



# Trojan hosts: the menace of invasive vertebrates as vectors of pathogens in the Southern Cone of South America

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**Abstract** Invasive alien species (IAS) can act as vectors for the introduction of pathogens in ecosystems and their transmission to threatened native species (TNS), leading to biodiversity loss, population reductions and extinctions. We assessed pathogens potentially occurring in a set of IAS in the Southern Cone of South America and identified TNS potentially vulnerable to their effects. Also, we assessed how risk analysis systems proposed or adopted by national authorities in the study region value the importance of pathogens. We identified 324 pathogens in the selected

IAS, which could potentially affect 202 TNS. Wild boar (*Sus scrofa*) was the IAS with the largest number of pathogens (91), followed by domestic dog (*Canis familiaris*) (62), red deer (*Cervus elaphus*) (58), rock dove (*Columba livia*) (37), American vison (*Neovison vison*) (18), European hare (*Lepus europaeus*) (17), common starling (*Sturnus vulgaris*) (12), common slider (*Trachemys scripta*) (6), and American bullfrog (*Lithobates catesbeianus*) (2). Most TNS were in the “vulnerable” IUCN category, followed by “endangered” and “critically endangered” species. Bacteria were the most frequently represented pathogens (112), followed by ectoparasites (78), viruses (69), protozoa and other (65). The direct effects of IAS on native wildlife are beginning to be addressed in South America, and their potential impact as pathogen spreaders to native wildlife has remained largely unexplored. Risk analysis systems associated with the introduction of IAS are scarce in this region. Although the existing systems contemplate hazard analyses for the co-introduction of pathogens, they underestimate the potential impact of diseases on TNS. Conservation efforts in the region would benefit from systems which give pathogen risk a relevant place, and from government agencies promoting targeted disease surveillance in IAS and wildlife.

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## Introduction

The introduction and spread of alien species and their pathogens has long been noted as a leading cause of biodiversity loss and species extinctions (McCallum 2012; Heard et al. 2013). Invasive alien species (henceforth IAS) can act as vectors for the introduction of new pathogens and become, at the same time, reservoirs for their maintenance in the new ecosystem and transmission to native species (“pathogen spillover”), increasing both pathogen richness and prevalence. Also, pathogens can cause declines in the abundance and diversity of native species (Daszak et al. 2000; Young et al. 2017).

Invasive species can affect the health of animals and plants immediately after their arrival in the new environment (Jeschke et al. 2014). For example, the invasion by European birds of the Hawaii islands brought avian malaria and birdpox to the area, which led to the extinction of a substantial proportion of Hawaiian avifauna in the late nineteenth century (van Riper et al. 1986). Another example is the collapse and extinction of several amphibian populations due to chytridiomycosis, a fungal infection associated with *Batrachochytrium dendrobatidis* (Bd) (O’Hanlon et al. 2018; Scheele et al. 2019). Notably, phylogenetic studies suggest that the invasive American bullfrog is contributing to the spread of Bd around the world (Byrne et al. 2019).

Pathogens and parasites cointroduced with IAS are often lethal to native species (Capinha et al. 2013; Collins et al. 2014). However, direct mortality is not the only mechanism which can mediate population effects; the fitness or fecundity of species can also be impaired, thus affecting breeding success or putting them at a competitive disadvantage (Vilcinskas et al. 2014). If the shared pathogen is more virulent in the new, native host (which is particularly likely with introduced pathogens), the disease could act as a “biological weapon” thus leading to a disease-mediated invasion (Vilcinskas 2015).

According to the Global Invasive Species Database (ISSG 2015), there are 142 terrestrial vertebrate species listed as invasive worldwide, with 33 of them (30.9%) potentially affecting native wildlife through the transmission of pathogens. In South America alone, there are 60 species of invasive reptiles, amphibians, birds, and mammals, and 19 of them

(31.7%) are considered potential disease spreaders to the native fauna (ISSG 2015).

Risk analysis systems associated with the introduction of IAS are scarce in South America. The existing systems contemplate hazard analyses for the co-introduction of pathogens, but they underestimate the potential impact of diseases on TNS. Conservation efforts in the region would benefit from systems that give pathogens a relevant place, and from government agencies promoting targeted disease surveillance in IAS and wildlife in general.

Existing risk analysis systems designed for the evaluation of terrestrial vertebrate introductions are based on three main components, namely (i) assessment of the risk that the species may escape from confinement and establish self-sustaining populations in natural or semi-natural environments; (ii) feasibility analysis for the effective control of the species in case of invasion, and (iii) evaluation of the effects it could have on biodiversity, economy and health. These kinds of assessments have been recently designed in different countries of the study region, including Argentina, Brazil and Chile, and the impact of IAS as agents of pathogen transmission to native wildlife is an integral component in all of them. While the direct effects of IAS on native vegetation, vulnerable wildlife and ecosystem processes are beginning to be addressed in conservation planning strategies in South America, their potential impact as pathogen spreaders to native wildlife has remained largely unexplored.

