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Original article

Linking invasive exotic vertebrates and their ecosystem impacts in Tierra del Fuego to test theory and determine action

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ABSTRACT

Understanding processes and impacts of biological invasions is fundamental for ecology and management. Recent reviews summarized the mechanisms by which invasive species alter entire ecosystems, but quantitative assessments of these mechanisms are lacking for actual assemblages to determine their relative importance, frequency and patterns. We updated information on introduced vertebrates in the Tierra del Fuego Archipelago (TDF) via an exhaustive literature review and new data to evaluate ecosystem impact mechanisms and provide management recommendations. To date, 24 exotic vertebrates have naturalized in TDF, outnumbering natives nearly 2:1, with the North American beaver (*Castor canadensis*) and muskrat (*Ondatra zibethica*) being the most widely distributed species and also impacting the ecosystem through the greatest number of mechanisms. Introduced vertebrates occupied most parts of the archipelago with human-inhabited islands having greater taxa richness. All exotics potentially altered ecosystems by one or more mechanisms: 100% food webs, 92% invasional meltdown, 42% habitat modification, 38% disease or parasite transmission, 21% soil property and disturbance regime changes. Impact to habitat structure was the main clustering criterion for this assemblage. Within the species that physically alter habitats, we found two sub-groups: 1) large herbivores and 2) "others" including beavers and muskrats. Species that did not alter habitat were divided further into those with predatory trophic effects (carnivorous mammals and trout, sub-group 4) and the rest with assorted impacts (sub-group 3). By establishing high quality information on archipelago-wide assemblage, distribution, impacts and mechanisms for exotic vertebrates, we recommend, based on ecological criteria, prioritizing the management of sub-group 2. A secondary priority might be given to the carnivores in sub-group 4, while species in sub-groups 1 and 3 are less urgent. As the first systematic survey of introduced fauna on an archipelago-scale, we identified knowledge gaps, such as population abundance and dynamics for specific species, which are needed to orient future work, but the notable progress made to date is highlighted.

1. Introduction

Strong cases have been made that population and community approaches to the study of introduced invasive species provide important insights into basic ecological theory (Shea and Chesson, 2002; Sax et al., 2007). As such, invasive species effects on native flora and fauna have been categorized as occurring through natural interspecies interactions like predation, competition, hybridization, transmission of parasites, spread of diseases, and modification of food webs, mechanisms that can cause both negative and positive impacts on other species (Clout and Russell, 2011). However, Simberloff (2011) pointed out that substantial changes in species abundances or composition ultimately can induce alterations in ecosystem processes. Therefore, it is likely that many biological invasions have previously unrecognized ecosystem-level impacts. Plus, these effects are expected to be magnified in isolated environments, like archipelagos (Courchamp et al., 2003; Phillips et al., 2012), where native species evolved in the absence of many predators, parasites or diseases.

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Recently, Ehrenfeld (2010) and Simberloff (2011) reviewed and summarized different mechanisms by which invasive species potentially alter ecosystems and noted that most of these modifications occurred via effects on habitat structure. Both authors also recognized that changes provoked by introduced species in nutrient cycling, soil properties, disturbance regimes (mainly fire) or food web dynamics had the potential to influence entire ecosystems. Additionally, Simberloff (2011) indicated that the impact of two or more invasive species could be more severe than each species separately. The facilitation between invasive taxa (or "invasional meltdown; Simberloff and Von Holle, 1999) is another ecological mechanism by which introduced species can act as agents of ecosystem change. Furthermore, the history of each introduction emerged as a key component to assess its influence on ecosystems, particularly original propagule pressure and lag times between introduction and invasion (Simberloff, 2011). Yet, despite having defined these potential mechanisms, the important review articles to date (Ehrenfeld, 2010; Simberloff, 2011) based their conclusions on descriptions of illustrative cases from the worldwide literature on invasive biota without analyzing an actual assemblage of invasive species to quantify the frequency of these mechanisms or their relative importance in discrete contexts.

We, therefore, decided to determine the patterns and processes of ecosystem impacts by invasive species on a specific biotic assemblage in the Tierra del Fuego (TDF) Archipelago (Fig. 1). TDF is considered one of the world's last remaining "wilderness" areas (Mittermeier et al., 2003). Despite its remoteness, this archipelago has a high number of introduced and invasive species (Lizarralde and Escobar, 2000; Anderson et al., 2006a). Additionally, the region displays a relatively species-poor assemblage of native vertebrates (Massoia and Chebez, 1993) that in many cases evolved in the absence of ecological analogs to the introduced species. An increasing research effort concerning this exotic and sometimes harmful flora and fauna has created a growing body of literature that studies the ecology of these taxa and analyzes how they compare to the same species in its native range (e.g., Anderson et al., 2009), as well as examining how research and management interact on the topic of invasive species (e.g., Anderson et al., 2011). Even so, no archipelago-wide evaluation of this assemblage has been attempted previously to assess fundamental ecological questions. Furthermore, published information is often not centrally located or indexed, and, thus, it is inaccessible to decision-makers. Finally, some early works need to be re-evaluated in the light of current knowledge and understanding of exotic species distributions and impacts.

Consequently, this paper (1) updates and synthesizes the available information on introduced vertebrates in the TDF Archipelago, providing historic context of each introduction, its known distribution, and its demonstrated and potential impacts on the native ecosystem; (2) analyzes the mechanisms by which these introduced species potentially affect the ecosystem, under the frameworks proposed by Ehrenfeld (2010) and Simberloff (2011) to study the frequency and relative importance of particular mechanisms in an actual introduced species assemblage in TDF; and (3) uses these results to suggest an ecologically-based prioritization of invasive species management strategies.

2. Methods

2.1. Data acquisition

We conducted a literature review from various sources for studies about introduced terrestrial and freshwater vertebrates, including peer-reviewed articles available on ISI Web of Science® and Scielo databases, scientific and historical books, and grey literature (e.g., technical reports, theses and dissertations). Additional

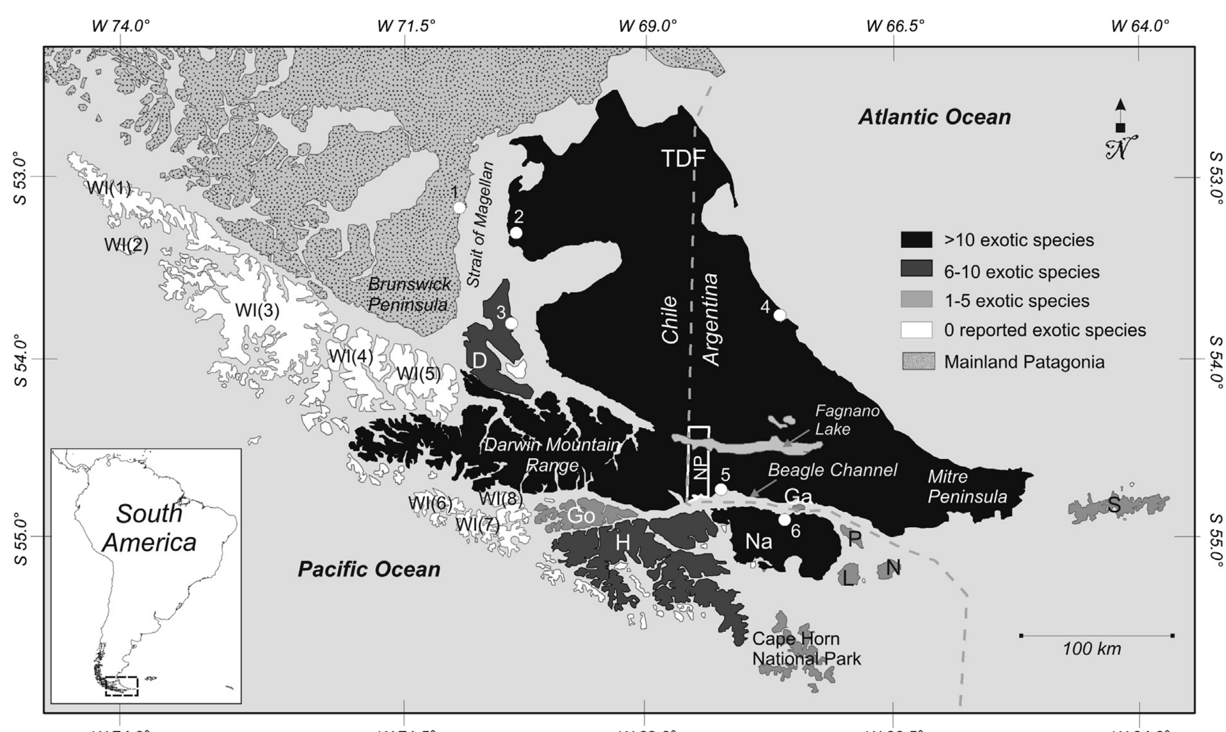

Fig. 1. Map of the Tierra del Fuego Archipelago, differentiating the islands according to the number of established exotic vertebrate species. Numbers correspond to cities or towns: 1) Punta Arenas, 2) Porvenir, 3) Puerto Harris, 4) Río Grande, 5) Ushuaia, and 6) Puerto Williams. Islands: D: Dawson, Ga: Gable, Go: Gordon, H: Hoste, L: Lennox, Na: Navarino, N: Nueva, P: Picton, S: Staten, TDF: Tierra del Fuego, WI: Western Islands were 1) Desolación, 2) Recalada, 3) Santa Inés, 4) Clarence, 5) Capitán Aracena, 6) Steward, 7) Londonderry, and 8) O'Brien. NP: Tierra del Fuego National Park. Cape Horn National Park includes 8 main islands (Bayly, Deceit, Freycinet, Grevy, Hermite, Herschel, Horn, and Wollaston).

assemblage and distribution data were derived from our own research, observations and informal interviews with local people. Research involved a variety of methods such as point count transects, censuses, opportunistic direct observations, signs surveys, various live and lethal trapping systems, mist netting, interviews with local people, hunting, and boat navigations throughout the archipelago.

