn et al. 2012). Introduction of animals into new areas removes geographical barriers and thus modifies the natural dispersal of hosts and parasites (Brooks and Hoberg 2007; Santicchia et al. 2015; Kołodziej-Sobocińska 2019). An introduced species may carry its natural parasites and transfer them to the hosts of the recipient community, or it may acquire parasites from the new environment (Kelly et al. 2009). Moreover, during the invasion process an introduced species may be released from the natural parasites that regulate its populations, promoting invasion success (Torchin et al. 2003, MacLeod et al. 2010). This statement is framed within the enemy release hypothesis (ERH), a comprehensive hypothesis with the underlying idea that invasive species are released from enemy pressure in the new range (Colautti et al. 2004; Prenter et al. 2004; Torchin and Mitchell 2004; Liu and Stiling 2006). This could be explained because their natural enemies are not co-introduced with the invasive species, or they may fail to establish, and also because the enemies in the new range cannot easily predate or parasitize the invasive species due to a lack of

adaptations to the new species (Jeschke and Heger 2018). This reduction of enemies might lead to an advantage for the invader in its new range. Some of the predictions (see Jeschke and Heger 2018) state that introduced populations harbour fewer natural enemies in comparison with native populations of the same species and that there may be a shift in the proportion of the “type of enemies” favouring generalist over specialist parasites species in introduced populations (Hufbauer and Torchin 2007). Another prediction of this Hypothesis is that introduced species may have a competitive advantage over native species because they are less likely to be affected by local parasites than native competitors (Keane and Crawley 2002; Hufbauer and Torchin 2007; Jeschke and Heger 2018). These expected outcomes lead to an enhanced performance of the invasive species in the new environment. This could be tested by parasitological analysis in combination with population density, occupation area and/or body mass of the new species in the invaded environment (Jeschke and Heger 2018).

The number of studies aiming to test the predictions of the main hypotheses that explain the success of invasive species has increased in the last 50 years (Jeschke et al. 2012; Lowry et al. 2013; Jeschke and Heger 2018). Studies referring to the ERH have yielded heterogeneous results depending on the prediction that was tested, how it was tested and the species that was studied (Prior and Hellmann 2015; Jeschke and Heger 2018). Based on the hierarchy of hypotheses (HoH) approach, it is useful to differentiate sub-hypothesis and clearly specify which indicators of enemy release (e.g. parasite abundance/richness) and which comparisons are intended to be made (e.g. invasive species in their native and their introduced ranges) (Heger and Jeschke 2014; Jeschke and Heger 2018). This will provide a better analytical approach for the role of enemy release in invasion success.

The red-bellied squirrel *Callosciurus erythraeus* is a sciurid rodent native to Southeast Asia that has been introduced in Argentina, Belgium, France, Hong Kong, Italy, Japan and the Netherlands (Lurz et al. 2013; Mazzamuto et al. 2016a). It was introduced in Argentina in 1970 but since 1995, the oldest and largest invasion focus in the Pampas has been the source of individuals transported and released in numerous sites within the country; its present distribution spreads over more than 20 districts in five

Argentinian provinces (Benitez et al. 2013; Guichón et al. 2015, 2019). It mainly occurs in rural, sub-urban and urban areas and although no native squirrels inhabit the areas invaded by *C. erythraeus* in Argentina, they are sympatric with other mammals such as introduced murids (genera *Rattus* and *Mus*) and native sigmodontine rodents (genera *Akodon*, *Oligoryzomys*, *Calomys*, *Oxymycterus* and *Scapteromys*) and caviids *Cavia aperea* (Gómez Villafañe et al. 2005; Patton et al. 2015). Also, the white-eared opossum *Didelphis albiventris* is frequently observed in trees used by *C. erythraeus* (personal observation). In urban and suburban habitats, parasitological studies of wild mammals are mainly restricted to introduced murids that host nematodes, cestodes and acantocephalans (Gómez Villafañe et al. 2004, 2008; Hancke 2016; Fitte et al. 2017; Gómez Muñoz et al. 2018).