With this background, identifying pathogens associated with populations of IAS is relevant in at least two respects: (i) it contributes information about biological agents with a potential to cause adverse health effects in TNS; and (ii) it informs risk analysis systems currently in place, while encouraging the creation of new ones in the study region.

The objective of our work was to assess the pathogens potentially prevalent in a set of selected IAS present in the Southern Cone of South America, and to identify native wildlife species which could be vulnerable to their effects. In addition, we assessed risk analysis systems currently in place in the study region to gain insight into the importance given to pathogens as they relate to vertebrate introductions. Specifically, we evaluated (a) whether issues related to the potential introduction of pathogens were considered, (b) how they were evaluated, and (c) the degree

of contribution of the pathogen component in the estimation of risk.

## Material and methods

The study region included the Southern Cone of South America, which comprises Argentina, Bolivia, Chile, Uruguay, Paraguay and southern Brazil (Rio Grande do Sul State), and covers 4,417,722 km<sup>2</sup>. This region spans 40 unique ecoregions, as defined by Olson et al. (2001).

From here on, definitions for “wild” and “feral” are used following OIE (2015), where wild is an animal that has a phenotype unaffected by human selection and lives independent of direct human supervision or control, and feral refers to a domesticated species that now lives without direct human supervision or control. We reviewed IAS databases to complete a list of exotic terrestrial vertebrates occurring in wild or feral populations in the Southern Cone of South America (Universidad Nacional del Sur and Ministerio de Ambiente y Desarrollo Sostenible de Argentina; Horus Institute for Environmental Conservation and Development, Brazil; ISSG 2015). A total of 37 IAS were reported as established in the study region. We selected a subset of these based on the following criteria: (i) presence of wild or feral populations in the study region, (ii) existence of peer-reviewed information about their pathogens in general, and (iii) availability of consistent distributional data. Nine invasive vertebrate species met these criteria and thus were included in the analyses. They were red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), European hare (*Lepus europaeus*), domestic dog (*Canis familiaris*), American mink (*Neovison vison*), rock dove (*Columba livia*), common starling (*Sturnus vulgaris*), common slider (*Trachemys scripta*), and American bullfrog (*Lithobates catesbeianus*). These IAS are expected to have varying invasive potential depending on each species’ ecological characteristics and the degree to which human activities can influence their dispersal. For example, since its introduction in 1906 (Navas 1987), wild boar have dispersed on their own across all but one ecoregion of Argentina, whereas American bullfrogs were dispersed by humans to nine of 23 provinces in the same country (Luchini 1995).

Dogs often have difficulties in maintaining populations without human support (Boitani et al. 2017), and for this reason, their populations rarely become feral (Reponen et al. 2014). To our knowledge, Navarino Island in Chile (Schüttler et al. 2018) and Tierra del Fuego in Argentina (Schiavini and Narbaiza 2015) have the only truly feral populations of domestic dogs in the study region. Therefore, in our study, we refer to free-roaming dogs.

## Spatial distribution of TNS and IAS

Data on the spatial distribution of the selected IAS were collected from peer-reviewed publications and personal communications (Online Resource 5), and from the databases mentioned above. The data used were presence-only records.

Ecoregions are likely to reflect the distribution of species and communities more accurately than do units based on other global and regional models (Olson et al. 2001), and the set of ecoregions where a species occurs can be taken as a realization of areas which have been accessible to the species over relevant time periods (Soberón 2010). Here, once the presence of the IAS was confirmed for a given location, it was assumed that the species could potentially find suitable combinations of environmental variables across the entire ecoregion (Soberón 2010; Barvea et al. 2011; Guisan et al. 2014), and the potential spatial distribution of each invasive species was calculated as the sum of the areas corresponding to the ecoregion/s where the species is known to occur. Then, the potential distribution of the IAS was assumed under the simplest case scenario, where ecoregions are accessible in their entirety (Soberón and Peterson 2005). Considering the spectrum of taxa and invasiveness of the different IAS considered here, the approach used to estimate their potential distribution is robust while also ascribing to the “precautionary principle”, weighing in favour of environmental protection in the case of uncertainty (Cooney 2004).

Data on the spatial distribution of all native species were downloaded from public databases (IUCN 2017; BirdLife International and NatureServe 2015). Initially, the distribution data of all the species included in the IUCN database was considered (10,423 species of birds, mammals, amphibians, and reptiles). After applying the spatial filters corresponding to the distribution of the invasive species considered here,

data were reduced to 5988 species: 2456 classified as vulnerable (VU), 2290 as endangered (EN) and 1242 as critically endangered (CR). The ecoregions spatial data used to estimate the potential distribution of each IAS were obtained from Olson et al. (2001).

### Threatened native species

Potentially exposed native wildlife was identified from the IUCN Red List (IUCN 2017), focusing on species listed as VU, EN and CR, which are henceforth jointly referred to as threatened native species (TNS). Although the IUCN Red List has its own limitations (IUCN Standards and Petitions Committee 2019), it is the most comprehensive resource detailing the global conservation status of plants and animals (Rodrigues et al. 2006).