2.2. Data analyses

We calculated the percentage of the total vertebrate assemblage that corresponded to exotic species. Non-native species confined exclusively within enclosures for domestic use with no feral populations (e.g., chickens, llamas [*Lama glama*]) were excluded. For each invasive species, we then assessed presence/absence on the archipelago's major islands and documented ecosystem impacts that included effects that were locally reported or cited elsewhere for this species as an exotic. Finally, we categorized these impacts as per the theoretical mechanisms proposed by Ehrenfeld (2010) and Simberloff (2011): (i) modifying habitat structure, (ii) affecting nutrient cycling, (iii) changing soil properties, (iv) altering disturbance regimes, (v) modifying food webs, either directly (predation) or indirectly (competition; being a new prey item), (vi) transmitting diseases or parasites, and (vii) being involved in invasional meltdown, either causing or being favored by positive interactions with other invasive species.

The invasive exotic vertebrate species in the archipelago then were grouped using Ward's method of hierarchical clustering and Euclidean distance measurement (Sokal and Rohlf, 1980), based on a matrix of the mechanisms by which these species affect the native ecosystem. Given the information included the matrix, the Euclidean distance is an indicator of relative proximity or similarity based on shared characteristics. Likewise, the main islands were compared and clustered through the same analysis, using instead the introduced assemblage of each island. All analyses were performed using Statistica 7.1 (StatSoft, 2005).

3. Results and discussion

3.1. Publication trends

A total of 85 publications were found about introduced vertebrate species in the TDF Archipelago (see Online Supplement 1 for full list). The earliest publications that provided critical information on species introductions were mostly historical texts (e.g., Bridges, 1949). After 2000, we found a >400% increase in peer-reviewed scientific literature, which parallels similar trends on the topic of invasion biology in Chile (Quiroz et al., 2009) and Latin America (Pauchard et al., 2011). Earlier publications mostly were in regional journals and technical/governmental reports, while later we see more international, indexed research papers (Fig. 2). Historically, the political border between Argentina and Chile clearly limited archipelago-wide research, and bi-national efforts in exotic species research are very recent (Anderson et al., 2009).

To date, most research has been focused on a single species (85%) and has come from a few human-inhabited islands (89%). The grey literature accounted for 38% of the total. Also, there was relatively little or no information available about exotic species in the western islands of the archipelago (Fig. 1). We also found a lack of experimental research; most studies were focused on descriptions of impacts and assemblage, a result that was also reflected in invasion biology in Chile (Quiroz et al., 2009).

While the first species introduction by humans in TDF occurred in the 17th century, when Europeans brought dogs (*Canis lupus familiaris*), most of today's exotic vertebrates were introduced between the second half of 19th century (livestock and pets) and the middle decades of the last century (mainly game and fur bearing species). The most recently recorded arrival of a deliberately introduced species was the large hairy armadillo (*Chaetophractus villosus*), while the detection of the chinook salmon (*Oncorhynchus tshawytscha*) in 2006 appears to be a range expansion from source populations (salmon farms) farther north on the Chilean coast (Table 1).

3.2. Exotic vertebrate assemblage and distribution

We identified a total of 24 exotic vertebrates with feral or semi-feral populations in the TDF Archipelago, comprising mammals, fish and birds (Table 1; see Online Supplement 2 for more details on specific histories and context of introductions and invasions). Nine of these introduced species are among the world's 100 worst invasive species (Lowe et al., 2000). Introduced mammals were the most diverse group with 62.1% (18 spp.) of the entire mammalian assemblage (29 spp.). Fifty percent of freshwater fish species were exotic (4 spp.). Only two non-native bird species maintained feral populations, which represented around 1.3% of the total avifauna. No exotic amphibian or reptile populations were confirmed in the area, although recently three separate discoveries of gray wood

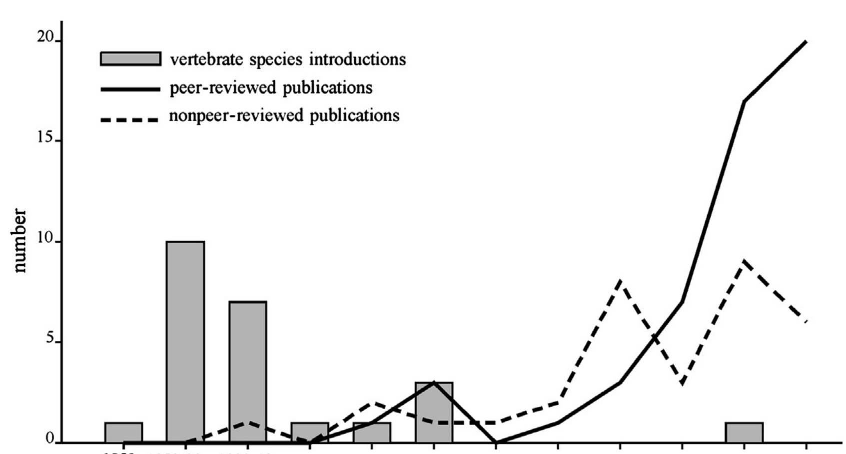

Fig. 2. Temporal trends in introductions (bars), peer-reviewed (solid line) and nonpeer-reviewed (dashed line) publications of exotic vertebrate species in the Tierra del Fuego Archipelago.

Table 1
Introduced vertebrate species in the Tierra del Fuego Archipelago with their current distribution (islands) and the date of first introduction. CH: Cape Horn National Park (8 islands), D: Dawson, Ga: Gable, Go: Gordon, H: Hoste, L: Lennox, Na: Navarino, N: Nueva, P: Picton, S: Staten, TDF: Tierra del Fuego, and WI: Western Islands (8 islands).

Common name	Scientific name	Islands												Introduction first date
		CH (8)	D	Ga	Go	H	L	Na	N	P	S	TDF	WI(8)	
Freshwater fish														
Brook trout	*Salvelinus fontinalis*	–	X	–	–	X	–	X	–	–	–	X	–	1931
Brown trout[a]	*Salmo trutta*	–	–	–	–	–	–	–	–	–	–	X	–	1931
Chinook salmon	*Oncorhynchus tshawytscha*	–	–	–	–	–	–	–	–	–	–	X	–	2006
Rainbow trout[a]	*Oncorhynchus mykiis*	–	–	–	–	–	–	X	–	–	–	X	–	1931
Birds														
House sparrow	*Passer domesticus*	–	–	–	–	–	–	X	–	–	–	X	–	1980's
Rock pigeon	*Columba livia*	–	X	–	–	–	–	X	–	–	–	X	–	1980's
Terrestrial and semi-aquatic mammals														
North American beaver	*Castor canadensis*	–	X	X	X	X	X	X	X	X	–	X	–	1946
Muskrat	*Ondatra zibethica*	–	X	X	X	X	X	X	X	X	–	X	–	1948
American mink	*Neovison vison*	–	–	X	X	X	X	X	–	–	–	X	–	1948
Feral cat[a]	*Felis silvestris catus*	X	X	–	–	X	X	X	–	X	–	X	–	1870–80's
Feral dog	*Canis lupus familiaris*	X	–	–	–	X	X	X	–	X	–	X	–	Before 1800
Feral pig[a]	*Sus scrofa*	–	–	–	X	X	–	X	–	–	–	X	–	1887
European rabbit[a]	*Oryctolagus cuniculus*	–	–	–	–	–	–	X	–	–	X	X	–	1880
Grey fox	*Pseudalopex griseus*	–	–	X	–	–	–	–	–	–	–	X	–	1950's
Silver fox	*Vulpes vulpes*	–	–	–	–	–	–	–	–	–	–	X	–	1948
Large hairy armadillo	*Chaetophractus villosus*	–	–	–	–	–	–	–	–	–	–	X	–	1982
Feral cow	*Bos taurus*	–	X	–	–	–	–	X	–	–	–	X	–	1884
Feral goat[a]	*Capra hircus*	–	–	–	–	–	–	–	–	–	X	–	–	1856
Feral horse	*Equus ferus caballus*	–	–	–	–	–	–	X	–	–	–	X	–	1885
Feral sheep	*Ovis orientalis aries*	–	–	–	–	–	–	–	–	–	–	X	–	1871
Red deer[a]	*Cervus elaphus*	–	–	–	–	–	–	–	–	–	X	–	–	1973
Brown rat[a]	*Rattus rattus*	–	–	–	–	–	–	–	–	–	X	X	–	1870–80's
House mouse[a]	*Mus musculus*	–	–	–	–	–	–	X	–	–	–	X	–	1870–80's
Norway rat	*Rattus norvegicus*	–	X	–	–	–	–	X	–	–	X	X	–	1870–80's
Total		2	7	4	4	7	5	15	2	4	5	22	0	

[a] Species listed among the world's 100 worst invasive species (Lowe et al., 2000).

frogs (*Batrachyla leptopus*) in Ushuaia (G. Martínez Pastur, pers. comm.) indicate a repetitive source of introductions, even though no evidence suggests that this species has a viable population. Two of the exotic mammals found on TDF Island (the grey fox, *Pseudalopex griseus*, and the armadillo) are native to mainland Patagonia, but were introduced to TDF.