Parasitological studies of *C. erythraeus* in its native range are particularly scarce. Actually, except for few exceptions (Huang et al. 2010; Zuo et al. 2011), information of parasites in native populations is based on taxonomic studies or checklists of ectoparasites found in specific populations (e.g. Jordan 1932; Hoogstraal and Kohls 1965; Traub 1972; Li et al. 1976; Durden and Musser 1994). On the contrary, quantitative parasitological studies have been conducted in introduced populations established in Argentina (Gozzi et al. 2013; 2014), Belgium and France (Dozières et al. 2010), Italy (Mazzamuto et al. 2016b) and Japan (Shinozaki et al. 2004; Miyabe et al. 2016).

The aim of this study was to analyse parasitological data of *C. erythraeus* obtained in native and introduced ranges under the framework of the ERH to better understand the ongoing invasion process in Argentina. Based on Hufbauer and Torchin (2007) and Jeschke and Heger (2018), we postulated two working hypotheses: (1) release of parasites and lack of specific parasites (from now on Community analyses): *C. erythraeus* has a low level of parasitism and has more generalist parasites in its introduced range in comparison with native sympatric species; we predicted (1.1) fewer parasites (richness, prevalence and mean intensity) of *C. erythraeus* in Argentina in comparison with native sympatric mammals and (1.2.) fewer or none specific parasites of *C. erythraeus* in Argentina in comparison with native sympatric mammals; (2) enhanced performance (from now on Biogeographical analyses): *C. erythraeus* has low level of parasitism

and an enhanced performance in introduced ranges in comparison with native range; we predicted (2.1) lower richness and prevalence of parasites of *C. erythraeus* in its introduced ranges in comparison with populations in native range and (2.2.) larger population density and spread of *C. erythraeus* in introduced ranges where level of parasitism is low in comparison with introduced ranges with intermediate or high level of parasitism (richness and prevalence). This analytical framework allowed us to evaluate all available information to find evidence in support or against the ERH. To our knowledge, this approach has not been undertaken yet for *C. erythraeus* and other sciurids.

Materials and methods

Community analyses

We studied ecto and endo-parasites (arthropods, protozoans and gastro-intestinal helminths) of *C. erythraeus* and co-inhabiting non-volant native mammals to assess its role as a new host in the invaded community. We described prevalence, abundance and identity of parasites recorded on *C. erythraeus* and sympatric native mammals in the main invasion focus of Argentina. As mentioned before, no sciurids are present in the Pampas region and potential mammalian competitors that share the same habitat include marsupials, and sigmodontine and caviomorph rodents, although no systematic studies have evaluated competitive interactions yet. The Luján invasion focus is the oldest and largest focus in Argentina, where *C. erythraeus* was introduced in 1970 (Benitez et al. 2013). Four decades since its introduction and a high density of *C. erythraeus* (Benitez et al. 2013) yielded an appropriate scenario to search for new host-parasite interactions. The Pampas region has been largely modified by agricultural activities and urban-industrial development; suitable arboreal habitat for *C. erythraeus* is highly fragmented and mainly composed of exotic tree species in small patches, wind barriers and tree lines along roads and railways, and in parks and streets of urbanised areas (Guichón and Doncaster 2008).

We live trapped small and medium sized mammals in four study sites in the Luján invasion focus (1: 34° 33' S, 59° 07' W; 2: 34° 34' S, 59° 3' W; 3: 34° 32' S, 59° W; 4: 34° 34' S, 59° 11' W) in autumn

(April–June) and spring (October–December) of 2010. The distances among all study sites exceeded the daily movements and dispersal distance expected for this species (Guichón and Doncaster 2008), and were considered replicates. In each study site, we set 30 cage traps (30 × 15 × 15 cm) on tree branches at fixed points 40 m apart to trap squirrels. Next to the trees with squirrel cage traps, we set on the ground 60 Sherman traps (8 × 9 × 24 cm) for small rodents and 20 Tomahawk traps (75 × 35 × 35 cm) for mid-sized mammals. Each trapping session in each site and season lasted four consecutive days and nights. We anaesthetised captured mammals to reduce their stress and facilitate proper and safe manipulation (Gannon and Sikes 2007). We collected ectoparasites and faeces samples separately for each captured individual. We marked each individual (haircut and bleaching) at first capture in each trapping session to avoid duplicate samples per season.

