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# Replacement of native by non-native animal communities assisted by human introduction and management on Isla Victoria, Nahuel Huapi National Park

Valeria L Martin-Albarracin, Martin A Nuñez, Guillermo C Amico

One of the possible consequences of biological invasions is the decrease of native species abundances or their replacement by non-native species. In Andean Patagonia, southern Argentina and Chile, many non-native animals have been introduced and are currently spreading. On Isla Victoria, Nahuel Huapi National Park, many non-native vertebrates were introduced ca. 1937. Records indicate that several native vertebrates were present before these species were introduced. We hypothesize that seven decades after the introduction of non-native species and without appropriate management to maintain native diversity, non-native vertebrates have displaced native species -given the known invasiveness and impacts of some of the introduced species-. We conducted direct censuses in linear transects 500m long (n=10) in parallel with camera-trapping (1253 camera-days) surveys in two regions of the island with different levels of disturbance: high (n=4) and low (n= 6) to study the community of terrestrial mammals and birds and the relative abundances of native and non-native species. Results show that currently non-native species are dominant across all environments; 60.4% of census records and 99.7% of camera trapping records are of non-native animals. We detected no native large mammals; the assemblage of large vertebrates consisted of five non-native mammals and one non-native bird. Native species detected were one small mammal and one small bird. Species with a highest trapping rate were red and fallow deer, wild boar, silver pheasant (the four species non-native) and chucao (a native bird). These results suggest that native species are being displaced by non-natives and are currently in very low numbers.

1 **Replacement of native by non-native animal communities assisted by human introduction**  
2 **and management on Isla Victoria, Nahuel Huapi National Park**

3

4 Valeria L. Martin-Albarracin<sup>1\*</sup>, Martin A. Nuñez<sup>1</sup>, Guillermo C. Amico<sup>1</sup>

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6 <sup>1</sup> Laboratorio Ecotono, INIBIOMA, CONICET-Universidad Nacional del Comahue, Bariloche,  
7 Río Negro, Argentina

8 \* Corresponding author; Address: Quintral 1250, 8400, Bariloche, Río Negro, Argentina; Phone  
9 number: 0054 0261 155737448; E-mail address: [valemartinalba@gmail.com](mailto:valemartinalba@gmail.com)

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## 36 Introduction

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38 Although the invasion by non-native species is currently recognized as one of the main threats to  
39 global biodiversity, historically this was not always the case. Throughout human history there  
40 have been many intentional introductions with the aim of naturalizing species considered  
41 valuable. For example, in Hawaii 679 species were purposely introduced and released between  
42 1890 and 1985 for the biological control of pest species; 243 (35.8%) of them have become  
43 established (Funasaki et al. 1988). Similarly, in the United States 85% of 235 woody species  
44 naturalized were introduced primarily for the landscape trade and 14% for agriculture or  
45 production forestry (Reichard 1994). Interestingly, many populations of non-native species  
46 known to have impacts are currently not managed or are protected because they constitute  
47 economic resources or have cultural importance (Lambertucci & Speziale 2011; Nuñez &  
48 Simberloff 2005). Moreover, intentional attempts to introduce new species are still common  
49 (Hulme et al. 2008). Together, these factors contribute to the colonization and success of  
50 invasive species.

51

52 One main objective of protected areas is the protection of native biodiversity (Naughton-Treves  
53 et al. 2005). However, without appropriate management, establishment of a protected area is not  
54 enough to protect native biodiversity (Leverington et al. 2010). Biological invasions in particular  
55 are an important threat to protected areas because they can have large impacts on native species  
56 (Simberloff et al. 2013). Moreover, an invasive species can be unintentionally introduced or  
57 reach a protected area by spreading from other sites (e.g. Fasola et al. 2011). If not controlled,  
58 these species can increase in abundance and become a serious problem.

59

60 We can expect three different scenarios as the result of the introduction of non-native species  
61 (MacDougall et al. 2009). One is a scenario where non-native species do not survive or are  
62 reduced to very low numbers, possibly owing to biotic resistance from native species (Zenni &  
63 Nuñez 2013). Another is where native and non-native species coexist, which could be explained,  
64 for example, by the existence of empty niches that are filled by non-native species (Azzurro et al.  
65 2014). The third scenario is where natives are gradually driven to extinction and replaced by  
66 non-natives (Blackburn et al. 2004; Woinarski et al. 2015). In this last scenario biological  
67 invasions become a very important threat to native biodiversity.