We found that since most previous reviews were conducted at the country or regional levels, they often lacked accurate data for this remote archipelago. These studies also always referred to political units, which are ecologically irrelevant. For example, the works for Argentina as a country (Novillo and Ojeda, 2008) and Argentine Patagonia (Bonino, 1995) omitted several species we confirmed in the TDF Archipelago (Table 1). Furthermore, both reports and those of Jaksic (1998) and Lizarralde and Escobar (2000) referred to the presence of reindeer (*Rangifer tarandus*) on TDF or Navarino Islands. Currently, though, reindeer are not present anywhere in the archipelago. Some other country-scale Chilean studies (Jaksic, 1998; Jaksic et al., 2002; Iriarte et al., 2005) also did not include several species for the TDF Archipelago that we found have established feral populations (domestic pets), asserted the absence of other species that are actually present (feral pig, *Sus scrofa*), and indicated the presence of species that we have removed from consideration due to lack of current evidence (reindeer) or to being only vagrants (cattle egret, *Bubulcus ibis*).

Island cluster analysis showed the greatest similarity between the exotic vertebrate assemblages on human-inhabited islands (TDF and Navarino; Fig. 3). These same islands also hosted the greatest taxonomic richness with 22 and 15 introduced vertebrate species, respectively (Table 1). The second cluster was composed of the adjacent islands (Hoste, Dawson, Lennox, Picton, Gable, Nueva and Gordon, in this order) with an average of five invasive species on each island. Finally, the most remote islands (Staten Island, Cape Horn National Park and the western islands) were grouped in a third cluster. These results indicate that the presence of human settlements have facilitated the introduction and invasion process either by increasing propagule pressure, facilitating establishment and expansion, or both.

North American beavers (*Castor canadensis*) and muskrats (*Ondatra zibethica*) were the most widely distributed introduced vertebrates in the archipelago (Table 1). Both semi-aquatic mammals had invaded the entire study area except for the most isolated islands, such as Staten Island and those of Cape Horn National Park. The red deer (*Cervus elaphus*) and the feral goat (*Capra hircus*) were the most spatially restricted species, only found on the western side of Staten Island.

3.3. Knowledge regarding ecosystem impacts

3.3.1. Fish

In numerous parts of the world, introduced trout and salmon have been shown to dramatically affect native fish and aquatic invertebrate populations by predation (Iriarte et al., 2005; Silva and Saavedra, 2008). They feed heavily upon and displace native galaxids (Pascual et al., 2002; Fernández et al., 2010), and in New Zealand have even driven native fish populations to local extirpation (Townsend, 1996). Moorman et al. (2009) showed that the presence of trout on Navarino Island reduced the abundance of native *Galaxias maculatus*, mainly in beaver ponds.

3.3.2. Birds

Both the rock pigeon (*Columbia livia*) and the house sparrow (*Passer domesticus*) apparently have limited impacts on entire natural ecosystems, as they are principally associated with human settlements (Jaksic, 1998; Anderson et al., 2006a). Yet, since sparrows on TDF Island do establish feral populations in the areas surrounding cities, it potentially displaces native passerines by

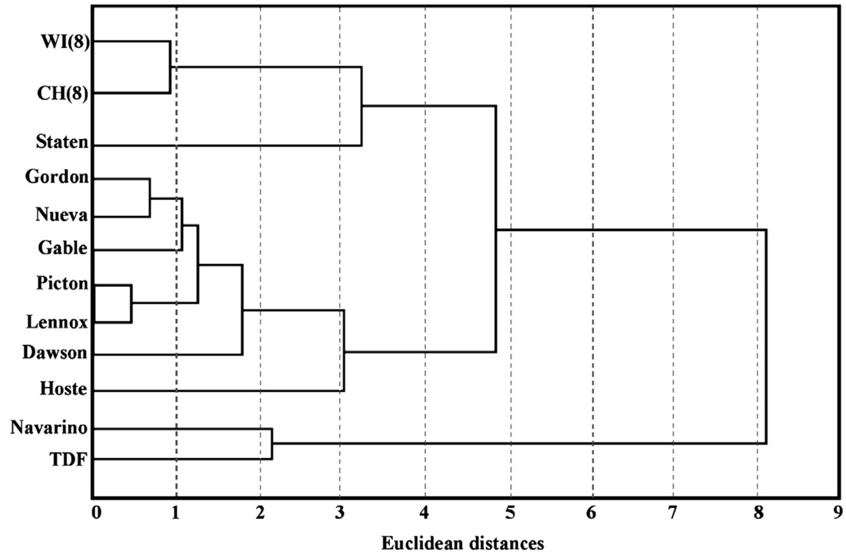

Fig. 3. Cluster analysis of the main islands in the Tierra del Fuego Archipelago, based on each island's exotic vertebrate assemblage using the Ward's method and Euclidean distance measurement. TDF: Tierra del Fuego, WI: Western Islands (include 8 principle islands), CH: Cape Horn National Park, including 8 principle islands.

competition for food and could cause localized community and ecosystem impacts. Pigeons are known to transmit parasites and diseases to native avifauna (Phillips et al., 2012). Consequently, even though exotic birds are few (~1.3%) and their ranges are still restricted, there is reason to expect that they could affect ecosystems by changing the food webs via competition or disease transmission.

3.3.3. Terrestrial and semi-aquatic mammals

The beaver was the most studied invasive species in the TDF Archipelago (68% of publications). These studies provided an ample body of evidence for ecosystem impacts, including effects on nutrient cycling and soil properties (Lizarralde et al., 1996; Ulloa et al., 2012) and stream food webs (Anderson and Rosemond, 2007, 2010; Moorman et al., 2009). All of these impacts resulted from modification (ecosystem engineering) of riparian and in-stream habitats (Wallem et al., 2007; Anderson et al., 2009). Beavers also facilitate other invasive species (i.e. invasional meltdown), such exotic plants in meadows (Anderson et al., 2006b; Martínez Pastur et al., 2006) and trout in ponds (Moorman et al., 2009). However, beavers damming also seem to favor native fish (*G. maculatus*), even under the likely increased depredation by introduced trout. Beavers have cultural impacts as well, since they flood archaeological sites (Piana et al., 2006).

Muskrats, like beavers, are semi-aquatic rodents, but are omnivorous. Their impacts in TDF appear to be similar to those in other parts of the world, where they are known to have trophic effects by consuming plants and small aquatic prey (freshwater mussels, crustaceans, fish) and habitat and nutrient cycling effects by burrowing into stream banks and wetlands (Anderson and Valenzuela, 2011). Additionally, in TDF, muskrats have been reported as prey for the introduced American mink (*Neovison vison*) (Schüttler et al., 2008; Ibarra et al., 2009; Valenzuela et al., in press-a).

The mink is a generalist and opportunist carnivore, and its largest impact in the TDF Archipelago is via predation on native prey species, mainly small rodents, fish and ground-nesting birds (Schüttler et al., 2008; Ibarra et al., 2009; Fasola et al., 2010; Valenzuela et al., in press-a). However, the relatively low representation of exotic species in its diet in the TDF Archipelago (Valenzuela et al., in press-a, in press-b) prevents us from concluding definitively that the invasion of this exotic predator in the region is facilitated through invasional meltdown. Furthermore, there is no evidence to suggest that it competitively excludes the southern river otter (*Lontra provocax*), an endangered and native mustelid which instead apparently out-competes and adversely affects the mink (Valenzuela et al., in press-b). At the same time, more studies are needed to assess the relative impact of mink on both native and exotic prey and predator populations.

Another widely distributed predator in the TDF Archipelago are dogs, which are found both as semi-feral (i.e. still maintaining some association with humans) or entirely feral (i.e. living in free packs). They prey on mammals and birds (Massoia and Chebez, 1993) and also use intertidal resources, as revealed from content of faeces found during carnivore surveys. Ranchers also reported packs of dogs attacking guanacos and livestock. Clearly, dogs could compete for prey with native predators such as the endemic and endangered culpeo fox (*Lycalopex culpaeus lycoides*). In the archipelago, no studies to date have addressed either their impacts on native fauna or the infectious diseases they may carry. However, Barun and Simberloff (2011) have shown that dogs can act as disease reservoirs that spread many wildlife and human pathogens, including rabies, salmonellosis and leptospirosis.