### Pathogens

Pathogens were considered regardless of their prevalence in host populations, time of reporting and geographical location. The rationale for this was that (a) disease survey efforts are seldom sustained over time in wildlife populations and prevalence data can be highly biased in most field studies due to small sample sizes, and (b) pathogens present in a IAS but that are considered exotic in the study region can be deemed as hazards under a scenario of new introductions. Different species and different serovars or strains of the same pathogen were considered as different entities. Reports including  $\leq 2$  cases and those made in captive populations were not included.

Reports of antibodies against pathogens were included as they most likely represent previous exposure to the agent and suggest a potential role of the IAS as pathogen spreader. It could be argued that serological diagnosis could overestimate prevalence due to lack of test validation, low test specificity, and cross-reactivity among other factors. Still, the presence of seropositive individuals in a population reflects the likely existence of conspecifics which are either currently infectious, experienced infection in the past and are now immune, or were infectious and remain as pathogen carriers while not suffering symptoms themselves. Carriers may become infectious and suffer symptoms or they may continue to infect others. Therefore, the presence of seropositive individuals reflects likely circulation of the pathogen

in the population and represents a potential risk if new individuals were translocated.

An online literature search was performed in peer-reviewed journals through PubMed Health with the term «disease» or «mortality» or «wildlife», combined with the terms corresponding to the common and scientific names of each IAS included in the analysis. Additionally, an exhaustive search was conducted using the Global Mammal Parasite Database (Stephens et al. 2017). To keep the analyses at a reasonable level of complexity, the following pathogen groups were considered: bacteria (including rickettsia), viruses (including prions), ectoparasites (mites, ticks, lice and fleas), and protozoa. Only one fungus (*Batrachochytrium dendrobatidis*) and two parasitic helminths (meningeal worm *Parelaphostrongylus tenuis* and heartworm *Dirofilaria immitis*) were considered, based on their proven capacity to affect populations of wild amphibians (Skerratt et al. 2007), cervids (Lankester 2010) and canids (Brzeski et al. 2015), respectively.

All pathogens were assigned to at least one of the following epidemiological categories: (1) GLOBIN (global + invasive), the pathogen has been detected in free-ranging populations of the IAS anywhere in the world; (2) ENDOM (endemic + domestic), the pathogen has been detected in populations of domestic animals in the study region; and (3) ENDIN (endemic + invasive), the pathogen has been reported in the IAS in the study region. The distribution of pathogens among these categories was analyzed using Venn diagrams for all IAS combined and for each one individually. In the first case, pathogens that were reported in more than one IAS were considered only once, and the one which could be included in the most epidemiological categories was chosen. In the case of individual IAS, all pathogens were included.

### Evaluation of national risk analysis systems

We performed a literature review and identified risk analysis systems designed to assess the potential impact of the introduction of exotic vertebrates in the study region and Colombia. For each system, we calculated the relative contribution made by pathogen-related aspects to the total potential risk attributable to an IAS. We included risk analyses for Chile, Argentina and Brazil. Also, we assessed the case of Colombia, which albeit outside the study region,

shares similar environmental and socio-political conditions with countries in the Southern Cone of America. Specifically, we evaluated if hazards related to the potential introduction of pathogens were considered in each system, how they were evaluated and the degree of contribution of the pathogen component in the estimation of risk.

### Data analysis

For the purpose of this work, TNS were considered as susceptible to pathogen transmission from an IAS if (i) the geographical distribution of TNS and IAS overlapped totally or partially, and (ii) the TNS and IAS shared the same taxonomic Class.

Ranaviruses (RV) can affect amphibians, reptiles, and fish, and have proven epidemic potential in populations of these groups. Also, cross-transmission of this pathogen between American bullfrogs, common sliders and TNS in either taxonomic group is possible. Therefore, the spatial analysis for the common slider and American bullfrog also included the spatial overlap with TNS of amphibians and reptiles, respectively.

