SAREM Series A
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VOLUME 3

INTRODUCED INVASIVE MAMMALS OF ARGENTINA

MAMÍFEROS INTRODUCIDOS INVASORES DE ARGENTINA

Alejandro E. J. Valenzuela, Christopher B. Anderson, Sebastián A. Ballari and Ricardo A. Ojeda, EDITORS

The Argentine Society for the Study of Mammals (Sociedad Argentina para el Estudio de los Mamíferos – SAREM) was created in 1983, and currently has about 300 members from several countries. SAREM is an interdisciplinary society of natural sciences professionals whose main goals are the promotion of scientific and technical research, the consolidation of national collections and research centers, and the publication and diffusion of research on living and/or extinct mammals. SAREM has organized scientific meetings for mammal researchers since 1994, publishes the journals *Mastozoología Neotropical* and *Notas sobre Mamíferos Sudamericanos*, and has edited books on the systematics, distribution and conservation of the mammals of southern South America, including *Libro Rojo de los mamíferos amenazados de la Argentina* (first ed. 2000, second ed. 2012) and *Mamíferos de Argentina. Sistemática y distribución* (2006), as well as contributing to the *Libro Rojo de los mamíferos y aves amenazados de la Argentina* (currently out of print).

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INTRODUCED INVASIVE MAMMALS OF ARGENTINA

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Mammalogical Research
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Introduced Invasive Mammals of Argentina / Alejandro Valenzuela … [*et al.*]. – 1ª ed. – Mendoza : Sociedad Argentina para Estudio de los Mamíferos SAREM, 2023.
Memoria USB, PDF

ISBN 978-987-98497-9-8

1. Mamífero. 2. Animales Exóticos. I. Valenzuela, Alejandro.
CDD 599.0982

Cover collage: Gabriela F. Ruellan

Cover photo credits: Kev on Pixabay (European hare) | Dorota Kudyba (dogs and horses) | Ruediger50 on Pixabay (water buffalo) | Sergio Anselmino (American mink) | Gabriela Ortega (cow hide) | efPercy05 on Pixabay (goat) | suksao on Freepik (chital) | Guillermo Deferrari (muskrat) | J. Cristóbal Pizarro (North American beaver damage) | Peter Chou (Pallas's squirrel) | Public Domain Pictures (red and fallow deer antlers) | marco on Pixabay (wild boar)

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Introduced invasive species are a major driver of local to global environmental change, including important negative impacts on biodiversity, ecosystem processes, economies, health and other social values. At the same time, however, different social actors can hold diverse representations of these species, particularly of introduced invasive mammals (IIMs). Such divergent values and perceptions can lead to conflicts regarding the management of IIMs, but also invite researchers and managers to be reflexive regarding their own work at a more fundamental level. Therefore, it is key that we advance towards a holistic understanding of IIMs and develop strategies to manage them based on solid technical information and plural perspectives regarding their multiple values. Despite a rich history of initiatives in Argentina to study and manage IIMs, until now there has not been an opportunity to assess the state-of-the-art knowledge in our country. This book seeks to provide rigorous, relevant and legitimate information to support research, policymaking and management decisions regarding IIMs in Argentina. With this objective in mind, the book presents a series of chapters selected to highlight priority topics concerning the conceptualization and implementation of IIM research and management. Then, fact sheets are provided for the different IIMs found in Argentina. Finally, beyond the realm of academic inquiry, the timing of this publication is ideal to re-enforce policy and decision-making, such as the recently approved National Invasive Exotic Species Strategy, which seeks to implement actions and enhance institutional capacities related to invasive species management in Argentina, and the Convention on Biological Diversity's new Global Biodiversity Framework, which also addresses biological invasions as part of broader efforts to attain the 2050 Vision for Living in Harmony with Nature.

Dr. Alejandro E.J. Valenzuela
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Editors, Vol. III SAREM Series A

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Foreword

Biological invasions by introduced species are one of the great changes rapidly transforming the globe today, with innumerable impacts on economics, human health, ecosystem services, and biodiversity. Mammals are among the most impactful of invasive species, transmitting diseases to humans, livestock, and native animals, trampling native grasslands, voraciously devouring vegetation from groundcover to saplings of forest trees, fouling water, causing erosion, and preying on and outcompeting native animals. They were among the first species humans introduced worldwide and in Argentina, both deliberately (*e.g.*, livestock) and inadvertently (*e.g.*, rats and mice). They have been introduced for sport (*e.g.*, deer, boar) and companionship (*e.g.*, cats, dogs), or simply as attractive ornamentals (*e.g.*, squirrels). Some that are meant to be kept in captivity, such as cats, dogs, and squirrels, escape and establish feral populations.

Argentina looms large in the history of biological invasions by introduced mammals. The earliest permanent European settlers of Buenos Aires in 1580 discovered huge herds of feral horses already on the pampas, and soon after, Vázquez de Espinoza described feral horses in Tucumán that were "in such numbers that they cover the face of the earth…". Many sheep were in Tucumán as well at that time, and of course later sheep were enormously numerous in Patagonia, effecting huge changes in the vegetation and driving land degradation and desertification to this day. When Charles Darwin visited the La Plata region in 1832 during the voyage of the Beagle, he reported that "…countless herds of horses, cattle, and sheep, not only have altered the whole aspect of the vegetation, but they have almost banished the guanaco, deer and ostrich. Numberless other changes must likewise have taken place; the wild pig in some parts probably replaces the peccari; packs of wild dogs may be heard howling on the wooded banks of the less-frequented streams; and the common cat, altered into a large and fierce animal, inhabits rocky hills."

Approximately 40 mammals have been introduced to South America, of which 25–30 have established populations; most of these are in the Southern Cone. In Argentina, I count 23 successfully introduced mammal species, including feral cats, dogs, and cows. Many, such as rats, rabbits, boar, and goats, are widely distributed around the world. By contrast, the hairy armadillo has been introduced nowhere else but from the mainland of Patagonia to Tierra del Fuego Island. Strikingly, except for the rats and house mouse, all these mammals were brought to Argentina deliberately; this is very different from, say, introduced insects. A few of these invasive mammals, like the squirrel, were not intended to be released, but I hesitate to term such invaders truly "accidental," because the people who brought them should have realized that escapes or later releases were almost inevitable. Of course, almost all of these mammals were introduced before the late twentieth century, which was when most scientists and the public began to recognize the extent and importance of impacts of introduced species. However, the squirrel and armadillo introductions were recent enough that potential impacts should have been foreseen. Things could be worse, of course—mammals deliberately brought to Argentina that either were released, but did not establish persistent populations or have not yet escaped from hunting preserves include reindeer, silver fox, mule deer, African buffalo, white-tailed deer, Père David's deer, thar, barbary sheep, wisent, mouflon, chamois, and ibex.

The technology of eradicating introduced invasive mammals has made enormous strides in the last thirty years—at least 31 mammal species have been eradicated from islands worldwide, including relatively large islands like South Georgia. Both Norway and ship rats have been eradicated hundreds of times, and house mice about 100 times. Most large mammals, such as deer and horses, are technologically easier eradication targets—many can simply be tracked and shot, for instance. However, mammals more than any other introduced species pose the complication that many people—especially hunters—simply do not want to eradicate them, and many animal welfare advocates, even those recognizing the damage some invaders cause, object to eradicating them by the only currently feasible means—killing them, humanely if possible. Even rat eradication has been impeded on animal rights/animal welfare grounds, and free-ranging dog and cat populations frequently are seen more as animal welfare issues than as conservation problems to broad sectors of some societies. In Argentina, the problem of implementing feasible eradication programs for invasive mammals is epitomized by the rather schizophrenic attitude taken by the National Parks Administration (Administración de Parques Nacionales – APN) towards red deer. The APN's conservation imperative is supported by the section of Law #22,351 that forbids propagating introduced animals, yet red deer, known to damage native species and ecosystems, are managed in Lanín National Park to foster ongoing hunting, and even to improve the size and quality of the deer for better hunting trophies. Additionally, there is often inconsistent and inadequate funding for managing and eradicating invasive mammals in protected areas, almost always constituting a supervening impediment even when a rational and effective goal is stated.