Globally, feral cats (*Felis silvestris catus*) have had disastrous effects on native species, mainly by predation. Their effects are stronger in insular systems where endemic species are often naïve to terrestrial predators (Courchamp et al., 2003). Like dogs, they can be reservoirs and vectors of diseases and parasites (Barun and Simberloff, 2011). In the TDF Archipelago, cats would appear to be less common than dogs, and their scats were not frequently observed during carnivore surveys. However, they are more secretive and do not travel in packs, meaning we cannot conclude *a priori* that they have a lower possibility of competing with native predators.

A preliminary study of the diet of the grey fox, another introduced predator in TDF, reported a high degree of niche overlap between this exotic opportunistic and generalist predator and the native culpeo fox (Gómez et al., 2010). Therefore, its potential effect on the endangered native species via competition is an issue of concern that requires more attention. Furthermore, hybridization with the culpeo fox has been described by natural resource managers (Gigli, 2001), but there are no genetic studies that support or reject this hypothesis. Plus, little is known about the grey fox regarding disease transmission. The silver fox, a melanistic form of red fox (*Vulpes vulpes*), could potentially affect the ecosystem by the same impact mechanisms as the grey fox.

Introduced feral pigs can negatively affect ground-nesting birds by trampling and consuming eggs and chicks (Long, 2003; Skewes et al., 2007). They are opportunistic omnivores, that do not only feed on plant matter and birds, but also insects, small mammals, and even newborn lambs and calves (Skewes et al., 2007; Novillo and Ojeda, 2008; Campbell and Long, 2009). They also have a wide range of ecosystem-level impacts (Barrios-García and Ballari, 2012). Through their rooting, digging, and nest building activities, feral pigs modify plant community composition, reduce plant diversity, facilitate the establishment of exotic plants, and reduce recruitment and growth of saplings in native forests (Hone, 2002; Skewes et al., 2007; Campbell and Long, 2009). Also, in northern Patagonia, pigs were shown to modify soil properties by thinning the forest litter, mixing soil layers and generating large extensions of bare ground (Vázquez, 2002; Novillo and Ojeda, 2008), which in turn can affect nutrient cycling and disturbance regimes (Crooks, 2002; Hone, 2002; Vázquez, 2002). Finally, this species potentially competes with native species, transmits diseases (Long, 2003; Novillo and Ojeda, 2008; Barrios-García and Ballari, 2012) and destroys archaeological sites.

Like pigs, European rabbits (*Oryctolagus cuniculus*) can modify habitats via burrowing and often decrease the structural complexity of vegetation by overgrazing (Crooks, 2002). They also alter forest and shrub habitats by consuming seedlings (Bonino, 1995; Jaksic, 1998). Rabbits can even prevent regeneration of *Nothofagus* forests farther north in Patagonia (Vázquez, 2002) and likewise affect the development of Patagonian grasslands (Novillo and Ojeda, 2008). Together, overgrazing and burrowing activities may decrease vegetation cover, thus reducing the amount of suitable habitat for ground-nesting birds (Courchamp et al., 2003) and increasing an increase in soil erosion (Crooks, 2002). Rabbits also directly compete for food with native herbivorous mammals (Jaksic, 1998), birds (Courchamp et al., 2003), and livestock (Jaksic et al., 2002). In addition, rabbits are prey for both native and exotic predators (Atalah et al., 1980; Valenzuela et al., in press-a, in press-b). Consequently, by enhancing predator populations, or by allowing them to persist when local prey is scarce, introduced rabbits could indirectly contribute to the decline of native fauna by becoming a resource subsidy to predators (Vázquez, 2002; Courchamp et al., 2003). On the Beagle Channel's coast, rabbits have cultural impacts, as well, given their preference for excavating their burrows in archeological sites (Piana et al., 2006).

The armadillo's burrowing activities similarly affect habitat structure, facilitating erosion, mixing the soil, generating bare ground and modifying soil properties (Abba et al., 2007). This species also consumes seedlings, insects, ground-nesting bird eggs and small vertebrates such as rodents and nestlings (Long, 2003; Poljak et al., 2007). Furthermore, armadillos could cause damage to buildings and oil industry structures and are also a vector of Chagas disease farther north in their range (Long, 2003). However, since this species has only been present for a short time in the archipelago, and its distribution is still limited, its full effects may not be evident yet.

Feral livestock such as horses (*Equus ferus caballus*), goats, sheep (*Ovis orientalis aries*) and cows (*Bos taurus*) have been shown to affect the regeneration, abundance, composition and spatial patterns of native *Nothofagus* forests through browsing and trampling (Vázquez, 2002). They also produce bare ground that facilitates the invasion of exotic plants and affects soil properties, potentially increasing erosion (Phillips et al., 2012). Additionally, feral livestock could affect the guanaco, the only large native herbivore in the archipelago, through competition for food (Vázquez, 2002). Finally, livestock could impact ground-nesting birds by altering their nesting sites or direct trampling. For example, we have recurrently observed cattle trampling on nest in a kelp gull (*Larus dominicanus*) colony on the north shore of Navarino Island, with the concomitant mortality of nestlings and eggs.

Besides livestock, the red deer was also introduced to Staten Island, and there is currently a red deer farm in the Chilean portion of TDF Island with about 300 individuals. Elsewhere in Patagonia, it is known to cause negative effects on native grasslands and alter the regeneration, composition and patterns of native forest (Bonino, 1995; Vázquez, 2002). In the case of Staten Island, Schiavini and Raya Rey (2001) reported that browsing and trampling by red deer and feral goats caused the replacement of forest with shrubs and grasses and also affected seabirds nesting sites.

Finally, with the expansion of human settlements in the archipelago, various commensal rodents have also become established, including Norway rats (*Rattus norvegicus*), black rats (*Rattus rattus*) and house mice (*Mus musculus*). Elsewhere, they consume native plants, invertebrates, small mammals and birds, while displacing native small cricetids via competition for food and disease transmission (Novillo and Ojeda, 2008; Drake and Hunt, 2009). Simberloff (2011) indicated that rat predation on islands could indirectly lead to effects on the entire ecosystem.

3.4. Mechanisms

The extant exotic vertebrate assemblage in the TDF Archipelago showed all the proposed mechanisms by which invasive species can affect native ecosystems (Table 2). All these species had the ability to modify food webs. Of these, 96% of the species have effects via competition for resources, while 50% are predators. Also, a very high percentage (92%) were species potentially involved in invasional meltdown, either by being facilitated (8 species, 33%) or facilitating other invasive taxa (17 species, 71%). Furthermore, 10 species (42%) had the ability to modify habitat structure. One of these, the North American beaver has landscape-level impacts (approximately 40% of riparian forests; Anderson et al., 2009). Nine species (37.5%) were potential disease and parasite vectors; five species (21%) could change soil properties; and three species (12.5%) had the ability to alter nutrient cycling or disturbance regimes.

Cluster analysis of the assemblage by ecosystem impact mechanisms showed two main clusters with two sub-groups each (Fig. 4). Clusters A and B segregate species that affect habitat structure from those that do not. Cluster A (habitat modifiers) was made up of species that have some of the most pervasive and damaging impacts generated by introduced species (Crooks, 2002). Within cluster A, sub-group 1 included feral livestock (horse, cow, goat and sheep) and the red deer, which besides habitat effects also potentially compete with native herbivores and domestic livestock and generate conditions that facilitate invasion by exotic plants. These species generally were not widely distributed and because of their size and behavior could be more easily removed. Furthermore, their expansion is exclusively dependent on humans, and consequently, re-introduction risk could be minimized. Yet, their management might also lead to social controversy, mainly because the control methods are perceived to be inhumane (Donlan et al., 2002; Forsyth, 2011).

Sub-group 2 in cluster A comprised species that affect ecosystems by several different mechanisms including habitat modification. The most similar species within this group were the beaver and the muskrat, which influenced the ecosystem by the greatest number of potential mechanisms. Sub-group 2 also

Table 2
Ecosystem impacts of the introduced vertebrate assemblage in the Tierra del Fuego Archipelago, based on the mechanistic typology proposed by Ehrenfeld (2010) and Simberloff (2011).

Introduced species	Habitat structure	Nutrient cycling	Soil properties	Disturbance regimes	Food webs (predation)	Food webs (competition)	Invasional meltdown (cause)	Invasional meltdown (effect)	Diseases transmission
Brook trout	–	–	–	–	X	X	X	X	–
Brown trout	–	–	–	–	X	X	X	X	–
Chinook salmon	–	–	–	–	X	X	X	–	–
Rainbow trout	–	–	–	–	X	X	X	X	–
House sparrow	–	–	–	–	–	X	–	–	–
Rock pigeon	–	–	–	–	–	X	–	–	X
North American beaver	X	X	X	X	–	X	X	–	–
Muskrat	X	X	X	–	–	X	X	–	–
American mink	–	–	–	–	X	X	–	X	X
Feral cat	–	–	–	–	X	–	–	X	X
Feral dog	–	–	–	–	X	X	–	X	X
Feral pig	X	X	X	X	X	X	X	–	X
European rabbit	X	–	X	X	–	X	X	–	–
Grey fox	–	–	–	–	X	X	–	X	–
Silver fox	–	–	–	–	X	X	–	X	–
Large hairy armadillo	X	–	X	–	–	X	X	–	X
Feral cow	X	–	–	–	–	X	X	–	–
Feral goat	X	–	–	–	–	X	X	–	–
Feral horse	X	–	–	–	–	X	X	–	–
Feral sheep	X	–	–	–	–	X	X	–	–
Red deer	X	–	–	–	–	X	X	–	–
Brown rat	–	–	–	–	X	X	X	–	X
House mouse	–	–	–	–	–	X	X	–	X
Norway rat	–	–	–	–	X	X	X	–	X
Total	10	3	5	3	12	23	17	8	9

contained the rabbit, the armadillo and the feral pig. Together, these species were recognized as potentially the most harmful, due to the fact that their impacts to ecosystems occurred via multiple pathways (Table 2). This group also includes the species with the greatest ranges and dispersal capacity (i.e. semi-aquatic mammals). Therefore, we recommend that they deserve special attention and prioritization in the planning of management strategies. Unlike sub-group 1, some of these species are capable of moving among islands by themselves.