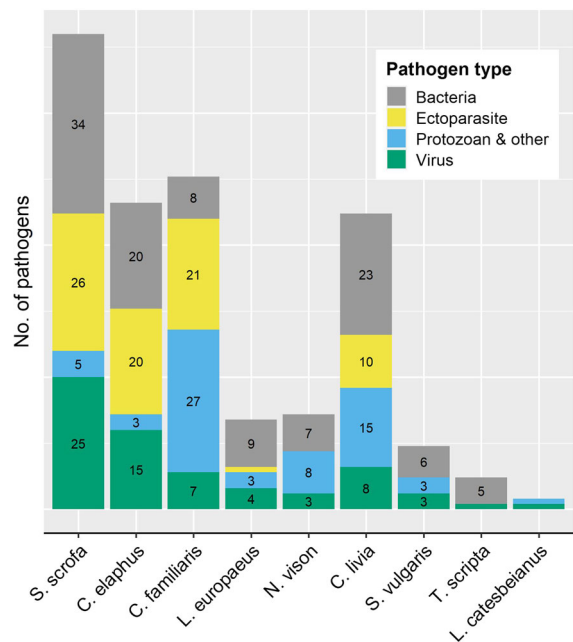
Since pathogens are not expected to affect all animal species across a taxonomic Class, the potential host range for each pathogen was further assessed through a literature review to more accurately approximate the number of TNS potentially affected. In general, the likelihood of pathogen transmission between different species (here, between IAS and TNS) is expected to be increased with taxonomic relatedness (Davies and Pedersen 2008). Therefore, the taxonomic closeness between each IAS and the TNS was assessed by grouping the set of TNS potentially affected into three groups, namely (i) TNS only sharing taxonomic Class with the IAS; (ii) TNS sharing taxonomic Class and Order with the IAS; and (iii) TNS sharing taxonomic Class, Order and Family with the IAS.

All spatial analysis and graphics were done using the packages “rgdal” (Bivand et al. 2017), “rgeos” (Bivand and Rundel 2017), “raster” (Hijmas 2018), “fastshp” (Urbanek 2014), “VennDiagram” (Chen 2018) and “ggplot2” (Wickham 2016) in the R software (R Core Team 2020).

## Results

We identified a total of 324 pathogens distributed among the nine studied IAS (Table 1; Online Resource 1). Bacteria were the most frequently represented pathogens (112), followed by ectoparasites (78), viruses (69), protozoa and other (65). Except for bullfrogs, all IAS were reported to harbor bacteria (Fig. 1). Fifty (15.4%) of these pathogens were reported in at least two of the IAS studied here. A total of 254 unique pathogen species remained when considering repeated records only once. Wild boar were associated with the greatest number of pathogens (91), followed by domestic dog (64), red deer (58), rock dove (56), American vison (18), European hare (17), common starling (12), common slider (6), and American bullfrog (2) (Fig. 1).

The potential spatial distribution of the IAS was highly variable and overlapped to varying degrees with a total of 202 TNS in the study region. Of all TNS, 5.4% (11) shared the highest taxonomic level considered here (Family) and 25.2% (51) shared Order with at least one IAS (Figure 1 in Online Resource 3). Wild boar shared Suborder (Suina) with 4.9% (2/41)

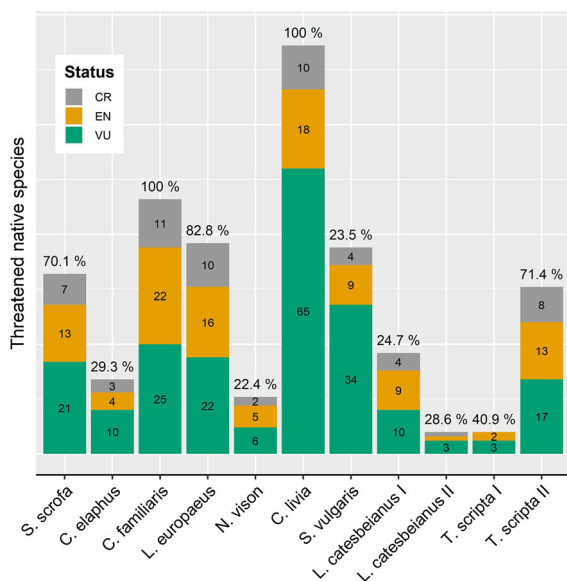


**Fig. 1** Frequency of pathogen types reported globally in nine invasive alien species present in the Southern Cone of South America. Stacks without numbers correspond to pathogen types represented by only one species



of TNS. When considering only species sharing Family with the IAS, our set of IAS was led by red deer with 17.6% (3/17) of TNS in the Cervidae family, followed by American mink with 15.4% (2/13) of TNS in the Mustelidae family, rock dove with 3.2% (3/93) of TNS in the Columbidae family, and domestic dog with 1.7% (1/58) of TNS in the Canidae family. The European hare, American bullfrog, common starling and common slider did not represent a risk for species in their respective families (Figure 1 in Online Resource 3). Most (44.1%) TNS were potentially at risk by one IAS, followed by those at risk by two (35.6%), three (11.9%), four (2.5%), and five (5.9%) IAS.

The number of potentially exposed TNS in each conservation category was dominated by VU species, followed by EN and CR species in all cases (Fig. 2). For each IAS-TNS group, the proportion of TNS potentially affected by each IAS in the study region ranged between 22.4 and 100% (Fig. 2). A complete list of TNS species potentially affected by each IAS is presented in Table 2 (Online Resource 2).