We combed and brushed the fur of each individual to collect ectoparasites. We filtered and stored arthropods in 96% ethyl alcohol and prepared them for their taxonomic identification using an optic microscope (Strandtmann and Wharton 1958; Furman 1972; Smit 1987; Welbourn 2006; Krantz and Walter 2009). We removed botfly larvae using forceps and used a stereomicroscope for taxonomic identification.

We collected faecal samples for the diagnoses of gastro-intestinal parasites by keeping captured individuals in a safe place within their traps until they defecated. We stored faeces in 10% formalin and inspected them to detect coccidian oocysts and gastro-intestinal helminth eggs by direct microscopical examination and using the sugar (Sheater's sugar solution) flotation method (Vignau et al. 2005). We used characteristics of the wall, shape and size of the eggs and oocysts to identify gastro-intestinal parasites.

We calculated prevalence (P%), mean intensity (MI) and parasite load (for gastro-intestinal parasites) of parasite species/taxonomic group for each host species per season (Bush et al. 1997). Parasite load was calculated as the mean fecal oocysts/eggs counts (hpg/opg: number of eggs or oocysts found in 1 gr of faeces per host species) of each species/taxonomic group for each host species, using the McMaster technique (Vignau et al. 2005). We also recorded total parasite richness (S) of each host species.

Biogeographical analyses

We analysed scientific papers and reports that included parasitological and/or population studies on *C. erythraeus* to describe its level of parasitism in native and introduced ranges, and to evaluate its association with population growth and spread in introduced populations. We used population density and spread (invaded area/time since introduction) as proxy variables of invasion success. Between 2008 and 2020 we have regularly searched for publications on *C. erythraeus* worldwide using Google Scholar and other public search engines, looking for all references on *C. erythraeus* cited in each paper found, and contacting researchers worldwide. We selected 35 publications with relevant and nonduplicated information about parasites of *C. erythraeus* and/or performance of introduced populations from which we extracted data on richness, prevalence and mean intensity of parasites, type of parasites (co-introduced or locally acquired, generalist or specific), population density/abundance of *C. erythraeus*, invaded area and time since introduction. We used parasitological data and population parameters estimated for the only or main invasion focus in each country. We calculated the number of macroparasite species (ectoparasites and helminths) to compare parasite richness in their native and introduced ranges (Argentina, Belgium, France, Italy and Japan). We compared parasite richness and prevalence among introduced populations taking into account squirrel density and spread described for those same populations. For these comparisons, parasite richness and prevalence in Japan are only for ectoparasite species (Shinozaki et al. 2004) and parasite richness in Argentina corresponds to studies on ectoparasites (Gozzi et al. 2013) and endoparasites (Gozzi et al. 2014) plus the results in the Community analyses of this study. We calculated Spearman correlation coefficient (r) using R 3.4.1 statistical software (R Development Core Team 2017) to analyse the relationship between mean parasite prevalence/richness and squirrel density/spread. We could not compare mean intensity of parasites among introduced ranges because data were insufficient or not comparable.