Introduced vertebrates that did not modify habitat structure were grouped in cluster B (Fig. 4). The species in sub-group 3 where those with restricted ranges and small effects on the native ecosystem (i.e. birds and house mouse). We would advise that these species are a lower management priority. Rats and salmon were grouped as well within sub-group 3 (i.e. the least harmful group). At present, these species are not widely distributed, and therefore have not yet caused major ecosystem impacts. However, both are known to cause large impacts when they become widespread.

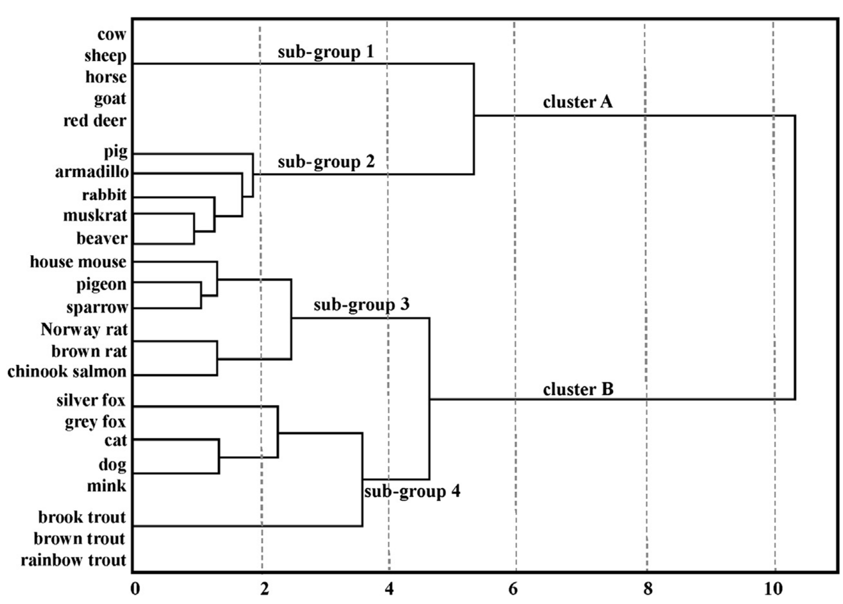

Fig. 4. Cluster analysis of introduced vertebrate species in the Tierra del Fuego Archipelago, based on their ecosystem impact according to mechanisms proposed by Ehrenfeld (2010) and Simberloff (2011), using the Ward's method and Euclidean distance measurement.

Finally, sub-group 4 was made up of predators that are favored by invasional meltdown: 1) terrestrial carnivores (mink, dog, cat and foxes) and 2) trout species. Predator introductions often constitute a major threat to local biodiversity, which implies serious impacts on food webs by predation and competition and consequently indirect ecosystem impacts (Courchamp et al., 2003; Clout and Russell, 2011). Also, it has been suggested that predation effects on native communities are quickly evident, compared to other species extinctions pathways (Sax et al., 2007). For instance, during interviews people often made reference to sites where birds do not nest anymore due to introduced predators. Therefore, subgroup 4 warrants management attention for both ecological and social reasons. The case of the trout, though, is more complex since sport fishing is a main tourism and economic activity throughout Patagonia. Consequently, the control of trout is not immediately plausible, and it would require consensus at a regional scale. Therefore, we suggest that managers initially focus on the terrestrial carnivores for control or eradication, because their negative effects are rapidly evident and native assemblage restoration would also be more feasible.

4. Conclusion

We found that crucial data on the history and consequences of 24 exotic vertebrates in the TDF Archipelago was widely dispersed and in various formats. By reviewing these data, we were able to update current knowledge to provide a more complete understanding of the region's novel vertebrate assemblage (see also Online Supplements 1 and 2). This is the first systematic analysis of the entire archipelago as a bi-national study unit to assess the invasive vertebrate assemblage and its potential impacts at the ecosystem level. Furthermore, by explicitly evaluating these ecosystem impacts under the typological framework proposed by Ehrenfeld (2010) and Simberloff (2011), we quantified these mechanisms in an actual introduced vertebrate assemblage. Negative effects via food web dynamics were found to be the most common way exotic vertebrates can impact ecosystems. Invasional meltdown was also a very common phenomenon among these species, but future studies should distinguish between whether a species facilitates or is facilitated by this mechanism. With 10 introduced species (42%) modifying habitat structure (including one ecosystem engineer), this mechanism constituted the most important clustering criteria for exotic vertebrates (Fig. 3). Habitat modification also clustered the species with the greatest or most pervasive ecosystem impacts.

Besides what this information tells us about basic ecology, knowledge of exotic species assemblages, distributions and associated impacts is also key to design effective management strategies (Genovesi, 2005). Our analysis demonstrated, for example, that human-inhabited islands had greater exotic species richness and that many of these species were brought for economic activities. Among these, the beaver and muskrat were the two most widely distributed species and also impacted the ecosystem through the greatest number of mechanisms. Based solely on ecological criteria, these species should be the highest management priority. Furthermore, introduced terrestrial carnivores are an important group to consider for management, due to their strong effects on native food webs. Finally, large, feral herbivores should have a lower ecological priority for management, due to their relatively restricted ranges and low population sizes. However, various other factors make their eradication perhaps more feasible (e.g., they have higher detection probability, lower dispersal capability and lower risk of reintroduction). Clearly, decisions regarding exotic species management require the involvement of the general public, as well as authorities (White et al., 2008). Consequently, ecological priorities should be complemented with an evaluation of the history of species introductions and invasions and their social, cultural, political and economical context (Bremner and Park, 2007).

Author contribution

A.V. and C.A. conceived the idea. All authors conducted the field work, analyzed the bibliography, contributed to the discussion of the results and wrote the manuscript, which was led by A.V.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.actao.2013.01.010.

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Online Supplement 1. Publications about introduced vertebrate species in the Tierra del Fuego Archipelago.