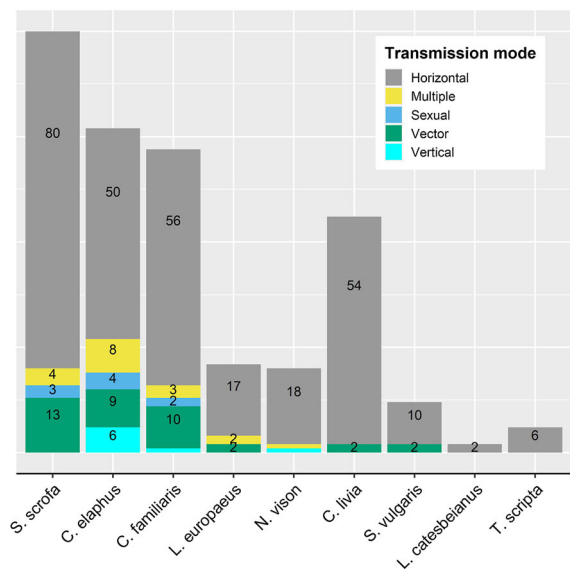


**Fig. 2** Number of threatened native species (TNS) potentially affected by each invasive alien species (IAS). TNS are classified according to IUCN Red List as critically endangered (CR), endangered (EN) and vulnerable (VU). Data for *T. scripta* and *L. catesbeianus* are divided according to reptiles (I) and amphibians (II). Percentages on top of bars represent the proportion of TNS potentially at risk by each of the IAS with respect to the total TNS present in the Southern Cone of South America

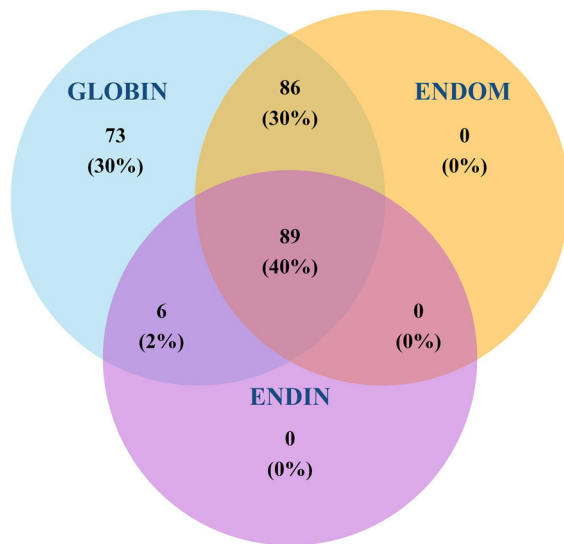
Considering all 324 pathogens, there were no TNS at risk for 12 (3.7%) of them, there were 34 (10.5%) pathogens which could potentially affect only one TNS, and 278 (85.8%) pathogens potentially affecting more than one TNS. The mean number and range of TNS potentially affected by pathogens in each IAS was 14.7 (1–58) for dogs, 7.4 (3–17) for red deer, 89.7 (1–93) for rock dove, 16.7 (0–48) for European hare, 5.0 for bullfrog, 6.4 (0–13) for American vison, 59 for common starling, 15 (0–41) for wild boar, and 36 (1–43) for common slider.

The largest proportion (90.2%;  $n = 229$ ) of pathogens reported here can be transmitted horizontally, followed by those transmitted by different biological vectors (10.6%;  $n = 27$ ) (Fig. 3). Remarkably, 100% ( $n = 27$ ) of pathogens with vectors in their life cycle could potentially find at least one of the invertebrate hosts required for their transmission to vertebrates in the study region. Of all the vector-transmitted pathogens reported, 29.6% ( $n = 8$ ) have been reported in at least one of the selected IAS the study region.

When considering all IAS combined (Fig. 4), there were no pathogens present in any of the IAS in the study region (ENDIN) without also being reported either globally (GLOBIN) or both globally and in domestic species (ENDOM) in the study region. Of all



**Fig. 3** Transmission mode for pathogens reported for nine invasive alien species present in the Southern Cone of South America. Stacks without numbers correspond to transmission modes for which there is only one pathogen



**Fig. 4** Venn diagram for the combined set of IAS in the Southern Cone of South America showing the distribution of pathogens between epidemiological categories and in their intersections. GLOBI: global + invasive; ENDOM: endemic + domestic; ENDIN: endemic + invasive

the pathogens reported globally, 37.4% (95/254) were also present in the selected IAS in study region. The proportion of pathogens found both globally and in the study region ( $GLOBIN \cap ENDIN$ ) varied widely between IAS, being 100% (2/2) for American bullfrog, 92% (59/64) for domestic dog, 50% (3/6) for common slider, 43.2% (16/37) for rock dove, 29.4% (5/17) for European hare, 22.2% (4/18) for American mink, 8.8% (8/91) for wild boar, 8.3% (1/12) for common starling, and 3.4% (2/58) for red deer (Figure 2 in Online Resource 3).

Regarding the analyzed risk analysis systems, the Brazilian (Horus Institute for Environmental Conservation and Development) and Argentine systems (Project GCP/ARG/023/GFF) share the same basic structure, including two specific questions (out of a total of 39) regarding the capacity of the taxon to spread pathogens to wildlife and about epizootics known to have affected the IAS. In these systems, the potential for pathogen transmission to native wildlife can contribute with a maximum of 6.5% to the total risk value assigned to the IAS under analysis.