68

69 In Andean Patagonia, southern Argentina and Chile, biological invasions are a serious problem,  
70 even in National Parks (Sanguinetti et al. 2014), where the highest invasion indices have been  
71 recorded in relation to other protected areas in Argentina (Merino et al. 2009). For example,  
72 studies on the diet of an assemblage of native carnivores found that their diet comprises almost  
73 exclusively non-native animals, indicating that these have replaced native species as a food  
74 source for native carnivores (Novaro et al. 2000). Similarly, the diet of the condor (*Vultur*  
75 *gryphus*), a scavenging bird of South America, was historically dominated by guanacos (*Lama*  
76 *guanicoe*) and lesser rheas (*Rhea pennata*), the dominant herbivores of the region, but now has  
77 shifted and comprises mainly non-native species (Lambertucci et al. 2009). Research in forests  
78 and shrublands of Patagonia shows that terrestrial communities are dominated by non-native  
79 mammals, including several invasive species such as *Cervus elaphus* (red deer), *Sus scrofa* (wild  
80 boar) and *Lepus europaeus* (European hare, Gantchoff et al. 2014). Moreover, the association of  
81 some of these species to human-disturbed environments such as roads or pine plantations can

82 increase their rate of spread (Gantchoff et al. 2014; Lantschner et al. 2012). Many of these data  
83 suggest that the actual problem is not a single species invasion, but a multi-species invasion.

84

85 Isla Victoria, located in the centre of Nahuel Huapi National Park, has a history of invasions,  
86 with many species of plants and animals actively introduced for several decades (Simberloff et  
87 al. 2002). In 1937 a zoological station was established on the island with the aim of exhibiting  
88 native and exotic fauna to tourists and promoting hunting (Daciuk 1978a). Non-native species  
89 included some of the most invasive vertebrates in the world; such as red deer (*C. elaphus*),  
90 fallow deer (*Dama dama*), and several pheasant species. The zoological station closed in 1959  
91 and animals were released. Since then, non-native species had not received any significant  
92 management, though various proposals have been advanced occasionally (Daciuk 1978a).  
93 Recently, records of native mammals on Isla Victoria have diminished drastically, and those of  
94 non-native mammals have become common.

95

96 The aim of this study is to assess the community composition of terrestrial mammals and birds in  
97 Isla Victoria several decades after the introduction of non-native species. Specifically, we  
98 recorded all species detected, and, for the more common species, we estimated the population  
99 density and their association with different disturbance levels. We hypothesize that (1) without  
100 appropriate management, non-native species have become dominant; and (2) that given the  
101 adaptation of some non-native species to human altered habitats, highly disturbed areas will  
102 harbor greater abundances and diversity of non-native animals than less disturbed areas.

103

104 **Methods**

105

106 Study site

107

108 The study was conducted in Isla Victoria, located in the core of Nahuel Huapi National Park, in  
109 the northern Patagonian Andes, Argentina (40° 57 S, 71° 33 W, APN research permit N° 1146).

110 This island is located in the center of Nahuel Huapi Lake, a glacial lake with 557 km<sup>2</sup> surface

111 that is located at an altitude of 770 masl. The island has a surface of 31 km<sup>2</sup> and a maximum

112 altitude of 1050 masl. The climate is cold and temperate with a pronounced seasonality. The

113 island is dominated by forests of native *Nothofagus dombeyi* (Coihue) and *Austrocedrus*

114 *chilensis* (Ciprés) (Simberloff et al. 2003). Since the beginning of the 20<sup>th</sup> century, this island has

115 been the focus of many animal and plant introductions, most of them conducted for economic

116 purposes.

117

118 Old World deer *C. elaphus* (red deer), *D. dama* (fallow deer), and *C. axis* (axis deer) were

119 introduced to this region between 1917 and 1922 as game animals (Simberloff et al. 2003). In

120 1937 a zoological station was constructed to raise animals for exhibition to tourists and to

121 promote hunting (Daciuk 1978a). The first two deer species successfully established and are

122 common in the island (Relva et al. 2009), while the last one became extinct. Several species of

123 phasianids were also introduced, including peacocks (*Pavo cristatus*), golden pheasants

124 (*Chrysolophus pictus*), silver pheasants (*Lophura nycthemera*), dark pheasants (*Phasianus* sp.),

125 and ring-necked pheasants (*Phasianus colchicus*) (Daciuk 1978a).