Results

Community analyses

We captured four mammalian species throughout the study, *C. erythraeus* ($n = 274$) and three native species: two sigmodontine rodents, the Azara's grass mouse *Akodon azarae* ($n = 66$) and the long-tailed mouse *Oligoryzomys* spp. ($n = 2$), and one marsupial, the white-eared opossum *Didelphis albiventris* ($n = 47$). We found ectoparasites in 67% of the samples of *A. azarae* (44/66), in all the samples of *Oligoryzomys* spp. (2/2) and in 49% of the samples of *D. albiventris* (23/47). Less than 1% (2/274) of the samples of *C. erythraeus* were positive for ectoparasites (Table 1). Helminths eggs or protozoans oocysts were found in 58% of the samples of *A. azarae* (26/45) and in 72% of the samples of *D. albiventris* (23/32). We found no gastro-intestinal parasites (helminths or protozoans oocysts) in *C. erythraeus* ($n = 103$) and in *Oligoryzomys* spp. ($n = 1$) (Table 1). Parasite richness of *C. erythraeus* was determined by the presence of only one ectoparasite species, the flea *Polygenis (Polygenis) rimatus* that was also present in *A. azarae* and *D. albiventris*. Parasite richness of sympatric mammals was 3–9, determined by ectoparasite, helminth and coccidian species (Fig. 1). In general, prevalence and mean intensity of the parasites found in native mammalian species reached higher values than obtained for *P. (P.) rimatus* in *C. erythraeus* (see Table 1).

Biogeographical analyses

Parasitological studies on *C. erythraeus* showed a relatively high number of macroparasite species in its native range ($S = 33$) in comparison with 3–11 species reported in introduced ranges (Fig. 2, lists of parasites recorded in native and introduced ranges are given in Online Resources 1 and 2, respectively). Parasite richness in Argentina ($S = 6$) was intermediate between Belgium and France ($S = 3$) and Italy ($S = 11$) and Japan ($S = 9$) (Fig. 2).

Both ecto and endoparasites (helminths) were reported in introduced ranges. One parasite species was introduced together with *C. erythraeus* into Belgium and France (the louse *Enderleinellus kumadai*, Dozières et al. 2010), four species into Japan (the lice *Neohaematopinus callosciuri* and *E. kumadai*, and

the nematodes *Strongyloides callosciureus* and *Brevistriata callosciuri*, according to Shinozaki et al. 2004; Kaneko 1954; Sato et al. 2007 and Asakawa 2005, respectively) and one into Italy (the nematode *Strongyloides callosciureus*, Mazzamuto et al. 2016b) (Fig. 2). However, in Argentina all parasites of *C. erythraeus* were acquired in the new environment from sympatric mammalian species (Fig. 2). Macroparasite species found in Argentina have low specificity in contrast to those described in Belgium, France, Italy and Japan considering that *S. callosciureus* is a common nematode of sciurids, and *E. kumadai*, *N. callosciuri* and *B. callosciuri* are specialist parasites of the Callosciurini tribe.

Performance of introduced populations taken as density was intermediate or high in all countries of introduction, particularly in Argentina, taking into account that population density of *C. erythraeus* in its native area ranges 0.5–7 ind/ha (Lin and Yo 1981; Tamura et al. 1989) (Table 2). Spread of *C. erythraeus* was high in the main invasion focus of Argentina, intermediate in Italy and Japan, and low in France and Belgium (Table 2). No correlation was found between parasite richness and population parameters (spread: $r_{\text{rich-spread}} = 0.78$, $p = 0.12$; density: $r_{\text{rich-dens}} = 0.78$, $p = 0.12$). A negative correlation between mean parasite prevalence and population parameters (spread: $r_{\text{prev-spread}} = -1$; density: $r_{\text{prev-dens}} = -0.9$, $p = 0.04$) was mainly due to the low parasite prevalence and high density and spread of *C. erythraeus* in Argentina (Table 2).

Discussion

Our results are in accordance with the first working hypothesis given that *C. erythraeus* in Argentina has lost its specific parasites, it is colonized by more generalist parasites and it is less parasitised than native sympatric mammals. *C. erythraeus* has acquired parasites present in the new environment; however, these acquisitions fail to compensate the parasite richness described in its native range (Online Resources 1 and 2). The encounter rate between host species and the infective stages of parasite species determines prevalence while the mean intensity could reflect the fitness of the parasite species (Wilson et al. 2002; Poulin 2007). Differences in the values of parasite prevalence and mean intensity found in *C.*

Table 1 Prevalence (P%), mean intensity (MI) and parasite load as mean fecal egg/oocyst count (MFE/OC) of parasites per host species in both seasons (A: autumn, S: spring). The range of parasite count is expressed in brackets