Argentine scientists have participated heavily in the rapid growth of modern invasion science since its inception in the 1980s, and they and overseas colleagues have conducted substantial research on the biology and impacts of many of the introduced invasive mammals in Argentina, as well as other invasive species. Some of the threats posed by these mammals have even become widely known to the general public in Argentina and beyond—the spread of the beaver from Tierra del Fuego to the mainland has been an international news story. *Introduced Invasive Mammals of Argentina* is therefore an exciting and timely addition to the literature on invasions in southern South America for both the Argentine public (and its political representatives and environmental managers) and scientists worldwide. The many authors assembled for this book explore how these biological invasions happened in the first place, how they spread, what they do to biodiversity, ecosystems, and human enterprises, what has been done about them so far, what can be done about them now, and what might be done with them in the future. The editors and authors are to be congratulated for an excellent exposition of the Argentine part of a growing global phenomenon.

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MAMÍFEROS INTRODUCIDOS E INVASORES: UNA PERSPECTIVA CONCEPTUAL E HISTÓRICA PARA ARGENTINA

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Abstract. Species that experience range expansions, high population growth and negative social or ecological impacts in a non-native location due to human actions are defined as both introduced and invasive. In particular, introduced invasive mammals (IIM) are more harmful than other vertebrates, and their social-cultural interactions are especially strong. IIMs in the Americas represent about 20% of mammal introductions worldwide, and their high species richness is concentrated in South America's Southern Cone. The aim of this chapter is to provide an overview of the state-of-the-art on IIMs in Argentina. We present the main concepts and applications of the biological invasion process, the major contributions of IIM studies in Argentina, and perspectives for future research. By viewing biological invasions as a multi-stage process with major drivers and a series of sequential steps, IIMs can be used as a relevant model and opportunity to promote a scientific agenda encompassing a diversity of topics and dimensions. Such a fundamental research program, coupled with strategic and integrated planning with governmental agencies, could provide the groundwork for aiding in the prevention of biotic homogenization and biodiversity loss in Argentina.

Resumen. Las invasiones biológicas facilitadas por los seres humanos constituyen uno de los aspectos más relevantes del cambio global. La propagación de especies invasoras ocurrió a lo largo de la historia, principalmente durante los siglos XIX y XX. La expansión del comercio, los desplazamientos humanos y el movimiento de continente a continente realizado por diferentes medios de transporte produjeron la dispersión y el aumento drástico de nuevas especies en diferentes regiones del planeta, con consecuencias ambientales inesperadas.

Muchas especies no nativas proporcionan beneficios y son componentes omnipresentes e integrales de la economía global. Especies utilizadas en la agricultura, la silvicultura, la piscicultura y otras actividades productivas de utilidad para el humano son no nativas. Sin embargo, los costos negativos de las especies no nativas surgen cuando estas alcanzan el estatus de introducidas, se naturalizan e invaden un nuevo ambiente. Las especies introducidas invasoras son definidas como toda especie introducida por el ser humano que se ha dispersado y establecido fuera de su área de distribución natural y constituye una amenaza para la biodiversidad (Convenio sobre la Diversidad Biológica,

CDB, 1992). Dichas especies en general son oportunistas y fácilmente adaptables a nuevos hábitats, lo que les permite aumentar sus números rápidamente, convirtiéndose en componentes dominantes en las comunidades invadidas; resultan además la causa principal de extinción, retracción y reestructuración de las poblaciones biológicas. Los daños y perjuicios ambientales producidos por las especies invasoras involucran costos económicos importantes para diversas actividades humanas, incluyendo además situaciones de riesgo para la salud, lo que las lleva a ser consideradas análogas a los desastres naturales.

Entendiendo que las especies introducidas invasoras en general, y los Mamíferos Introducidos Invasores (MII) en particular, son un fenómeno mundial con gran relevancia a escala local, el objetivo del presente capítulo es proporcionar una visión global del estado del arte en la investigación sobre MII en Argentina. En las dos primeras secciones introducimos aspectos conceptuales claves de las invasiones biológicas, proceso de invasión y teoría de nicho aplicada a las invasiones. En las dos últimas secciones abordamos y analizamos la historia y el contexto de las investigaciones de MII en Argentina.

Fundamentalmente, el éxito de las especies invasoras es resultado de la conjunción de factores: 1) intrínsecos de la especie (tasa de reproducción, masa corporal, abundancia, tamaño del área de distribución natural) y 2) extrínsecos, o del hábitat que invaden (disponibilidad de nichos vacantes y recursos alimenticios, clima, entre otros). Sin embargo, no es posible establecer generalizaciones que permitan caracterizar la invasión de una especie, ya que este proceso varía de región a región y de ecosistema a ecosistema.

En particular, los mamíferos son uno de los grupos de invasores biológicos más exitosos y sus interacciones socioculturales son especialmente fuertes. Los MII en América representan alrededor del 20% de las introducciones de mamíferos en todo el mundo, y su mayor densidad se concentra en América del Sur. De un total de 37 especies citadas, el 76% (excluyendo las especies domésticas) ocuparon el cono sur de Argentina y Chile. La mayoría de las introducciones de mamíferos fueron hechas deliberadamente por el ser humano para posibilitar su caza deportiva, realizar actividades de explotación económica o confinar los animales en explotaciones privadas, rurales, criaderos, parques o zoológicos donde constituyeron poblaciones asilvestradas. En ausencia de regulaciones específicas, estas introducciones ocasionaron perjuicios de amplio impacto por la expansión de varias especies, en ciertos casos incontrolables, como el jabalí (*Sus scrofa*). La tendencia en la investigación de MII en Argentina entre los años 1978 y 2021 se enfocó principalmente en abordajes biológicos y ecológicos, así como de impacto ambiental. Menor importancia presentan las aproximaciones en investigación aplicada, mostrando que aún existen importantes vacíos, tanto en estudios de impactos económicos, sociales y culturales como de desarrollo de políticas de manejo.

La comunidad científica ha identificado a las invasiones biológicas como un fenómeno de disrupción y amenaza al mantenimiento de la biodiversidad. Algunos autores también consideran a las especies invasoras como organismos modelo que podrían proporcionar una comprensión más general de la naturaleza y de problemas aplicados, como la extinción, funcionamiento de ecosistemas y respuestas al cambio climático. Más aún, las invasiones biológicas abarcan una amplia gama de dimensiones de investigación que va desde los aspectos biológicos-ecológicos a consideraciones socio-económicas, análisis de riesgos y desarrollo de políticas.

Al estudiar las invasiones biológicas como un proceso multifacético con grandes impulsores y una serie de pasos secuenciales, los MII ofrecen un modelo único y una oportunidad para una agenda de investigación que engloba una gran diversidad de temas y dimensiones. Tal programa de investigación fundamental, junto con la planificación estratégica e integrada con organismos gubernamentales, agencias estatales en varios niveles y diferentes sectores sociales, políticos y económicos, debe proporcionar las bases para prevenir la homogeneización biótica y la pérdida de biodiversidad en los principales ecosistemas de Argentina.