In 2014, Chile proposed its first national strategy on invasive alien species (Comité Operativo para el Control de las Especies Exóticas Invasoras 2014). As part of this initiative, risk analysis systems were

developed to evaluate the introduction of vertebrates and invertebrates, both terrestrial and aquatic (Wallem and Ulloa 2013). The terrestrial vertebrate questionnaire includes a module on “Biological Interactions”, with one question specifically inquiring whether the species is host or vector of pathogens, especially non-native ones, and representing 9.4%, or three points of a total potential risk score of 319.

Outside the study region but still in South America, Colombia has made significant progress in the management of IAS, with a working risk analysis system for the introduction of vertebrates (Baptiste et al. 2010). Therein, the entire system encompasses 23 questions (maximum of 170 points), of which six questions (maximum of 60 points) address specifically the potential impact of the IAS. Among the latter, one question (maximum of five points) focuses on the risk of pathogen introduction and transmission to humans, native species or commercially important species and can add up to 8.3% (5/60) of the total risk attributable to the potential impact, or 2.9% (5/170) of the maximum possible risk derived from the entire system.

## Discussion

Our findings suggest that the risk for pathogen transmission between IAS and TNS in the Southern Cone of South America is largely underestimated, despite representing a major threat to the conservation of regional biodiversity. We base this on the high pathogen diversity observed in the selected IAS, on the large number of TNS potentially at risk for transmission, and on the marginal relevance given by risk analysis systems in the study region to the introduction and dissemination of pathogens.

Pathogenicity depends largely on host susceptibility and immune response, and it was not specifically addressed in our work. Therefore, it is difficult to offer generalizations; a pathogen that is highly pathogenic in one host or age class might be non-pathogenic in another. For similar reasons, we have not discussed the influence of population structure, social contact networks, or overall biodiversity on pathogen invasion and spread, since these are highly context- and species-dependent.

All the pathogens reported in the selected IAS in the study region have also been described globally in the

same species. Contrarily, with the exception of the domestic dog and American bullfrog, not every pathogen reported globally was also present in the IAS in the study region. These differences might be a consequence of insufficient disease surveillance and underreporting in these IAS in the study region. Other alternative explanations cannot be ruled out, such as stochastic founder effects and genetic drift (Biedrzycka et al. 2020), pathogen release (Torchin et al. 2003), reduced pathogen burdens in the introduced stocks due to sanitary controls in animals originating from breeding facilities or originally imported as game species, or that some of the diseases reported elsewhere are recent findings.

The focus of our discussion is on three IAS which either have long been associated with disease spillover to native endangered wildlife (i.e., domestic dog and American bullfrog) or are considered as having enormous potential to do so (i.e., wild boar).

Dogs can harbor pathogens of global conservation concern, such as rabies and canine distemper virus (CDV), which have been linked to local extinctions and population declines of wild canids (e.g., Kat et al. 1996; Marino et al. 2017) and felids (Roelke-Parker et al. 1996; Seimon et al. 2013; Gilbert et al. 2014). Importantly, disease transmission was reported as the third most prevalent cause of population declines associated with dogs worldwide, and South America was the fourth region in terms of number of affected native species (Doherty et al. 2017).

In our study, 100% of dog pathogens reported globally have also been found in the study region; however, there are only two reports of wildlife mortality in the region which could be linked with CDV transmission from dogs (Ferreira et al. 2009; Acosta-Jamett et al. 2011). Also, CDV transmission was suggested between dogs and wild cats in Brazil (Nava et al. 2008), and CDV antibodies were found in foxes and wild cats in Argentina (Martino et al. 2004; Uhart et al. 2012), and in mustelids in Brazil (Megid, et al. 2013).

The most recent and reliable global population estimation of dogs ranges from 700 million to nearly one billion (Hughes and Macdonald 2013; Gompper 2014). Until 2012, Argentina and Brazil ranked among the top six countries in the world with largest dog population growth since 2007, with the latter having the largest number of dogs in the world, second only to the US (Bradley and King 2012). With this

background and the existing evidence suggesting disease transmission to wildlife, management planning of dog populations and active disease surveillance in co-existing populations of wild carnivores becomes crucial in the study region.

The wild boar has become an increasing concern for animal and public health globally (Miller et al. 2017) and in the study region (Barrios-García and Ballari 2012). In their study, Miller et al. (2017) found that 87% of swine pathogens can cause clinical disease in livestock, poultry, wildlife, or humans, and underlined the importance of transmission between wild pigs and bovids, which in turn can spill pathogens back to wildlife populations (Meagher and Meyer 1994). In the study region, research and policy addressing wild boar diseases have received increased attention in recent years (Carpinetti et al. 2014, 2016; Maciel et al. 2017).