Parasite species	<i>C. erythraeus</i>			<i>A. azarae</i>			<i>Oligoryzomys</i> spp.			<i>D. albiventris</i>							
	P%			P%			P%			P%							
	A	S	MI-MFE/OC ^b	A	S	MI-MFE/OC	A	S	MI-MFE/OC	A	S	MI					
Siphonaptera (fleas)																	
Rhopalopsyllidae																	
<i>Polygenis (P.) rimatus</i>	0	1.7	a	1.5	10	25	1.6	1.6 [1–3]	1.25 [1–3]	0	–	a	–	34.6	52.4	1.33 [1–3]	10.4 [2–36]
Pulicidae																	
<i>Ctenocephalides felis felis</i>	0	0	a	a	0	0	a	a	a	0	–	a	–	15	10	1.5 [1–2]	1
Acari																	
Laelapidae (mites)																	
<i>Androlaelaps fahrenheitzi</i>	0	0	a	a	32	6.2	2.2 [1–7]	1	1	0	–	a	–	7.7	4.8	1.5 [1–2]	1
<i>Androlaelaps aff. rotundus</i>	0	0	a	a	82	43.8	10.7 [1–51]	9.3 [1–25]	9.3 [1–25]	0	–	a	–	0	0	a	a
<i>Laelaps manguihosi</i>	0	0	a	a	0	0	a	a	a	100	–	3.5 [3–4]	–	0	0	a	a
<i>Laelaps paulistanensis</i>	0	0	a	a	2	0	1	a	a	50	–	11	–	0	0	a	a
<i>Gigantolaelaps wolffsohni</i>	0	0	a	a	0	0	a	a	a	100	–	3 [2–4]	–	0	0	a	a
<i>Mysolaelaps microspinosus</i>	0	0	a	a	2	0	1	a	a	100	–	12.5 [5–20]	–	0	0	a	a
Diptera																	
Oestridae (botflies)																	
<i>Cuterebra</i> sp.	0	0	a	a	22	12.5	1.8 [1–2]	1	1	0	–	a	–	0	0	a	a
Protozoa																	
Coccidia																	
Eimeriidae																	
<i>Eimeria</i> spp.	0	0	a	a	0	0	a	a	a	0	–	a	–	92.8	55.6	11,242 [280–69,040]	5089 [20–16,480]
Helminths																	
Cestoda																	

Table 1 continued

Parasite species	<i>C. erythraeus</i>			<i>A. azarae</i>			<i>Oligoryzomys</i> spp.			<i>D. albiventris</i>					
	P%		MI-MFE/OC ^b	P%		MI-MFE/OC	P%		MI-MFE/OC	P%		MI			
	A	S	A	S	A	S	A	S	A	S	A	S			
Cyclophyllidea	0	0	a	a	0	0	160	60	-	a	-	0	0	a	
[140–180]															
Nematoda															
Ascaritrida, Aspidoderidae	0	0	a	a	6	8.3	a	a	-	a	-	0	6	a	40
<i>Aspidodera</i> sp.	0	0	a	a	0	0	410	112.5	-	a	-	0	6	a	140
Enoplida, Trichuridae	0	0	a	a	0	0	410	112.5	-	a	-	0	6	a	140
<i>Trichuris</i> spp.	0	0	a	a	0	0	410	112.5	-	a	-	0	6	a	140
[40–280]															
Spirurida, Kathlamidae	0	0	a	a	0	45.4	a	a	-	a	-	78.6	55.6	a	171.5
<i>Cruzia</i> sp.	0	0	a	a	0	45.4	a	a	-	a	-	78.6	55.6	a	171.5
Unidentified	0	0	a	a	0	0	a	120	-	a	-	0	22	a	64.7 [20–134]
[20–733]															