Introduction

> "…Few countries have undergone more remarkable changes, since the year 1535, when the first colonist of La Plata landed with seventy-two horses. The countless herds of horses, cattle, and sheep, not only have altered the whole aspect of the vegetation, but they have almost banished the guanaco, deer and ostrich. Numberless other changes must likewise have taken place; the wild pig in some parts probably replaces the peccari; packs of wild dogs may be heard howling on the wooded banks of the less-frequented streams; and the common cat, altered into a large and fierce animal, inhabits rocky hills." (Darwin, 1833).

Species that experience rapid range expansions into a non-native location via human actions are defined as being both introduced and invasive (Lockwood *et al.*, 2007). These species also provoke changes in ecological, economic, and social systems as a result of their new interactions in the recipient environment (Simberloff *et al.*, 2013; Blackburn *et al.*, 2014). The impact upon the new region is context-dependent and is contingent on both the identity of the invader (*i.e.*, on its biological traits) and the recipient community or ecosystem (*i.e.*, on the biological traits of resident species) (Valéry *et al.*, 2008). Typically, ecologists also have identified biological invasions as an ecological disturbance and a threat to biodiversity (Vitousek *et al.*, 1996).

However, non-native and even invasive species also can provide benefits to some stakeholders and conceptually are a source of opportunities to understand fundamental ecological and evolutionary processes of ecosystems (Sax *et al.*, 2007). The benefits from some non-native species are pervasive and integral components of our global economy. For example, fiber-producing crops, such as cotton, are often grown outside of their native range to great advantage, and livestock, such as sheep, that produce food and material for clothing; these benefits are typically received from managed species (Sax *et al.*, 2007). The negative costs of introduced species usually come from those that have become naturalized and invasive; that is, those which have established self-sustaining populations in the absence of human assistance and expanded their range across the recipient environment. These invasive species have caused or contributed to the extinction of many native species, as exemplified by rats and cats introduced onto islands (Blackburn *et al.*, 2005; Medina *et al.*, 2011; Harper and Bunbury, 2015 and references therein). Thus, biological invasions can generate enormous environmental damage and have been considered analogous to natural disasters (Ricciardi *et al.*, 2011).

Globally, the list of human-introduced species increases, as does the number of those that become invasive and have significant ecological, economic, and cultural effects (Mooney and Hobbs, 2000). Therefore, biological invasions are actually socio-ecological phenomena because humans are involved as both a driver and recipient in the entire invasive process: they serve as vectors for introductions (accidental or intentional), suffer the consequences, and possess the capacity to act and make decisions for managing these species (García Llorente *et al.*, 2008) (see Anderson and Pizarro, this volume). Environmental decision-makers and scholars recognize the need to integrate the social dimension into biological invasions research and extend it beyond the fields of biology and ecology, encompassing sociological, political and economic aspects of the problem that must be understood to develop effective policies and management solutions (Van Wilgen *et al.*, 2014; Estévez *et al.*, 2015; Schiavini *et al.*, 2016).

In this context, introduced invasive mammals (IIMs) stand out for being more invasive than other vertebrates, and their social-cultural interactions are especially stronger (Jeschke, 2008; Ballari *et al.*, 2016). IIMs in the Americas represent about 20% of mammal introductions worldwide, and their high species richness is concentrated in South America's Southern Cone (Novillo and Ojeda, 2008; Ballari *et al.*, 2016). The aim of this chapter is to provide an overview of the state-of-the-art on IIMs in Argentina. In the **first section,** we introduce key concepts of the biological invasion process, using IIM examples in Argentina. The **second section** discusses niche theory applied to biological invasions and some case studies for the country. In the **third section,** we examine the main contributions of IIM research in Argentina. Finally, we propose IIMs as a research model to better understand ecological processes (*e.g.*, niche, competition, disturbance dynamics, etc.) and as a tool for the conservation and management of biodiversity.

Invasion process of introduced invasive mammals in Argentina

A "biological invasion" is the end product of a multi-staged process (Lockwood *et al.*, 2007), which is not necessarily linear. Each stage includes a series of barriers or ecological filters, and species must pass these to advance to the next stage in the invasion process (Richardson *et al.*, 2000; Colautti and MacIsaac, 2004). At the same time, each stage is associated with a term that indicates the degree of progress: introduction, naturalization/establishment, expansion, and invasion. Here, we use the term IIMs to refer to introduced mammals that have passed the stages of establishment and expansion in Argentina (*i.e.*, are or are becoming "invasive").

The terminology, definitions and stage numbers of the biological invasion process vary among authors (Valéry *et al.*, 2008; Blackburn *et al.*, 2011), generating different interpretations and some confusion regarding concepts and theory (Colautti and MacIsaac, 2004). In this contribution, we follow the neutral theoretical framework suggested by Colautti and MacIsaac (2004) with seven distinct stages, attempting to avoid preconceived terms and imprecisions (Fig. 1). The model begins with a "Stage 0," defined by the potential invading propagules resident in a main donor region (previous to primary dispersal stage). If these propagules go through the primary dispersal filter, into the transport vector, they pass to "Stage I". If they survive the transport vector and release filter, they pass to "Stage II." Those propagules that become established and proliferate, survive in the new environment and go through the reproduction filter in a novel region pass to "Stage III." Finally, there are four categories of established species, based on two filters: local dispersal, and environment and community suitability. Thus, local dispersal of individuals (*i.e.*, propagule pressure) determines which Stage III species (localized, but rare) reach "Stage IVa" (widespread, but rare), or which "Stage IVb" species (localized, but dominant) reach "Stage V" (widespread and dominant). Also, environment and community suitability filters determine if species at stage III reach stage IVb, or which stage IVa species go on to Stage V (Fig. 1). Three factors affect the probability that a potential invader will pass through each filter: propagule pressure (PP); environmental requirements of the potential invader (physico-chemical) (ER), and community interactions (CI).

The IIMs in Argentina exhibit intrinsic (*i.e.*, high dispersal capacity, high reproductive capacity, broad diet, habitat generalists) and extrinsic attributes (*i.e.*, vacant niches, natural enemy release, diversity of resources, climate matching), as well as factors associated with human activity (*i.e.*, game hunting or commercial purposes, transport vectors and pathways, propagule pressure), that can explain successful invasions. For example, the Pallas's