Number	Publication	Type	Taxa Studied	Location(s)	App
1	Amaya (1981)	*Technical Report - Instituto Nacional de Tecnología Agropecuaria*	beaver	Ga, Na, TDF	5
2	Anderson et al. (2006a)	*Peer-reviewed ISI - Biodiversity and Conservation*	beaver, muskrat, pig, cow, dog, cat, mink, grey fox, rabbit, horse, house mouse, Norway rat, brown trout, rainbown trout, brook trout, sparrow, pigeon	Archipelago	1,2
3	Anderson et al. (2006b)	*Peer-reviewed ISI - Biological Conservation*	beaver	Na	4
4	Anderson and Rosemond (2007)	*Peer-reviewed ISI - Oecologia*	beaver	Na	4
5	Anderson et al. (2009)	*Peer-reviewed ISI - Mammal Review*	beaver	Na, TDF	4
6	Anderson and Rosemond (2010)	*Peer-reviewed ISI -Hydrobiologia*	beaver	Na	4
7	Anderson et al. (2011)	*Scientific Book Chapter*	beaver	Na, TDF	4,5
8	Andrade (2000)	*Technical Report - Fondo de Desarrollo Tecnológico y Productivo*	beaver	TDF	5
9	Arismendi et al. (2008)	*Peer-reviewed no ISI - Revista Bosque*	beaver	TDF	4
10	Atalah et al. (1980)	*Peer-reviewed no ISI - Anales del Instituto de la Patagonia*	grey fox	TDF	3
11	Bahamonde (2007)	*Undergraduate Thesis*	beaver	TDF	5
12	Baldini et al. (2008)	*Peer-reviewed no ISI - Revista Bosque*	beaver	TDF	4
13	Bonino (1995)	*Technical Report - Instituto Nacional de Tecnología Agropecuaria*	beaver, mink, muskrat, rabbit, pig, red deer, reindeer	TDF	1,2
14	Bridges (1949)	*Non-Scientific Book*	horse, dog, pig, rabbit, sheep, cow	TDF	1,2
15	Briones et al. (2001)	*Peer-reviewed no ISI - Anales del Instituto de la Patagonia*	beaver	TDF	3
16	Bugnest (1995)	*Technical Report - Tierra del Fuego National Park*	mink	TDF	1
17	Caibul (2008)	*Undergraduate Thesis*	beaver	TDF	5
18	Castillo (2006)	*Undergraduate Thesis*	beaver	TDF	4
19	Coronato et al. (2003)	*Peer-reviewed no ISI - Ecología Austral*	beaver	TDF	4
20	Crisosto (2010)	*Ms Thesis*	pig, cow, dog, cat, mink, grey fox, rabbit, horse, beaver, muskrat, house mouse, Norway rat, sheep, rainbown trout, brook trout, sparrow, pigeon, cattle egret	Na	1,4
21	Davis et al. (2012)	*Peer-reviewed ISI - Annales Zoologici Fennici*	mink	Na	5
22	Deferrari et al. (1996)	*Technical Report - Folleto Instituto de la Patagonia*	muskrat	TDF	3
23	Deferrari (2007)	*Ph. D Thesis*	muskrat	TDF	2,3
24	Escobar et al. (1996)	*Technical Report - Folleto Instituto de la Patagonia*	beaver	TDF	5
25	Estay (2007)	*Undergraduate Thesis*	beaver	Na, TDF	5
26	Fabbro (1989)	*Technical Report - Tierra del Fuego Natural Resource Office*	red deer, goat, reindeer, beaver, muskrat, rabbit, grey fox, silver fox, mink	TDF	1,2
27	Fasanella et al. (2010)	*Peer-reviewed no ISI - Mastozoologia Neotropical*	beaver	Da, TDF	3
28	Fasola (2009)	*Ph. D Thesis*	mink	TDF	1,3
29	Fasola et al. (2010)	*Peer-reviewed ISI - European Journal of Wildlife Research*	mink	TDF	2,4
30	Fernandez et al. (2010)	*Peer-reviewed ISI - Biological Invasions*	chinook salmon	TDF	1
31	Gigli (2001)	*Technical Report - Tierra del Fuego Natural Resource Office*	muskrat, beaver, grey fox, mink, brown trout, rainbown trout, brook trout, dogs, cow	TDF	1
32	Gómez et al. (2010)	*Peer-reviewed ISI - Polar Biology*	mink, grey fox	TDF	3
33	Goodall (1979)	*Scientific Book*	rabbit, grey fox, beaver	TDF	1,2
34	Haider and Jax (2007)	*Peer-reviewed ISI - Biodiversity and Conservation*	beaver	Na	5
35	Ibarra et al. (2009)	*Peer-reviewed ISI - Oryx*	mink	Na	3,4
36	Iriarte et al. (2005)	*Peer-reviewed ISI - Revista Chilena de Historia Natural*	rainbow trout, brown trout, beaver, muskrat, pigeon, sparrow, rabbit, Norway rat, black rat, house mouse, mink,	Na, TDF	1,2
37	Jacksic and Yañez (1983)	*Peer-reviewed ISI - Biological Conservation*	rabbit, grey fox	TDF	4,5
38	Jaksic (1998)	*Peer-reviewed ISI - Biodiversity and Conservation*	beaver, muskrat, rabbit, reindeer, grey fox, cattle egret, mink, pigeon, sparrow, Norway rat, house mouse, black rat, red deer	Na, TDF	1,2
39	Jaksic et al. (2002)	*Peer-reviewed ISI - Biological Invasions*	rabbit, beaver, muskrat, mink, red deer, grey fox,	Na, S, TDF	1,2
40	Larson (2005)	*Peer-reviewed no ISI - Chile Forestal*	beaver	TDF	1,2
41	Lizarralde (1993)	*Peer-reviewed no ISI - Ambio*	beaver	TDF	2,4
42	Lizarralde (1996)	*Technical Report - Folleto Instituto de la Patagonia*	beaver	TDF	3
43	Lizarralde et al. (1996)	*Peer-reviewed no ISI - Ecología Austral*	beaver	TDF	4
44	Lizarralde et al. (1997)	*Technical Report - Folleto Instituto de la Patagonia*	beaver, muskrat	TDF	5
45	Lizarralde and Escobar (2000)	*Peer-reviewed no ISI - Ciencia Hoy*	beaver, muskrat, rabbit, reindeer, grey fox, Norway rat, black rat, house mice, horse, mink, silver fox, dog, cat, blue fox, lama, goat, sheep, cow, red deer	TDF	1,2
46	Lizarralde et al. (2004)	*Peer-reviewed no ISI - Interciencia*	beaver	TDF	2,3,4
47	Lizarralde et al. (2008)	*Peer-reviewed ISI - Biological Invasions*	beaver	TDF	3
48	Maley et al. (2011)	*Peer-reviewed no ISI - Anales del Instituto de la Patagonia*	mink	Na	4
49	Martinez Pastur et al. (2006)	*Peer-reviewed ISI - Applied Vegetation Science*	beaver	TDF	4
50	Martinic (1973)	*Non-Scientific Book*	goat, cow, horse, sheep	Archipelago	1,2
51	Massoia and Chebez (1993)	*Scientific Book*	beaver, mink, muskrat, red deer, grey fox, rabbit	H, Na, S, TDF	1,2
52	Mella (1994)	*Technical Report - Proyecto Río Cóndor*	beaver	TDF	1,2
53	Menvielle et al. (2010)	*Peer-reviewed no ISI - Aliens*	beaver	Archipelago	5
54	Merino et al. (2009)	*Peer-reviewed no ISI - Natural Areas Journal*	beaver, muskrat, goat, rabbit, mink	TDF	1
55	Moorman et al. (2006)	*Peer-reviewed no ISI - Anales del Instituto de la Patagonia*	beaver, mink	Go, O, TDF	1,2
56	Moorman et al. (2009)	*Peer-reviewed ISI - Transactions American Fisheries Society*	beaver, rainbow trout, brook trout	H, Na	4
57	Novillo and Ojeda (2009)	*Peer-reviewed ISI - Biological Invasions*	mink, beaver, muskrat, reindeer, rabbit, goat, Norway rat, brown rat, house mice	S, TDF	1,2
58	Orquera and Piana (1999)	*Scientific Book*	dog	Archipelago	1
59	Paillacar (2007)	*Undergraduate Thesis*	beaver	TDF	5
60	Parkes et al. (2008)	*Technical Report - Servicio Agrícola y Ganadero*	beaver	Archipelago	5
61	Poljak et al. (2007)	*Peer-reviewed ISI - Revista Chilena de Historia Natural*	armadillo	TDF	1,2,4
62	Ramirez Silva (2006)	*Undergraduate Thesis*	beaver	TDF	4
63	Rojel (2009)	*Undergraduate Thesis*	beaver	Archipelago	3,4,5
64	Rozzi and Sherriffs (2003)	*Peer-reviewed no ISI - Anales del Instituto de la Patagonia*	mink	Na	1
65	Schiavini and Raya Rey (2001)	*Technical Report - Project ARG/97/G31 GEF/PNUD/MRECIC*	goat, red deer, Norway rat, black rat, rabbit	S	1,2
66	Schüttler et al. (2008)	*Peer-reviewed ISI - Revista Chilena de Historia Natural*	mink	Na	3,4
67	Schüttler et al. (2009a)	*Peer-reviewed ISI - Biodiversity and Conservation*	mink	Na	2,3
68	Schüttler et al. (2009b)	*Peer-reviewed ISI - Biological Conservation*	mink	Na	4
69	Schüttler et al. (2011)	*Peer-reviewed ISI - Journal of Nature Conservation*	beaver, mink	Na	5
70	Sielfeld (1977)	*Peer-reviewed no ISI - Anales del Instituto de la Patagonia*	muskrat	H	1
71	Sielfeld and Venegas (1980)	*Peer-reviewed no ISI - Anales del Instituto de la Patagonia*	beaver	Na	1,2,4
72	Silva and Saavedra (2008)	*Peer-reviewed ISI - Revista Chilena de Historia Natural*	beaver, muskrat, mink, rabbit, pig, rainbow trout, brown trout, river trout, grey fox	H, Na, TDF	1,2
73	Simanonok et al. (2011)	*Peer-reviewed ISI - Forest Ecology and Management*	beaver	TDF	2,4,5
74	Skewes et al. (1999)	*Technical Report - Servicio Agrícola y Ganadero*	beaver	Na, TDF	2,3,4,5
75	Skewes et al. (2006)	*Peer-reviewed ISI - European Journal of Wildlife Research*	beaver	Na, TDF	1,2
76	Soto and Cabello (2007)	*Technical Report - Servicio Agrícola y Ganadero*	beaver, mink, muskrat, grey fox, dog, pig	Archipelago	1,5
77	Ulloa et al. (2012)	*Peer-reviewed ISI - Latin American Journal of Aquatic Research*	beaver	Na	2,4
78	Valdebenito (2011)	*Undergraduate Thesis*	red deer	TDF	5
79	Valenzuela (2011)	*Ph.D Thesis*	mink	TDF	2,4,5
80	Valenzuela et al. (in press a)	*Peer-reviewed ISI - Mammalian Biology*	mink	TDF	4
81	Valenzuela et al. (in press b)	*Peer-reviewed ISI - Biological Invasions*	mink	TDF	4,5
82	Vázquez (2002)	*Peer-reviewed ISI - Biological Invasions*	beaver, muskrat, rabbit	TDF	1,4
83	Vila et al. (1999)	*Peer-reviewed ISI - Revista Chilena de Historia Natural*	rainbow trout, brown trout	TDF	1
84	Wallem et al. (2007)	*Peer-reviewed ISI - Revista Chilena de Historia Natural*	beaver	Na, TDF	2
85	Wallem et al. (2010)	*Peer-reviewed ISI - Biological Invasions*	beaver	TDF	4,5

List of publications on introduced vertebrate species in the Tierra del Fuego Archipelago, indicating whether they are peer-reviewed ISI (included in the Institute for Scientific Information database), peer-reviewed non-ISI, non-scientific book/document, technical report, thesis/dissertation, and scientific book/chapter. For each publication, the following information is listed: i) exotic taxa studied, ii) location of the study, and iii) the approach (App) of the study, whereby each was classified as studying (1) presence/absence , (2) distribution/patterns, (3) autoecology, (4) impacts, and/or (5) management/social dimensions of the exotic assemblage. Islands were: Da: Dawson, Ga: Gable, Go: Gordon, H: Hoste, Na: Navarino, O: O'Brien, S: Staten, TDF: Tierra del Fuego.