All six disease agents reported in wild boars in the study region are also endemic in local populations of domestic animals, which suggests that spillover and spill-back between domestic species, wild boars, and TNS is a possibility. In particular, the role of wild boar as host of *Mycobacterium bovis* and bovine diarrhoea virus (BVDV) in the study region raises concern (La Sala et al. 2017; Pérez Aguirreburualde et al. 2017; Griffa et al. 2018), especially considering that some of the *M. bovis* spoligotyping signatures found in wild boars matched those reported in axis deer (*Axis axis*) and cattle from the same areas (La Sala et al. 2017; McCormick et al. 2018).

It is worth noting the report of vampire bats (*Desmodus rotundus*) feeding on invasive feral pigs (*Sus scrofa*) and native ungulates in the Brazilian Atlantic forest (Galetti et al. 2016), where about 1.4% of vampire bats are infected with rabies virus (Scheffer et al. 2007). Also, during rabies outbreaks in cattle in Argentina associated with vampire bats, the disease was also observed in different species of native wildlife (Delpietro et al. 2009). Despite rabies virus not being detected in wild boars in the study region, it has long been present in the dog population (Delpietro et al. 1997), suggesting a potential role for wild boar and free-roaming dogs in the maintenance of sylvatic cycle of this disease and potential transmission to susceptible wildlife.

Considering the potential role of wild boars as spreaders of diseases to livestock and native wildlife, it is desirable that institutions dealing with animal



health and pest management ramp up disease surveillance and control efforts in wild boar populations, especially in areas where boars cohabit with TNS of particular concern.

The American bullfrog has been introduced throughout the world over the past two centuries (Lever 2003). The species started expanding in South America as a consequence of the growing trade of live animals for food (Hanselmann et al. 2004), and currently, wild bullfrog populations are present in the majority of South American countries, with Brazil and Argentina having the most extensive feral populations in the region (Giovanelli et al. 2008; Akmentins and Cardozo 2010).

As mentioned above, this species can act as a vector for the fungus Bd. In the study region, Bd was isolated from bullfrogs (Ghirardi et al. 2011; Giovanelli et al. 2008) and 12 native amphibian species in Argentina (Agostini et al. 2015; Lescano et al. 2013; Herrera et al. 2005; Ghirardi et al. 2009, 2014), Chile (Bacigalupe et al. 2017; Soto-Azat et al. 2013), Uruguay (Borteiro et al. 2009), Bolivia (Barrionuevo et al. 2005), and Rio Grande do Sul in southern Brazil (Toledo et al. 2006). Also, the fungus was isolated in museum specimens of Andean aquatic birds, which could represent an additional route of pathogen dispersion (Burrowes and De la Riva 2017).

Bd appears to cause mortality in at least one native amphibian species in Argentina (Arellano et al. 2009) and has been associated with most historical amphibian declines observed in areas of Brazil bordering our study region (Carvalho et al. 2017) and in Chile (Soto-Azat et al. 2013). Despite this, there is no direct evidence showing a direct role of bullfrogs in the transmission of Bd in the region, which makes research in this topic a priority for amphibian conservation.

Bullfrogs can also host potentially lethal viruses of the genus *Ranavirus* (RV), which are widely distributed and have been identified as a threat to amphibian populations (e.g., Teacher et al. 2010; Price et al. 2014). Among the six currently recognized species of RV, Frog virus 3 (FV3) can infect fish, reptiles and amphibians (Duffus et al. 2015) and therefore is capable of threatening whole communities (Price et al. 2014). Cross-species infection has been documented (Stöhr et al. 2013). In South America, FV3 infection and disease have been primarily associated with American bullfrog farms in Brazil

(Mazzoni et al. 2009) and Uruguay (Galli et al. 2006), and until now only one case of infection has been reported in Argentina, involving a wild amphibian population of a Patagonian frog (*Atelognathus patagonicus*) (Fox et al. 2006). In this work, we report six species of reptiles and 23 species of amphibians that could be exposed to either BD or FV3, or both. Therefore, American bullfrog and these two pathogens represent a notable example of invasive host–pathogen systems which could lead to population declines, extirpations and extinctions in amphibians, reptiles and fish populations in the study region.

Most pathogens are capable of infecting more than one host species. This includes the 61.6% of human pathogen species that are zoonotic, 77.3% of pathogens found in livestock and 90.0% in carnivores (Cleaveland et al. 2001). Related hosts may share pathogens because they have similar immunological responses and life-history traits (Perlman and Jaenike 2003). However, many of the most virulent emerging infectious diseases in humans and wildlife are thought to be related to host shifts (Daszak et al. 1999, 2000; Walsh et al. 2003; Roelke-Parker et al. 1996).