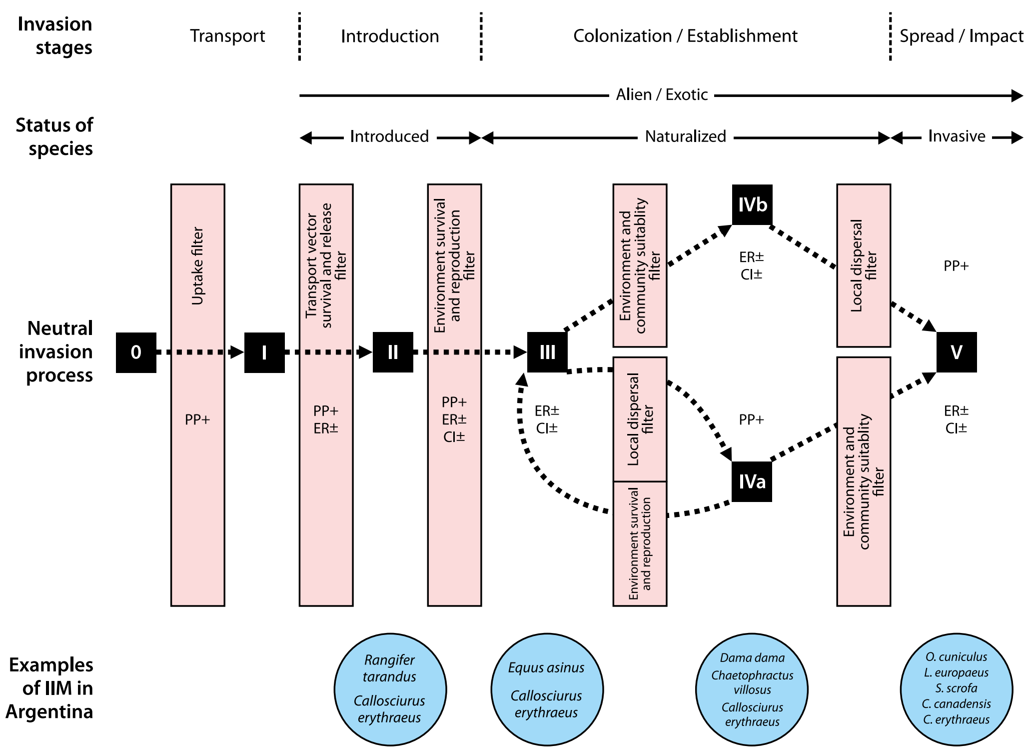

Figure 1. The biological invasion process defined using a proposed neutral theoretical framework (modified from Colautti and MacIsaac, 2004), merging the stages in the process with commonly used terms and the status of species (Catford *et al.*, 2009). In the lower portion of the figure, several introduced invasive mammals are categorized based on their status in different parts of Argentina. For example, Pallas's squirrel (*Callosciurus erythraeus*) was introduced to two sites in the city of Buenos Aires (**Stage II**). Pallas's squirrel have established, but localized populations in Salto (Buenos Aires province) (**Stage III**). Pallas's squirrel is localized and dominant (**Stage IVb**) in Arrecifes (Buenos Aires province), as well as the hairy armadillo (*Chaetophractus villosus*) in Tierra del Fuego's main island (**Stage IVa**). Pallas's squirrel is widespread and dominant in Luján (Buenos Aires province) (**Stage V**).

squirrel (*Callosciurus erythraeus*) was able to successfully colonize a broad area, starting with 10 initial individuals that have kept expanding to become one of the country's main foci of invasion (Aprile and Chicco, 1999; Benitez *et al.*, 2013). Furthermore, given their charismatic appeal, these squirrels are transported and released by people, which provides new invasion points due to translocation events (Guichón *et al.*, 2015). This case also allows us to establish different stages of the invasion process for different squirrel focal points (see Fig. 1). Thus, the Pallas's squirrel shows high invasive potential in Argentina, due to its charismatic appeal combined with high reproductive potential, the probability of establishment from a few founding individuals, its ability cope with modified environments and a lack of natural enemies (see also Guichón *et al.*, this volume; Gozzi *et al.*, this volume). For its part, the American mink (*Neogale vison*) is another successful invader in Argentina, introduced for fur farming and subsequently establishing itself in the wild (Fasola and Valenzuela, 2014). The American mink shows remarkable ecological adaptability, as a carnivore with a generalist and opportunistic diet, a high reproductive rate, particular reproductive features (*e.g.*, delayed implantation), and high genetic variability that allows it to inhabit a wide range of habitats (Valenzuela *et al.*, 2016; Malerba *et al.*, 2018).

In particular, the niche requirements of an introduced species can be used as predictors of potential invasion risk in areas of introduction and establishment (Qiao *et al.*, 2017). Environmental factors (biotic and abiotic) in the native range would pre-adapt populations for similar habitat types in the invaded range (*i.e.*, habitat suitability) (Lee, 2011). For example, many IIMs occupy ecoregions similar to their native ranges, which provide good climate niche matching, but some species have even experienced range expansions to completely new habitat types (Novillo and Ojeda, 2008; Ojeda *et al.*, 2010), which are discussed in the next section.

Niche theory applications for invasive species

A given species can persist under a limited set of habitat conditions. Therefore, a habitat's biotic and abiotic factors are relevant for enabling an organism to survive and reproduce, determining its environmental niche (Hutchinson, 1959) (Fig. 2). Niche differentiation between native and recipient ranges may result from changes in either the fundamental niche of the species (*i.e.*, the requirements of a species to maintain a positive population growth rate, disregarding biotic interactions) or the realized niche (*i.e.*, the fundamental niche constrained by biotic interactions) (Broennimann *et al.*, 2007).

The distinction between realized and fundamental niches is important for describing and understanding niche dynamics—expansion, contraction or shift of a species' niche- (Pearman *et al.*, 2008). Thus, when propagules are transported to a novel range, there could be a match between their realized niche and at least one habitat in the area of introduction (*i.e.*, habitat compatibility) to enable their survival at initial stages of invasion (Steinmaus, 2011). In other words, a proportion of the native niche should be overlapping the introduced niche (*i.e.*, niche stability) (Guisan *et al.*, 2014) (Fig. 2). The challenges imposed by abiotic and biotic factors in novel ranges could induce a rapid evolutionary response and introduced species would undergo niche shifts (Lee, 2011). Thus, introduced species

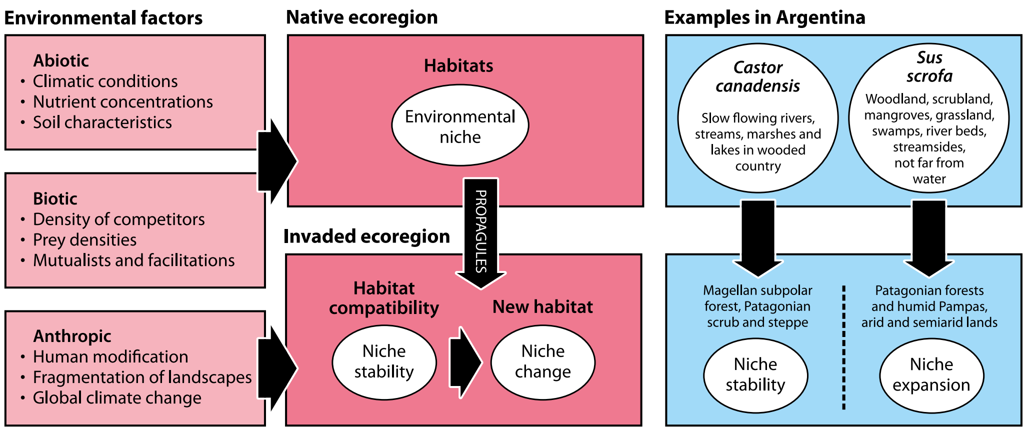

Figure 2. Representation of native and invaded ecoregions showing environmental factors that determine environmental niche (**left**); changes in the niche (stable, changed or expanded) (**center**) and possible examples with introduced invasive mammals in Argentina (**right**).

experience changes in their ecological processes in a new geographic range. For example, release from natural enemies in the new environment could influence their environmental niche (Pearman *et al.*, 2008). In this sense, niche shift may be a factor in mediating the establishment and expansion success of the organism introduced into a novel environment (Broennimann *et al.*, 2007).