Number of ectoparasite samples analysed per season (A: autumn, S: spring): *C. erythraeus*: n_A = 154, n_S = 120; *A. azarae*: n_A = 50, n_S = 16; *Oligoryzomys* spp.: n_A = 2, n_S = 0; *D. albiventris*: n_A = 26, n_S = 21. Number of faeces samples per season: *C. erythraeus*: n_A = 68, n_S = 35; *A. azarae*: n_A = 33, n_S = 12; *Oligoryzomys* spp.: n_A = 1, n_S = 0; *D. albiventris*: n_A = 14, n_S = 18

^aNo hosts were infected

^bMFE/OC is expressed in oocysts or helminth eggs per gram of faeces (opg/hpg)

–: No samples were available

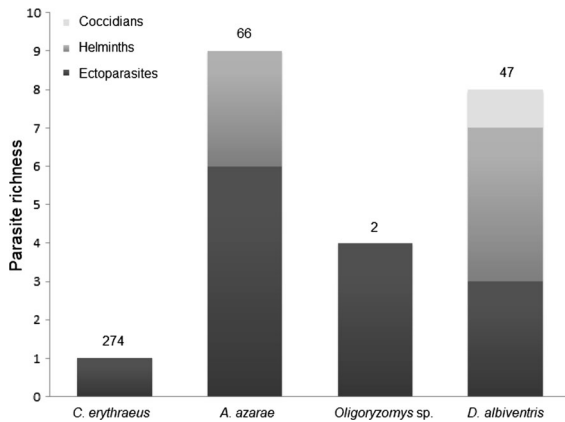


Fig. 1 Number of parasite species found in *C. erythraeus* and native sympatric mammals in Luján invasion focus, Argentina. The number of analysed individuals of each host species is indicated above each bar

erythraeus in comparison with sympatric mammals suggest that associations between *C. erythraeus* and its parasites in Argentina are occasional or accidental. Prevalence, intensity and load of parasites described for *C. erythraeus* were lower than for sympatric mammals, even if a much larger number of samples were analysed for *C. erythraeus*. The loss of its natural parasites could be due to its history of introduction or to the absence of appropriate intermediate hosts or adequate conditions (i.e. climate) for the perpetuation of its natural parasites in the new environment. In addition, compatibility and ecological filters (i.e. herbivory, arboreal habits) and the absence of phylogenetically close host mammals (sciurids) or ecological equivalents could determine the low acquisition of parasites with higher host specificity (Combes 2001; Poulin 2007). It is therefore more likely the acquisition of generalist ectoparasites, whose alternation of stages on and off the host allows them to “explore” new species as potential hosts (Marshall 1981; Poulin 2007). Ectoparasites acquired by *C. erythraeus* are generalist species previously described for sympatric rodent and marsupial species (Lareschi and Mauri 1998; Lareschi et al. 2016; summarised in Gozzi 2015). This is the case of the flea *P. rimatus* that has a South American distribution and it is considered a generalist species found in a diversity of mammals, mainly rodents (Smit 1987; Linardi and Guimarães 2000). However, *Cuterebra* botflies would be an exception to the condition of generalist species given