Here, the potential spatial distribution of the selected IAS overlapped with varying numbers of TNS sharing different levels of taxonomic relatedness (i.e., Class, Order, or Family). Very few TNS were in the same Family as the studied IAS, and most shared Class or Order. In addition, the vast majority of pathogens reported are capable of infecting more than one host species. Under this scenario, where host-shifts are likely and a wide variety of generalist pathogens are reported, even distantly related hosts may share pathogens and geographical proximity becomes crucial for pathogen transfer (Antonovics et al. 2002).

Epidemiological theory and observations suggest that where a pathogen drives a host species to extinction, there is likely a reservoir host in which the pathogen has a reduced effect (McCallum 2012). In our study, vector mediation was the second most frequent type of transmission, which involved several species of invertebrate hosts such as hard ticks, mosquitoes, triatomid bugs and tabanids. Moreover, among the vector-transmitted pathogens that have not been reported in the study region, most could eventually find the suitable vector/s necessary for transmission in the region. This, we believe, raises special concern with regards to the potential impact of these

pathogens if they were to be introduced in the study region.

The general impact of introduced pathogens on native fauna can be even more worrying if the synergistic effects with other threats are considered. Habitat loss and fragmentation are widely regarded as the most important factors driving extinctions (Sih et al. 2000; Cushman 2006), and research confirms that habitat fragmentation could promote pathogen persistence and disease outbreaks (White et al. 2018). Additionally, although transmission spillover can take place directly between IAS and TNS, mediation by domestic animals, including livestock, poultry and pets could play an important role in the dispersal of diseases to wildlife (Daszak et al. 2000).

Also, the impact of animal movements in the spread of diseases to wildlife and livestock can be enormous (Fèvre et al. 2006). In this regard, domestic animal and human contact networks represent important transmission routes that can affect wildlife in distant regions (Craft 2015; Rwego et al. 2008). There are no overriding rules to control these movements, and much of the trade depends on treaties and agreements between countries, on the World Trade Organization and the Sanitary and Phytosanitary Agreement ([http://www.wto.org/english/tratop\\_e/sps\\_e/spsagr\\_e.htm](http://www.wto.org/english/tratop_e/sps_e/spsagr_e.htm)), and on existing international standards (OIE 2019a; b). Also, detailed guidelines have been developed by the World Conservation Union (IUCN) to minimize disease risks associated with the intentional movement of wildlife for conservation or game management purposes (Cooper and Rosser 2002). With this background, the role of effective animal health service infrastructure and planning becomes crucial to minimize the risks of exotic disease incursion and spread, as has been emphasized elsewhere (e.g., Thiermann 2004).

The design and implementation of risk analysis systems which encompass pathogen introductions by way of IAS is crucial, but unfortunately they are rare in the region and limited to those mentioned in this work. Moreover, the few existing ones are in early stages of implementation, and decisions dealing with introductions are mostly based on expert judgment. On the other hand, while government agencies dedicated to agricultural and animal health assess disease status of imported animals, their focus is on the early detection of pathogens that affect livestock, and have so far ignored direct threats to biodiversity.

Our review of risk analysis systems in the region reveals that all of them deal, at least to some extent, with the introduction of pathogens; however, the relative valuation given to the problem in these systems ranges only between 1 and 6.5%, which shows that the problem is far from being fully acknowledged. We suggest that the relevance of pathogens is severely underestimated in these systems, which leads to risk estimations that can be biased in favor of potentially harmful introductions at best, and completely ignore pathogens with potentially devastating effects at worst. Moreover, the way in which pathogen transmission capacity is addressed in these systems is overly simplistic; for example, the systems proposed for Argentina, Brazil and Chile enquire about the IAS's capacity to transmit pathogens, without further pondering other relevant aspects such as the severity of associated diseases or their potential impact on vulnerable wildlife.

At the international level, the Invasive Species Environmental Impact Assessment (ISEIA) protocol of Belgium (Vanderhoeven et al. 2015) is among one of the most consistent systems that has recently been complemented with risk screening tools focusing on pathogens (D'hondt et al. 2015). These initiatives should pave the way for improving those still under development in the study region.

In conclusion, our work highlights the potential of invasive terrestrial vertebrates to affect native wildlife in the Southern Cone of South America through pathogen transmission and the associated diseases. Transmission could be elicited either through the introduction of new IAS, the introduction of new individuals of IAS already present in the region, or the expansion of their established populations. At the same time, the synergism between the introduction/dispersion of pathogens and other causes of biodiversity loss, such as land use change, makes it reasonable to foresee increasingly widespread and more serious effects in the future. Compared to other impacts associated with IAS, unfortunately, this threat has just begun to be realized in tools to manage biological invasions in the region.

We suggest that pathogens and risk for their transmission should lie at the core of any set of criteria guiding IAS prevention and control policies. In particular, those systems assessing the risks associated with the introduction of new species or the import of organisms already present in the region should benefit

from a detailed identification of pathogens posing a risk, and also include decision-making rules based on the potential impact of transmissible pathogens and the vulnerability of native wildlife. Conservation efforts would benefit immensely from transversal efforts which also consider the ramping up of targeted wildlife surveillance by government agencies.

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