Nevertheless, ecological and evolutionary theory suggests that niche conservatism ought to be more common than niche shifts (Qiao *et al.*, 2017). Niche shifts confound the idea of fundamental niche with aspects of condition availability across real-world landscapes. Thus, the use of new environments by invasive species in the invaded range may require conditions that are unavailable or inaccessible in the native range (Fig. 2). For example, the wild boar (*Sus scrofa*) occupies a broad range of habitats in Argentina, from the Patagonian forests and humid pampas to arid and semiarid regions (Cuevas *et al.*, 2013a). In the temperate Monte Desert, wild boar could be invading a new environment, therefore experiencing a niche expansion (Ojeda *et al.*, 2010) (Fig. 2). On the other hand, the North American beaver (*Castor canadensis*) inhabits slow-flowing rivers, streams, marshes and lakes in wooded country in North America, from Alaska south to northern Mexico (Long, 2003). In Tierra del Fuego, it occupies ecosystems, such as the Magellanic subpolar forest and Patagonian scrub and steppe, limited mainly by hydrological resources (Wallem *et al.*, 2007) (Fig. 2). Another good example is the establishment of the European rabbit (*Oryctolagus cuniculus*) in central Chile, where the climate matches that of its native range (Mediterranean-type climate). When the rabbit population expanded towards Argentina (Neuquén and Mendoza provinces), it initially established in two different environments: one to the west where a rainy Mediterranean climate prevails and another one to the east with semiarid Mediterranean characteristics. Therefore, the principal invaded distribution in Argentina also shows a climate regime similar to that of the native range (Bobadilla *et al.*, 2021). This is reflected in the good match between native and invaded ecoregions and partially explains the successful establishment of this IIM.

In summary, niche dynamics occur during the biological invasion process as a result of differences in the realized niche (*i.e.*, where the biotic interactions are important) or adaptation to new conditions (*i.e.*, where rapid evolutionary responses are important) (Broennimann *et al.*, 2007; Steinmaus, 2011). In this way, extrinsic factors (*e.g.*, transport vectors and release filter, local dispersal filter; see Fig. 1) impose challenges and opportunities for invading species, while intrinsic properties of organisms and populations (*i.e.*, body size, locomotion, reproductive rate, population size, habitat and trophic ecology) dictate their response to extrinsic factors via mechanisms like phenotypic plasticity or evolutionary adaptation (Lee, 2011).

Historical context of IIM research in Argentina

Like in many other regions, biological invasions pose a serious threat to biodiversity in South America, where 41 out of the 100 most invasive species in the world are already established (Speziale *et al.*, 2012; Ballari *et al.*, 2016). In this way, the publication trend on biological invasions at the regional level has been shown to correlate with or even exceed that seen at the global level, and Argentina is the Latin American and Caribbean country with the most ISI-indexed publications on this subject (Pauchard *et al.*, 2011). The same trend is shown for research on IIMs where the number of studies published in South America has increased exponentially since the beginning of the 21st century, and Argentina has shown a marked increase, especially between 2006 and 2010 (Fig. 3). Despite this, Speziale *et al.* (2012) showed that research trends in non-native species are not of major concern for South American countries. This could reflect a low level of social interest due to historical and recent socio-cultural particularities. For example, South American societies are often dominated by more recent immigrants or a rural to urban transformation could suffer "generational amnesia," meaning urban residents are not aware of the past biological environmental conditions (Speziale *et al.*, 2012). Overall, an historical understanding of species introductions demonstrates how they have been driven largely by human social practices that have existed and, in some cases, still exist, whereby native species are either less known or less valued than those brought from other parts of the world to "improve" local ecosystems (Anderson and Valenzuela, 2014; Archibald *et al.*, 2020; Anderson and Pizarro, this volume). Particularly, introduced mammals are associated with human activities and the principal reasons why they were brought to southern South America were hunting, livestock, fur trade, pets, aesthetic purposes and so on (Long, 2003; Ballari *et al.*, 2016).

In Argentina, the first assessments of introduced mammals occurred before the 1980s with the contribution of Daciuk (1978), who studied the Araucana sub-region. This author provided the first data on the introduction of red deer (*Cervus elaphus*) into Chubut province and reindeer (*Rangifer tarandus*) to Tierra del Fuego Island and South Georgia Island. Nowadays, there are no reindeer on Tierra del Fuego, and they have been eradicated from some sectors of South Georgia Island (Adalbjornsson, 2018). Some years later, Jackson (1985) documented the status, population trends and expansion of the blackbuck (*Antilope cervicapra*) across some regions of the country. Since 1990, with the consolidation of invasion biology as a subdiscipline of ecology, research on the IIMs in Argentina has begun to

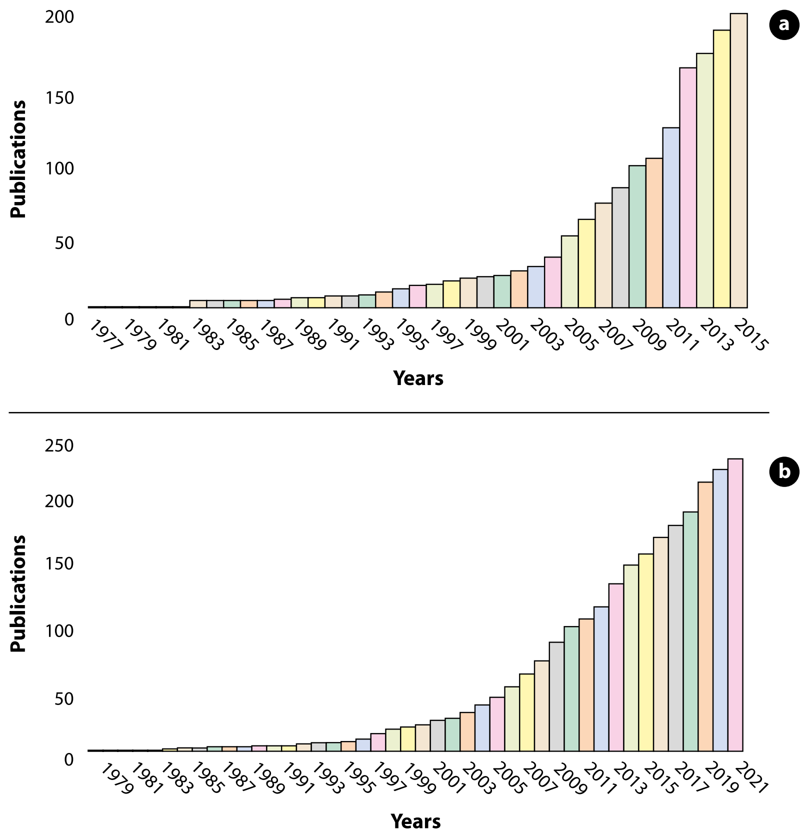

Figure 3. a. Number of papers published on introduced invasive mammals in South America, represented cumulatively between 1977 and 2014 (Ballari *et al.*, 2016); **b.** Number of scientific publications on introduced invasive mammals in Argentina graphed cumulatively between 1977 and 2021 (reviews not included).

flourish, starting with seminal studies of the impact of North American beavers in Tierra del Fuego (Lizarralde, 1993) and the diet and habitat use of the American mink in Patagonia (Previtali *et al.*, 1998).

A synthesis of IIM research in Argentina is presented in Table 1, where we have considered 1) the type of study carried out: biological and ecological, of impacts (inside protected areas or in unprotected areas) or management, and 2) the taxa studied. We found 248 IIM studies published in Argentina between 1978–2021. Forty-one percent (n=102) of the studies have been focused on the biology and ecology of the mammal species, principally on their habitat and diet (18%) and dispersal and population (16%). To a lesser extent, 33% (n=82) of the studies have been focused on the impacts, where the most evaluated environment consequences are inside protected areas (19%). The most studies in unprotected areas were about zoonotic diseases (13%), and only two studies quantify economic impacts. Only 8% of publications have been focused on applied research. Of these studies, only 2% were on social and education topics, while the 6% were about policy development and management. Finally, a category of "other," including reviews and inventories, represented 18% of the total (Table 1).

Table 1. Summary of the principal literature on introduced invasive mammals in Argentina, identifying the characteristics of each publication. For this analysis, feral domestic mammals, such as horses, dogs, cats and livestock, are not included.