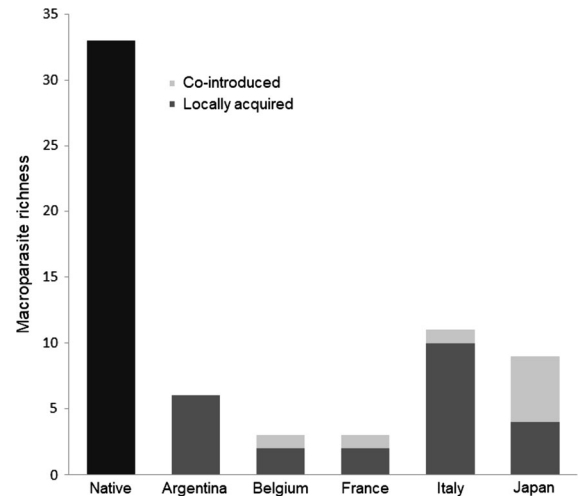


Fig. 2 Macroparasite richness of *C. erythraeus* in its native and introduced ranges. Studies that recorded macroparasites in native range included at least seven subspecies of *C. erythraeus* and at least six study sites in Southeast Asia (sources: Jordan 1932; Myers and Kuntz 1964; Hoogstraal and Kohls 1965; Schmidt et al. 1967; Durette-Desset 1970; Blagoveshchenskiy 1972; Traub 1972; Kliks and Durette-Desset 1976; Li et al. 1976; Chin 1979; Fischthal and Kuntz 1981; Wang 1981; Liu et al. 1982; Durden and Musser 1994; Shinozaki et al. 2004; Huang et al. 2010; Zuo et al. 2011; Lurz et al. 2013; Durden and Beaucournu 2014). For introduced ranges, we used parasitological studies conducted in: Argentina (this study—section “Community analyses”—and two previous publications; Gozzi et al. 2013, 2014), Japan (n = 6; Kaneko 1954; Matsudate et al. 2003; Shinozaki et al. 2004; Asakawa 2005; Sato et al. 2007; Miyabe et al. 2016), France (n = 1, Dozières et al. 2010), Belgium (n = 1; Dozières et al. 2010), and Italy (n = 1; Mazzamuto et al. 2016b) (complete lists of parasites and additional data are given in Online Resources 1 and 2)

their affinity for hosts of the genus *Akodon* (Zuleta and Vignau 1990). Unfortunately, competitive interactions of *C. erythraeus* in Argentina have not been studied yet although resource use overlap could be high with *D. albiventris* (Chemisquy and Martin 2019; Guichón et al. 2019; personal observation). Also, other taxa deserve attention as potential competitors, such as some bird species (Messetta et al. 2015). Further studies monitoring new interactions through time and space (e.g. new invaded areas with a different community composition or the same invaded area at different times since introduction) would provide more evidence for or against the ERH in the invasion success of *C. erythraeus*.

Regarding the biogeographical analyses, we found partial support to our second working hypothesis (enhanced performance). In accordance to the first

Table 2 Characteristics of the invasion foci of *C. erythraeus* used for comparison among countries (study site in each country) indicating year of introduction, invaded area (year of estimation), spread, density (year of estimation/technique), parasite richness (year of parasitological study), range of parasite prevalence (mean prevalence) (year of parasitological study), and information sources

	Year of introduction	Invaded area (km ²)	Spread (km ² /year)	Density (ind/ha)	Parasite richness	Parasite prevalence (mean)	Sources
Argentina (Luján)	1970	1336 (2009)	34.26	15 (2006–2007/point transect)	6 (2010)	0.15–2.5 (1.2) (2010)	Benitez et al. (2013), Gozzi et al. (2013, 2014); Community analyses
Belgium ^a (Dadizele)	2005	0.15 (2011)	0.03	6 (2007/trapping)	3 (2008)	5–70 (40) (2008)	Dozières et al. (2010), Adriaens et al. (2015)
France (Antibes)	1970	18 (2010)	0.45	4 (2010/line transect)	3 (2008)	7–55 (23) (2008)	Dozières et al. (2010, 2015)
Italy (Varese)	2007	90 (2015)	11.25	8 (2011–2015/trapping)	11 (2011–2014)	1–50 (10.8) (2011–2014)	Mazzamuto et al. (2016a, b)
Japan (Kamakura)	1950	304 (2002)	5.85	7 (1982–1988/census routes)	3 (2001–2003)	1–21 (11.5) (2001–2003)	Shinozaki et al. (2004); Tamura et al. (1989); Tamura (2004)

^aAn eradication campaign was conducted between 2005 and 2011 (Adriaens et al. 2015)