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Online Supplement 2. History and context of invasive vertebrate introductions and invasions in the Tierra del Fuego (TDF) Archipelago.

Fish

Trout were introduced at multiple times in Tierra del Fuego for aquaculture and sport fishing (Anderson et al., 2006; Fernández et al., 2010; Moorman et al., 2009). The first formal record discovered for fish introductions in the area dated from 1931 and included brook (*Salvelinus fontinalis*), brown (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiis*), brought by the Argentine government to TDF Island (Gigli, 2001; Fernández et al., 2010). Currently, the government of TDF Province (Argentina) continues hatchery raising and introducing juvenile trout every year for sport fishing. Currently, exotic trout were confirmed on TDF, Navarino and Hoste Islands (Anderson et al., 2006; Moorman et al., 2009; Pascual et al., 2002; Vila et al., 1999). Rainbow and brook trout have been recorded on Navarino Island, but only brook trout were sampled on Hoste Island (Moorman et al., 2009). We also confirmed that brook trout are on Dawson Island, and all three species are well established on TDF Island. Electrofishing on Gable Island registered no exotic fish species (D. Fernández and C. Boy, pers. comm.). Since the late 1980's, expanding salmon aquaculture in Chile (Pascual et al., 2002) has provided a new source of salmonid introductions via escapees. In 2006, exotic chinook salmon (*O. tshawytscha*) were first reported in a river on the Beagle Channel coast of TDF Island (Fernández et al., 2010), which would be a natural range expansion of this exotic species from the north rather than a deliberate introduction. Besides the first record of chinook salmon on TDF Island, there is no information about its presence or absence in freshwater bodies on other islands or in marine channels throughout the archipelago. However, due to the presence of salmon and trout farms in the bays around Capitán Aracena Island and plans to install them in the bays of Navarino Island, the extent of the salmon invasion is likely to increase and is perhaps unavoidable, in light of the experiences farther north in Patagonia (Becker et al., 2007). Nevertheless, there is no indication that chinook salmon numbers in TDF were great enough yet to produce ecosystem impacts, but our review also highlighted that there was no research on exotic fishes in marine environments.

Birds

The only two exotic bird species recorded in the area were the house sparrow (*Passer domesticus*) and the rock pigeon (*Columbia livia*). The house sparrow's presence in the archipelago is apparently the result of natural range expansion from the mainland (Anderson et al., 2006), as it is found throughout Patagonia in association with human settlements, even around houses at isolated ranches. In contrast, the pigeon is known to have been deliberately released to the town of Puerto Williams (Chile) in the 1990's (Anderson et al., 2006), and currently it is also found associated with other Chilean settlements such as Porvenir on TDF and the Puerto Harris Naval Base on Dawson Island. Until recently, the pigeon was absent from Argentine TDF, but now individuals of unknown origin have been sighted in Ushuaia and Río Grande.

Terrestrial and semi-aquatic mammals

North American beaver (*Castor canadensis*)

The Argentine government released 25 beaver pairs on TDF Island in the Claro River area along the north shore of Fagnano Lake in 1946 (Lizarralde, 1993). By the late 1990's, estimates placed its numbers as high as 100,000 individuals, found throughout most of the archipelago (Lizarralde, 1993; Skewes et al., 2006). Today, the beaver has been confirmed on most islands, except the far southern islands around Cape Horn, Staten Island and some of the extreme western islands; its expansion onto the mainland Brunswick Peninsula in the 1990's lead to a binational treaty signed between Argentina and Chile in 2008 to seek to eradicate this invasive species and restore riparian forests (Menvielle et al., 2010). Little research was done on this species in the early decades of the invasion (Anderson et al., 2011). Yet, since the late 1990's, the beaver has become the most studied invasive species in the TDF Archipelago with 68% of the total publications on exotic fauna. Finally, the research on invasive beavers stands out in this review with regards to the explicit efforts that also have been made to link ecological studies with decision making, such as specific recommendations for eradication and subsequent ecosystem restoration and joint publication between scientists and managers (Anderson et al., 2009; 2011).

Muskrat (*Ondatra zibethica*)

Muskrats were introduced to TDF Island for their fur by the Argentine government in the same period as beavers (Fabbro, 1989). However, the exact locations and numbers of these introductions remain unclear, but reports coincided that there were various sites and at least several dozen individuals (Deferrari, 2007). The population grew and expanded quickly, leading the Argentine Agriculture and Livestock Ministry to declare it a harmful species in 1954 (Resolution 1227). Even so, effective control measures are still lacking (Deferrari, 2007). We found that its range in the archipelago includes TDF, Navarino, Hoste, Nueva, Picton and Lennox Islands (Anderson et al. 2006). However, our new records extend its confirmed distribution to Gordon (E. Davis pers. comm.), Gable and Dawson Islands. Recently, we have also captured two individuals on the Chilean mainland (Laguna Parrillar National Park on the Brunswick Peninsula, Cabello et al., unpublished results). With the exception of one Ph.D. dissertation (Deferrari, 2007), almost no primary research has been conducted on muskrats in TDF. At the same time, it is an invasive introduced species in 42 countries in South America and Eurasia with widely documented impacts (Anderson and Valenzuela, 2011). It is also of note that this species was successfully eradicated from Great Britain in the 1930's (Gosling and Baker, 1989), which demonstrates the feasibility of its control on a large scale.

American mink (*Neovison vison*)

Between 1948 and 1953, *N. vison* was introduced to the Argentine sector of TDF Island to establish fur farms near the city of Río Grande (Lizarralde and Escobar, 2000; Massoia and Chebez, 1993). According to the former provincial director of wildlife (N. Loekemeyer), another farm operated in Aguirre Bay on Mitre Peninsula. These farms, however, were closed by 1961 (Godoy, 1963) due to financial problems, and several mink were released near Los Cerros Ranch and around the Irigoyen River (Fabbro, 1989). Lizarralde and Escobar (2000) reported the presence of small groups of feral mink in the Mitre Peninsula and in the central part of TDF Island by 1988 and along the coasts of the Beagle Channel by 1990. Bugnest (1995) noted that the first American mink sighting in TDF National Park was in 1994. In 1998, minks were observed in the central and north areas of the Chilean sector of TDF Island (Jaksic et al., 2002), and since 2001, the expansion of this species in the archipelago has been confirmed with its first capture on Navarino Island (Rozzi and Sherriffs, 2003). Later, it was recorded on Hoste Island in 2005 (Anderson et al., 2006) and on Lennox Island in 2009 (Davis et al., 2012). Currently, based on new sightings of individuals, prints and scats, we also confirmed mink presence on Gordon and Gable Islands in the western and eastern Beagle Channel, respectively. While minks are semi-aquatic and therefore likely able to swim among some of the closer islands, fisherman also reported to us that they have accidentally transported minks hidden in their boats, mainly between Navarino and Lennox Islands. Despite a series of publications that have been produced in the last eight years, more studies are needed to specifically assess the relative impact of mink on prey populations and the relationships with native predators, such as the endemic and endangered culpeo fox (*Lycalopex culpaeus lycoides*) or birds of prey, and other exotic carnivores, such as grey fox and feral pets.

Feral pets

Before European arrival, the southernmost record of dogs (*Canis lupus familiaris*) for the Americas was in mainland Patagonia (Prates et al., 2010), and dogs have never been found in archeological sites in the TDF Archipelago (E. Piana, pers. comm.). Therefore, the presence of dogs in this region can be dated to post-European discovery. Bridges (1949) and Orquera and Piana (1999) indicated that the Yamana (or Yahgan) people (nomadic inhabitants of the Beagle Channel coasts and islands located to the south) adopted introduced dogs mainly for assisting in hunting activities for otters, birds and guanacos (*Lama guanicoe*). Currently, we confirmed feral dogs, either solitarily or in packs, widespread on TDF, Navarino, Hoste, Lennox and Picton Islands. Furthermore, until recently naval families stationed at outposts in Cape Horn National Park and elsewhere were allowed to keep dogs and cats (*Felis silvestris catus*) as pets.