Species	Biology and ecology	Impact	Social perception and education	Policy development and management	*Other
Chaetophractus villosus	Abba *et al.,* 2005[1] Poljak *et al.,* 2007[2] Abba *et al.,* 2014[2] Cabello *et al.,* 2017[1] Gallo *et al.,* 2020[2] Poljak *et al.,*2020[4]				Valenzuela *et al.*, 2014 Ezquiaga *et al.*, 2016 Gallo *et al.*, 2019
Lycalopex gymnocercus	Funes *et al.,* 2006[3] APN, 2007[2] Gómez *et al.,* 2010[1]				Jaksic *et al.*, 2002 Zanini *et al.*, 2006 Valenzuela *et al.*, 2014 Luengos Vidal *et al.*, 2019
Neogale vison	Previtali *et al.,* 1998[1] Gómez *et al.,* 2010[1] Fasola *et al.,* 2011[2] Valenzuela *et al.,* 2013a[1] Valenzuela *et al.,* 2013b[1] Guichón *et al.,* 2016[2] Fasola and Roesler, 2018[1] Malerba *et al.,* 2018[3] Failla and Fasola, 2019[2]	Peris *et al.*, 2009[5] Fasola *et al.*, 2009[6] Roesler *et al.*, 2012[5]		Fasola and Valenzuela, 2014 Fasola and Roesler, 2016	Daciuk, 1978 Jaksic *et al.*, 2002 Novillo and Ojeda, 2008 Merino *et al.*, 2009 Valenzuela *et al.*, 2014 Valenzuela *et al.*, 2019
Sus scrofa	Merino and Carpinetti, 2003[2] Pescador *et al.*, 2009[2] Cuevas *et al.*, 2010[1] Cuevas *et al.*, 2013a[1] Cuevas *et al.*, 2013b[1] Gantchoff *et al.*, 2013[1] Lantschner *et al.*, 2013[1] Nuñez *et al.*, 2013[1] Ballari *et al.*, 2015b[1] Gantchoff and Belant, 2015[1] Guichón *et al.*, 2016[2] Soteras *et al.*, 2017[1] Caruso *et al.*, 2018[1] Sagua *et al.*, 2018[4] Acosta *et al.*, 2019[4] Ballari *et al.*, 2019c[1] Panebianco *et al.*, 2019[1]	Campos and Ojeda, 1997[5] Vázquez, 2002[6] Meier and Merino, 2007[5] Pérez Carusi *et al.*, 2009[5] Cohen *et al.*, 2010[6] Sanguinetti and Kitzberger, 2010[5] Barrios-García and Ballari, 2012[5] Cuevas *et al.*, 2012[5] Barrios-García and Simberloff, 2013[5] Barrios-García *et al.*, 2014[5] Winter *et al.*, 2019[6] Ballari *et al.*, 2020[5] Cuevas *et al.*, 2020[5] Bercê *et al.*, 2021[5]		Ballari *et al.*, 2015a Gürtler *et al.*, 2018 Gürtler and Cohen, 2021 Nicosia *et al.*, 2021	Daciuk, 1978 Jaksic *et al.*, 2002 Novillo and Ojeda, 2008 Merino *et al.*, 2009 Valenzuela *et al.*, 2014 Ballari and Barrios-García, 2014 Cuevas *et al.*, 2016 Sanguinetti and Pastore, 2016 Ballari *et al.*, 2019a

Table 1. (Continued).

Species	Biology and ecology	Impact	Social perception and education	Policy development and management	*Other
Dama dama	Frisina and Frisina, 1997[1] Relva and Caldiz, 1998[1] Flueck, 2010[2] Barrios-García *et al.*, 2012[1] Ballari *et al.*, 2019c[1]	Veblen *et al.*, 1989[5] Veblen *et al.*, 1992[5] Vázquez, 2002[6] Simberloff *et al.*, 2003[5] Nuñez *et al.*, 2008[5] Relva *et al.*, 2009[5] Relva *et al.*, 2010[5] Relva and Nuñez, 2014[5] Relva *et al.*, 2014[5]			Daciuk, 1978 Novillo and Ojeda, 2008 Merino *et al.*, 2009 Barrios-García *et al.*, 2019
Axis axis	Burgueño *et al.*, 2021[1]	Relva and Veblen, 1998[3]		Gürtler *et al.*, 2018 Gürtler and Cohen, 2021 Nicosia *et al.*, 2021	Daciuk, 1978 Novillo and Ojeda, 2008 Merino *et al.*, 2009 Fracassi *et al.*, 2010 Tellarini *et al.*, 2019
Cervus elaphus	Bahamonde *et al.*, 1986[1] Relva and Caldiz, 1998[1] Flueck *et al.*, 1999[1] Flueck, 2001[2] Flueck *et al.*, 2003[2] Flueck, 2004[3] Flueck *et al.*, 2005[2] Ortiz and Bonino, 2007[1] Soler *et al.*, 2007[4] Aller *et al.*, 2009[4] Flueck, 2010[2] Flueck and Smith-Flueck, 2011[4] Barrios-García *et al.*, 2012[1] Gantchoff *et al.*, 2013[1] Lantschner *et al.*, 2013[1] Nuñez *et al.*, 2013[1] Guichón *et al.*, 2016[2] Ballari *et al.*, 2019c[1]	Veblen *et al.*, 1989[5] Veblen *et al.*, 1992[5] Relva and Veblen, 1998[5] Relva and Sancholuz, 2000[6] Vázquez, 2002[6] Simberloff *et al.*, 2003[5] Flueck and Jones, 2006[6] Meier and Merino, 2007[5] Nuñez *et al.*, 2008[5] Relva *et al.*, 2009[5] Relva *et al.*, 2010[5] Flueck and Smith-Flueck, 2012[6] Relva and Nuñez, 2014[5] Relva *et al.*, 2014[5] Reissig *et al.*, 2016[6] Charro *et al.*, 2018[6] Reissig *et al.*, 2018[6]		Sanguinetti *et al.*, 2014	Daciuk, 1978 Jaksic *et al.*, 2002 Novillo and Ojeda, 2008 Merino *et al.*, 2009 Relva and Sanguinetti, 2016 Relva *et al.*, 2019
Antilope cervicapra	Jackson, 1985[1] Frisina and Frisina, 1997[1] Carpinetti, 2001[2]				Novillo and Ojeda, 2008 Merino *et al.*, 2009 Ballari *et al.*, 2019b

Table 1. (Continued).