prediction, macroparasite richness of *C. erythraeus* was lower in introduced than in native range, which may contribute to its invasion success (Torchin et al. 2003). Even though the list of parasites in native range was obtained from a larger number of sites and studies (n = 19) than for introduced ranges (n = 10), it must be noted that studies in native range mostly reported parasite taxonomic descriptions, records and checklists. Unfortunately, the lack of data on parasite prevalence and mean intensity/abundance in native range prevented further comparisons. The second prediction was partially supported given that parasite richness was not associated with population density and spread in introduced ranges. We did find a negative correlation between mean parasite prevalence and population parameters. However, the strong effect of just one site (Luján, Argentina) in this correlation suggests caution for generalisations and the need of further studies to fully comprehend if the ERH could play a more important role in Argentina than in other introduced regions. These comparisons were conducted using data of parasite prevalence obtained in the same sites where population density and spread have been recorded (based on available bibliography, see references in Table 2). Although different methodological techniques could hinder comparisons, we consider that these data are valid to search for general trends and attain a global picture. As stated by Krasnov and Poulin (2010), population regulation could be caused by the presence of a subset of infesting parasite species and might not be related to parasite species richness in a host population. Therefore not only parasite richness or prevalence, but also the taxonomic identity and characteristics of the parasites (e.g. specific vs. generalist) should be taken into account when comparing parasites of a species in its native and introduced ranges (Colautti et al. 2004). Further studies are still needed for a comprehensive understanding of the role of enemy release of *C. erythraeus* in introduced ranges, such as regulatory effects of specific parasites, as those described in France, Belgium, Japan and Italy (Shinozaki et al. 2004; Dozières et al. 2010; Mazzamuto et al. 2016a, b) and of other enemies, i.e. predators. Also, further comparisons regarding parasites and performance of introduced populations versus populations in native range would provide more evidence for or against the ERH in the invasion process of this species (Prior et al. 2014, 2015).

Concluding remarks

Parasitological studies of introduced species covering not only biogeographic aspects but also comparisons within the invaded community provide more evidences to evaluate the role of the ERH in invasion success. These studies also reveal new associations between parasites and hosts due to parasites exchange between native and introduced species. As explained before, the ERH states, in a broad sense, that the absence of natural enemies in the exotic range promotes invasion success (Torchin et al. 2003; Jeschke and Heger 2018). This reduction of enemies might lead to an advantage for the invader in its new range. However, the relationship between the release of enemies and the enhanced performance is not always straightforward and other factors may contribute to invasion success (Prior et al. 2014). The fact of enunciating which aspects of the ERH are going to be tested improves the analyses using available and new information on the invasion process and sheds light on other variables and comparisons that need further analyses. The release of parasites of *C. erythraeus* in comparison to native and other introduced ranges, the low level of parasitism, the acquisition of only generalist parasites and the high population performance in Argentina are mostly in agreement with the expected outcomes of the ERH. The lack of efficient predators could also support the ERH and should be thoroughly studied; unfortunately no systematic studies have been conducted so far on this subject in Argentina. This partial support to the ERH does not discard that other factors related to habitat features and resource availability could also favour invasion success (e.g. empty niche hypothesis) (Shea and Chesson 2002). The apparently high competitive pressure in its native range where *C. erythraeus* is sympatric with several arboreal squirrel species (e.g. Timmins and Duckworth 2008, Kobayashi et al. 2019; Koyabu et al. 2012) and the lack of sciurids in the areas invaded in Argentina, could result in fewer competitors rendering a favourable environment that facilitates invasion (Hufbauer and Torchin 2007; Dunn et al. 2012). Ongoing studies regarding ecological interactions of *C. erythraeus* in invaded areas will improve the understanding of its success in Argentina and other regions to fully comprehend the relative importance of the ERH in this process (Prior and Hellmann 2015). Future studies could also show

whether these parasite acquisitions that until now are occasional/accidental in Argentina may progress into more stable associations (Torchin and Mitchell 2004; Poulin 2007; Gendron et al. 2012). This would provide insight into how the level of parasitism may translate into an ecologic advantage at different invasion stages (Hufbauer and Torchin 2007; Dunn et al. 2012).

Acknowledgements The authors thank all the volunteers that collaborated in the field and laboratory work, and the owners of the properties where we conducted the fieldwork in Luján invasion focus (ACA, Huellas, Santa Elena ranch and Universidad Nacional de Luján). Comments of two anonymous reviewers helped to improve the manuscript. This study was supported by the Universidad Nacional de Luján (Grant No. Finalidad 3.5).

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