There were no detailed records for feral cat introductions to the TDF Archipelago, but in accordance with what is known globally, cats likely arrived in the 19th and 20th centuries by travelling as human commensals or being taken as pets for rodent control (Nogales et al., 2004). Domestic cats are very adaptable and can become feral even under inhospitable conditions (Barun and Simberloff, 2011). Lizarralde and Escobar (2000) and Anderson et al. (2006) were the only authors to list feral cats among the exotic species for the archipelago and reported their presence on TDF, Hoste, Lennox, Picton and Navarino Islands. In addition, Anderson et al. (2006) found that naval outposts in remote places like Cape Horn National Park have historically been allowed to keep cats as pets. Plus, even small islets (e.g., Holger Islets) were observed to have cats, indicating their placement there by fishermen. We also provide new data here to confirm that feral cats are present on Dawson Island. While elsewhere experiences with feral cats raise fears about their potential impact, their effects on native fauna in TDF have been largely undocumented, but they were implicated in the extermination of a penguin colony on Horn Island (Anderson et al., 2006).

Feral pig (*Sus scrofa*)

The first documentation discovered for pig introductions was on TDF Island in 1887, when the Bridges family, the first permanent Europeans inhabitants in the archipelago, released a group due to over-reproduction at the farm and problems with feeding them during winter (Bridges, 1949). This author also indicated that those wild pigs were heavily hunted during the subsequent years, but there is no information about the survival of that original population. The current feral animals likely come from multiple escapes and releases from farms since the late 1800's. Curiously, Massoia and Chébez (1993), Jaksic et al. (2002) and Novillo and Ojeda (2008) indicated that feral pigs were not present in the TDF Archipelago, but we have confirmed the presence of this introduced species not only on TDF Island, but also Gordon, Hoste and Navarino. While no research has been conducted on this species in the region, introduced feral pigs are known to have a wide range of ecosystem-level impacts (Barrios-García and Ballari, 2012). No systematic feral pig control efforts have been made in TDF Archipelago, except for sporadic hunting.

European rabbit (*Oryctolagus cuniculus*)

Thomas Bridges introduced European rabbits to several small islands (two or three pairs per island) in the Beagle

Channel near Ushuaia around 1880 with the aim of securing a food supply for explorers (or even themselves when travelling), but taking deliberate care to not introduce this species to the main island for fear it would wreak havoc on farming (Bridges, 1949). Jaksic et al. (2002) reported that these rabbits were then spread by naval boats and local residents to southern TDF and Navarino Islands. However, it is not known whether these subsequent introductions and translocations were successful nor if they are the source of today's rabbit population in southern TDF Island. A separate introduction of rabbits took place near the Chilean town of Porvenir on TDF Island in 1936 (Fabbro, 1989; Massoia and Chebez, 1993), when sheep ranchers released two pairs (Jaksic et al., 2002). By 1953, the population was estimated at 35 million individuals and had invaded the entire northern part of the island (Massoia and Chebez, 1993). Apparently, several rabbits were brought later by the municipal government of Ushuaia to the Beagle Channel coast around 1950 (Goodall, 1979). Due to the damaging effect of rabbits on ranching activities, in 1954 the myxomatosis virus was used to successfully reduce their numbers in the north part of the island (Jaksic and Yañez, 1983). During the 1980's, rabbits were still common along the Argentine coast of the Beagle Channel (E. Pianna, pers. comm.), but their numbers appear to have declined after fox hunting was banned (Provincial Laws 1422/78 and 101/93). Currently, we confirmed two rabbit populations on TDF Island: i) on the southern shore, restricted to the Beagle Channel coast from Yendegaia Bay (Chile) to Ushuaia Bay (Argentina) and including TDF National Park; and ii) on the northwest side of TDF, near the town of Porvenir (Chile). Despite the great impact of the myxomatosis virus on the rabbit population from Navarino Island, Anderson et al. (2006) also reported sighting several individuals on the island's northwestern tip in 2004. A separate introduction of European rabbits occurred in the 19th century on Staten Island, specifically to San Juan del Salvamento Bay and later to the adjacent Observatorio Island in 1902 (Schiavini et al., 1999). Jaksic et al. (2002) suggested that subsequent introductions occurred on Staten Island at least until 1973. By 2000, rabbits were identified as one of the most common invasive mammals on portions of Staten Island (Schiavini and Raya Rey, 2001). However, no research has been conducted specifically on rabbits in the TDF Archipelago.

Foxes

The grey fox (*Pseudalopex griseus*) was introduced to the northern steppe ecosystems of TDF Island in the 1950's as a biological control agent to reduce the invasive rabbit population (Fabbro, 1989). Twenty four animals were brought to Onaisín, near Porvenir, in 1951 (Jaksic et al., 2002). Lizarralde and Escobar (2000) and Gigli (2001) indicated that 32 individuals were also released at Cullen Ranch, on the northeast side of TDF Island. By 1980, they were widespread in the northern half of the island (Atalah et al., 1980), and as recently as the mid-1990s, they were still unconfirmed south of Fagnano Lake (Massoia and Chebez, 1993). In 1997, however, this species was recorded on the Beagle Channel coast by rangers in TDF National Park (P. Kunzle, pers. comm.). Nowadays, grey fox are widespread and abundant across much of TDF Island, except the southwestern portion (Darwin Mountain Range and Agostini National Park). Additionally, during carnivore surveys on Gable Island, we frequently sighted individuals and their signs. The grey fox is an opportunistic and generalist predator. However, their actual impact on native prey populations by consumption is currently unknown. A preliminary study reported a high degree of niche overlap between the grey fox and the native culpeo fox (Gómez et al., 2010). Therefore, its potential effect on the endangered native species via competition is an issue of concern that requires more attention and should be addressed. Furthermore, hybridization with the culpeo fox has been described by natural resource managers (Gigli, 2001), but there are no genetic studies that support or reject this hypothesis. Plus, little is known about the grey fox regarding disease transmission.

Two fur farms of silver fox, a melanistic form of red fox (*Vulpes vulpes*), opened in 1948 on TDF Island (Fabbro, 1989): i) north of Río Grande and ii) at Aguirre Bay on Mitre Peninsula. These fur farms closed before 1961 (Godoy, 1963), however, and the animals were released to the wild (Lizarralde and Escobar 2000). Although it is currently unknown if this species became successfully established, Lizarralde and Escobar (2000) described silver fox presence in some sectors of TDF Island. Like the grey fox, this species could potentially affect native species by predation, competition and disease transmission.

Large hairy armadillo (*Chaetophractus villosus*)

Native to mainland Patagonia, this armadillo species is the most recently documented deliberate vertebrate introduction to the archipelago. By 1975 this species expanded its southern range to the mainland side of the Strait of Magellan (Atalah, 1975). On TDF Island, eight individuals were released for aesthetic reasons in 1982, after which there were at least three more introduction events up until 2005 by oil company employees, presumably for food (Poljak et al., 2007). These authors suggested that currently armadillos only occupy a thin strip of Atlantic coast north of Río Grande and that their burrows are highly associated with the underground network of oil pipelines.

Feral livestock

Domestic horses (*Equus ferus caballus*), goats (*Capra hircus*), sheep (*Ovis orientalis aries*) and cows (*Bos taurus*) were introduced by the earliest European colonizers around the world. Subsequent escapes or releases resulted in the establishment of feral and semi-feral populations of these species in the TDF Archipelago. Goats were deliberately introduced to Staten Island in 1856 (Fabbro, 1989) and later to Navarino Island in 1867 (Martinic, 1973). Sheep were brought to TDF Island in 1870 and released into the wild in 1871, cows were present on the island by 1884, and in 1885 the Argentine Navy released a few horses (Bridges, 1949). Currently, feral cows are found on Dawson, Navarino and TDF Islands. We confirmed feral horses on TDF and Navarino Islands, while feral goats are only on Staten Island. Semi-feral sheep appeared to only be an issue on TDF Island.

Red deer (*Cervus elaphus*)

Red deer were released onto Staten Island in 1973 (Fabbro, 1989), and their descendants can be found today. In spite of the fact the red deer is listed as one of the world's 100 most invasive species (Lowe et al., 2000), the Chilean Livestock and Agricultural Service authorized in 2000 a farm for this species on TDF Island, which currently maintains approximately 300 individuals.

Mice and rats

Despite being extensively studied around the world (Pascal, 2011), Norway rats (*Rattus norvegicus*), black rats (*Rattus rattus*) and house mice (*Mus musculus*) were not subject of research in the TDF Archipelago. The exact introduction dates of these species remain unknown, but most likely occurred by the late 19th century in incidental arrivals due to increased colonization and shipping to the region. Only a few works have reported their presence and distribution (Lizarralde and Escobar, 2000; Schiavini and Raya Rey, 2001; Anderson et al., 2006). To date, Norway rats were reported on Dawson, Navarino, Staten and TDF Islands, black rats were recorded on TDF and Staten Islands, and house mice were observed only on TDF and Navarino Islands. These species were previously described as restricted to human settlements in the TDF archipelago (Jaksic et al., 2002; Iriarte et al., 2005; Anderson et al., 2006). However, we have confirmed their presence in the diet of American mink away from human-inhabited areas (Valenzuela et al., in press a; b).

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