Species	Biology and ecology	Impact	Social perception and education	Policy development and management	*Other
Callosciurus erythraeus	Guichón *et al.*, 2005[2] Guichón and Doncaster, 2008[2] Bridgman *et al.*, 2012[2] Benitez *et al.*, 2013[2] Gabrielli *et al.*, 2014[4] Guichón *et al.*, 2015[2] Coniglione and Zalba, 2018[2] Zarco *et al.*, 2018[1] Guichón *et al.*, 2020[2]	Gozzi *et al.*, 2013a[6] Gozzi *et al.*, 2013b[6] Gozzi *et al.*, 2014[6] Messetta *et al.*, 2015[6] Bobadilla *et al.*, 2016[6] Pedreira *et al.*, 2017[7] Gozzi *et al.*, 2020[6] Pedreira *et al.*, 2020[7]	Borgnia *et al.*, 2013	Benitez *et al.*, 2010 ENEEI, 2016	Aprile and Chicco, 1999 Fasola *et al.*, 2005 Novillo and Ojeda, 2008 Cassini and Guichón, 2009 Guichón *et al.*, 2019
Castor canadensis	Lizarralde, 1993[2] Lizarralde *et al.*, 2004[2] Lizarralde *et al.*, 2008[4] Fasanella *et al.*, 2010[4] Pietrek and González-Roglich, 2015[1] Davis *et al.*, 2016[1] Pietrek *et al.*, 2016[1] Pietrek *et al.*, 2017[2] Eltall *et al.*, 2019[2] Feldman *et al.*, 2020[1] Huertas Herrera *et al.*, 2020[2]	Lizarralde *et al.*, 1996[5] Vázquez, 2002[6] Martínez Pastur *et al.*, 2006[6] Anderson and Rosemond, 2010[5] Wallem *et al.*, 2010[6] Simanonk *et al.*, 2011[6] Ulloa *et al.*, 2012[5] Anderson *et al.*, 2014[5] Henn *et al.*, 2014[6] Henn *et al.*, 2016[5] Westbrook *et al.*, 2017[5] García and Rodríguez, 2018[6] Francomano *et al.*, 2021[6]	Estévez *et al.*, 2014 Santo *et al.*, 2015 Anderson *et al.*, 2017 Santo *et al.*, 2017	Sanguinetti *et al.*, 2014 Anderson *et al.*, 2015 ENEEI, 2016 Schiavini *et al.*, 2016 Jusim *et al.*, 2020 Pastur *et al.*, 2021	Daciuk, 1978 Jaksic *et al.*, 2002 Coronato *et al.*, 2003 Wallem *et al.*, 2007 Anderson *et al.*, 2009 Pietrek and Fasola, 2014 Valenzuela *et al.*, 2014 Anderson *et al.*, 2019
Ondatra zibethicus	Deferrari *et al.*, 1996[2] Deferrari, 2011[1]	Vázquez, 2002[6] Deferrari, 2006[5]			Daciuk, 1978 Novillo and Ojeda, 2008 Valenzuela *et al.*, 2014 Deferrari, 2019
Mus musculus	Miño *et al.*, 2007[1] León *et al.*, 2007[2] Gómez *et al.*, 2008[2] Guidobono *et al.*, 2009[3] Cavia *et al.*, 2009[1] Vadell *et al.*, 2010[4] León *et al.*, 2013[1]	Larrieu *et al.*, 2004[5] Aristegui *et al.*, 2015[6] Fitte and Kosoy, 2021[6]			Novillo and Ojeda, 2008 Valenzuela *et al.*, 2014 Cavia *et al.*, 2019a
Rattus rattus, R. norvegicus	Gómez Villafañe and Busch, 2007[1] Gómez Villafañe *et al.*, 2008[2] Cavia *et al.*, 2009[1] Vadell *et al.*, 2010[4]	Cueto *et al.*, 2008[5] Shepherd and Ditgen, 2012[5], 2013[5] Gómez Villafañe *et al.*, 2013[6] Alonso *et al.*, 2019[6] Fitte and Kosoy, 2021[6]			Novillo and Ojeda, 2008 Valenzuela *et al.*, 2014 Cavia *et al.*, 2019b Cavia *et al.*, 2019c

Table 1. (Continued).

Species	Biology and ecology	Impact	Social perception and education	Policy development and management	*Other
Lepus europaeus	Grigera and Rapoport, 1983[2] Bonino and Montenegro, 1997[4] Campos *et al.*, 2001[1] Puig *et al.*, 2007[1] Nabte *et al.*, 2009[2] Bonino *et al.*, 2010[2] Galende and Raffaele, 2008[1] Galende and Raffaele, 2013[1] Gantchoff *et al.*, 2013[1] Lantschner *et al.*, 2013[1] Gantchoff and Belant, 2015[1] Puig *et al.*, 2015[1] Puig *et al.*, 2017[1]	Bonino *et al.*, 1997[5] Vázquez, 2002[6] Delibes *et al.*, 2003[5] Kleiman *et al.*, 2004[6] Puig *et al.*, 2006[5] Kufner *et al.*, 2008[5] Raffaele *et al.*, 2011[5] Palacios *et al.*, 2012[5] Zanón Martínez *et al.*, 2012[5] Reus *et al.*, 2013[5] Scioscia *et al.*, 2013[6] Puig *et al.*, 2014[5] Barbar *et al.*, 2018[5] Barbar and Lambertucci, 2019[6] Aguirre *et al.*, 2021[6]			Daciuk, 1978 Hiraldo *et al.*, 1995 Donázar *et al.*, 1997 Novaro *et al.*, 2000 Jaksic *et al.*, 2002 Donadio *et al.*, 2005 Monserrat *et al.*, 2005 Campos *et al.*, 2008 Merino *et al.*, 2009 Monteverde *et al.*, 2019
Oryctolagus cuniculus	Howard and Amaya, 1975[2] Bonino and Soriguer, 2004[2] Bonino and Borrelli, 2006[1] Bonino and Soriguer, 2008[4] Galende and Raffaele, 2008[1] Bonino and Soriguer, 2009[2] Nabte *et al.*, 2009[2] Cuevas *et al.*, 2011[2] Laspina *et al.*, 2013[1] Galende, 2014[2] Guichón *et al.*, 2016[2] Udrizar Sauthier, 2017[2]	Vázquez, 2002[6] Delibes *et al.*, 2003[5] Veblen *et al.*, 2004[6] Bonino, 2006[6] Barbar and Lambertucci, 2019[6] Bobadilla *et al.*, 2020[5]			Daciuk, 1978 Hiraldo *et al.*, 1995 Donázar *et al.*, 1997 Jaksic *et al.*, 2002 Aparicio *et al.*, 2004 Donadio *et al.*, 2005 Aparicio *et al.*, 2006 Bonino and Donadio, 2010 Valenzuela *et al.*, 2014 Cuevas *et al.*, 2019

*Includes reviews, inventories and general topics.
Type of research is noted using numbered superscripts (1–7) for Biology and ecology ([1]Habitat and diet, [2]Population and dispersal, [3]Behavior, [4]Reproduction and genetics); Impacts: Environmental impacts ([5]Protected areas / [6]Non-protected areas) and [7]Economic impacts.

Among the 248 publications, the most-studied orders were Cetartiodactyla (37%), Rodentia (32%), Lagomorpha (20%), and Carnivora (8%), followed by Cingulata (3%). The most-studied species were the red deer (13%), wild boar (13%), North American beaver (13%), European hare (*Lepus europaeus*) (12%), European rabbit (9%), and Pallas's squirrel (8%).

IIM research highlights per taxonomic order

Cingulata. A particular example is the large hairy armadillo (*Chaetophractus villosus*), endemic to southern South America, but introduced and invasive on Tierra del Fuego's main island since about 20 years ago (Poljak *et al.*, 2007).

Carnivora. There are studies on American mink related to its diet and habitat use (Valenzuela *et al.*, 2013a,b). However, several relevant issues, such as population trends, behavior and genetics, have not been well addressed. Within this group, the grey fox (*Lycalopex gymnocercus*) is another example of a native species from the South American mainland, but that has been introduced and become invasive to Tierra del Fuego Island (Ojeda *et al.*, 2016).

Cetartiodactyla. The red deer has been rather well studied, but this is not the case for the blackbuck. Some studies on fallow deer (*Dama dama*) have been associated with red deer on Argentina's Patagonian steppe (Frisina and Frisina, 1997). Various aspects of the wild boar have been studied, such as diet and habitat use in different ecoregions like Patagonia (Soteras *et al.*, 2017), Monte (Cuevas *et al.*, 2010, 2013a) and Espinal (Caruso *et al.*, 2018). However, studies on reproduction and behavior have not been explored.

Rodentia. Cosmopolitan species, such as the brown rat (*Rattus norvegicus*), black rat (*Rattus rattus*) and house mice (*Mus musculus*), have been the subject of different studies, particularly epidemiology (Gómez Villafañe *et al.*, 2013; Aristegui *et al.*, 2015). Muskrats (*Ondatra zibeticus*) have few studies about habitat use and ecological trends (Deferrari *et al.*, 1996, Deferrari, 2006, 2011), but there is no research about their impact or management. A substantial body of knowledge has been produced by multiple studies on the Pallas's squirrel in periurban and urban areas (Guichón *et al.*, 2015; see also Guichón *et al.*, this volume, and Gozzi *et al.*, this volume) and on the North American beaver, as an invasive ecosystem engineer in Tierra del Fuego Archipelago (Anderson *et al.*, 2009; Schiavini *et al.*, 2016).

Lagomorpha. From 1980 onwards, there has been an increase in research on the European rabbit and European hare, aiming to provide information about its, morphology, distribution, diet, diseases (*e.g.*, myxomatosis) and interspecific interaction (Galende and Raffaele, 2008, 2013; Gantchoff *et al.*, 2015; Bobadilla *et al.*, 2020), but there are no data about management for both species in Argentina. A recent publication by Bobadilla *et al.* (2022) deals with the ecology of the European rabbit in its invading front range in central Argentina.

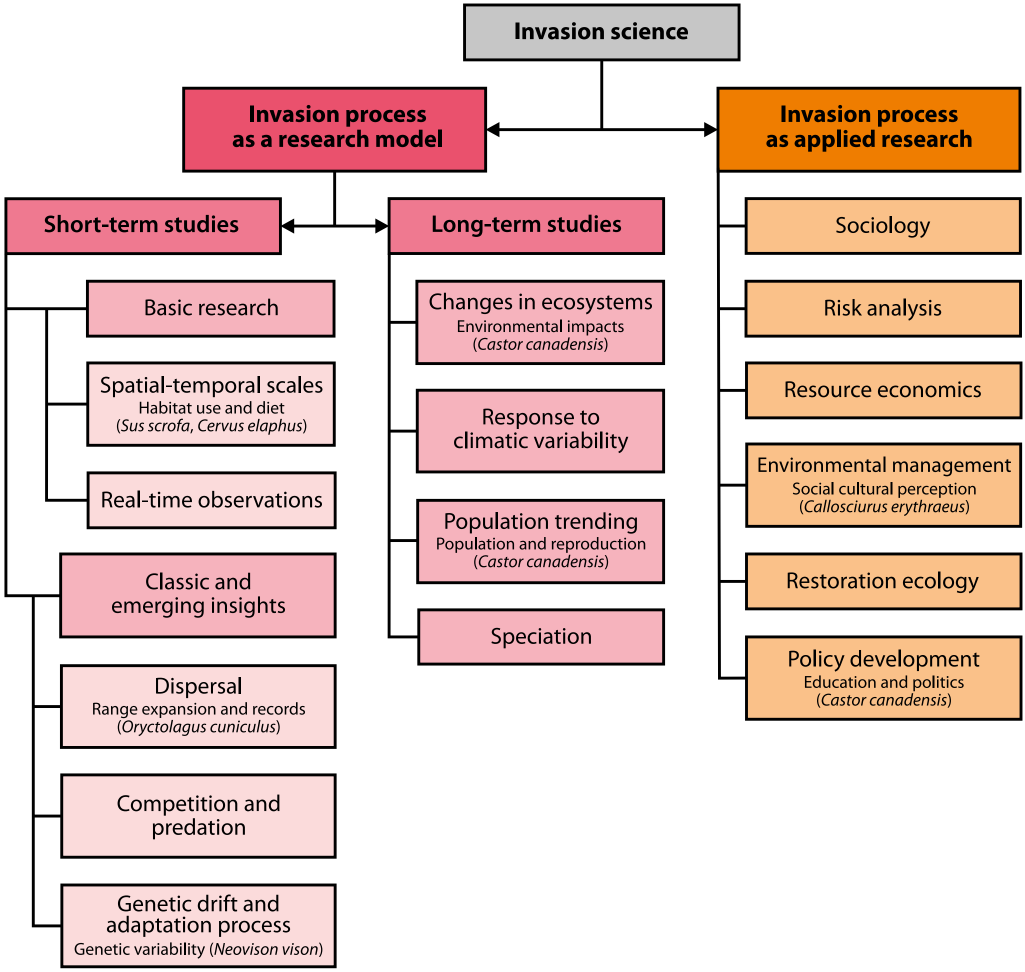

Figure 4. Invasion science research fields and examples for introduced invasive mammals in Argentina (modified from Sax, 2007).

Conclusions

Although significant advances have been made in the understanding of the phenomenon of biological invasions in South America (Jaksic and Castro, 2021, and references therein), there are still important gaps to fill (Lowry *et al.*, 2013; Ojeda, 2016). For example, more than half of the studies have been short-term and oriented to basic research on the biology and ecology of the IIMs in Argentina. Quite a few studies have quantified the ecological impacts of these species, but economic or social impacts are much less studied. However, perhaps the principal gap is in the generation of applied research and interdisciplinary studies, similar to those initial approaches that have been carried out with the North American beaver and the Pallas's squirrel (Fig. 4). At the same time, there is an overrepresentation of a few species (*e.g.*, red deer and North American beaver), while others (*e.g.*, muskrat) are almost not being studied at all. According to Pauchard *et al.* (2011), these differences in effort could be fundamentally due to contributions of the taxon or theme to general hypotheses or theories, or impacts of the taxon in conservation biology or novel taxa for the region.

IIMs provide the focus for a wide array of research dimensions, from biogeography, evolutionary biology, macroecology and community ecology, to ecosystem ecology, restoration ecology, risk analysis, and policy development, among others. A good synthesis of the diversity of research and fertile areas for future studies in the field of biological invasions is provided by Richardson (2011). There is no doubt that introduced invasive species are the research focus of a wide range of scientists and wildlife resource managers, particularly conservation biologists (Sakai *et al.*, 2001). IIMs provide the opportunity to address basic research questions in different disciplines (*e.g.*, ecology, biogeography, evolution, genetics, and conservation biology, among others) that could be used to understand the natural world in a better way. In this way, biological invasions are real-time, natural experiments, offering a scenario where processes occur faster than in most natural systems (Sakai *et al.*, 2001; Sax *et al.*, 2007). Among several examples are the unplanned experiments regarding island invaders and their ecological impacts, eco-evolutionary processes dealing with competition and character displacement, genetic change, rate of range expansion, introduction of pathogens, among others (Sax *et al.*, 2007). In this regard, the research on the North American beaver in the island of Tierra del Fuego is a good example since it represents a natural laboratory for biological and ecological studies (Fig. 4). Invasive species offer unique opportunities to study basic processes in population biology (*i.e.*, life history, demographic models, and so on), evolution (*e.g.*, rapid adaptive evolution), and ecology of interactions between invasive and native species. Some examples of these opportunities are the ecological studies on diet and habitat associations of the American mink or the invasion of new environments by the wild boar (Fig. 4).

Our main purpose in this chapter was to provide a global overview regarding the state-of-the-art in research on introduced invasive mammals in Argentina. By viewing biological invasions as a multifaceted process with major drivers and a series of sequential steps, IIMs offer an especially useful model and opportunity for a research agenda encompassing a rich diversity of topics and dimensions. Such a fundamental research program, coupled with strategic and integrated planning with governmental organisms, state agencies at several levels and different social, political and economic sectors, should provide the grounds for preventing biotic homogenization and biodiversity loss in major ecosystems of Argentina.

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