126

127 *Sus scrofa* (wild boar) was seen for the first time in the island in 1999. This species was  
128 introduced to Patagonia in the early 1900s and probably reached the island swimming from the  
129 nearby Huemul Peninsula (Simberloff et al. 2003; see Fig. 1), although is also possible that it  
130 was illegally and covertly introduced. They are now reproducing regularly and are widespread  
131 along the island (Barrios-Garcia et al. 2014). Other non-native species more recently established  
132 on the island is *Neovison vison* (American mink), introduced to Patagonia in 1940s and currently  
133 spreading (Fasola et al. 2011). Domestic cats, *F. domesticus*, were brought to the island by the  
134 first settlers (date unknown). Several cats escaped from domestication and are now living and  
135 reproducing in a wild state. Non-native rodents of the genera *Mus* and *Rattus* can be found in the  
136 most intensively used ports of the island - Anchorena, Piedras Blancas, and Radal (Fig. 1).  
137 Several of these non-native species have been introduced in other regions of the world with  
138 reported ecosystem impacts (Barrios-Garcia & Ballari 2012; Fasola et al. 2011; Relva et al.  
139 2010; Woinarski et al. 2015). The list of species introduced and naturalized on isla Victoria is  
140 presented on Table 1.

141  
142 The original assemblage of native terrestrial vertebrates on Isla Victoria was relatively simple,  
143 consisting on a subset of few species respective to the total fauna of Nahuel Huapi National Park  
144 (Table 2) (Grigera et al. 1994). It was composed of several lizards of the genus *Liolaemus*, a  
145 snake, two terrestrial birds and some small mammals (Contreras 1973; Daciuk 1978b). Two  
146 native cervids were observed on Isla Victoria in early 1900s, *Pudu pudu* (pudú) and  
147 *Hippocamelus bisulcus* (Austral huemul, Daciuk 1978b; Koutché 1942). References indicate that  
148 *H. bisulcus* was common on the island at the beginning of the 20<sup>th</sup> century. Remains of this  
149 species have been found in excavations at Puerto Tranquilo, in the north coast of the island (E.



150 Ramilo, personal communication). On the contrary, there is not enough evidence to say that *P.*  
151 *pudu* inhabited the island. Instead, individuals observed probably reached the island from  
152 populations surrounding Nahuel Huapi Lake (Eduardo Ramilo, Personal Communication). *Pudu*  
153 *pudu* was introduced to the island at the zoological station, and some recent sightings indicate  
154 that it is still present, although it appears to be very scarce; however, there are no reported  
155 sightings of *H. bisulcus* from the last decades  
156 ([http://www.sib.gov.ar/area/APN\\*NH\\*Nahuel%20Huapi#eves](http://www.sib.gov.ar/area/APN*NH*Nahuel%20Huapi#eves)).

157

## 158 Sampling Design

159

160 To study the composition of the community of terrestrial vertebrates in Isla Victoria we installed  
161 one camera trap in each of eight 500m-transects from winter 2011 to autumn 2012 (Fig. 1).  
162 Transects were associated with two different levels of human disturbance: high (4 transects) and  
163 low (4 transects). High disturbance occurred in regions where tourist activities are developed,  
164 with tens to hundreds of people walking along paths daily. These regions include plantations of  
165 non-native trees and shrublands with high abundances of non-native plants. Regions with low  
166 disturbance were occasionally visited by people who inhabit the island. These regions are  
167 dominated by forests of *N. dombeyi* and *A. chilensis* and by mixed shrublands dominated by  
168 native plants. We used eight heat and motion-triggered infrared cameras; six were model  
169 Bushnell Trophy Cam 119736C (Bushnell, Overland Park, Kansas), and the other 2 were Stealth  
170 Cam Unit IR (Stealth Cam, Grand Prairie, Texas). Cameras were located haphazardly along  
171 transects, installed at a height of 30-50cm and programmed to take videos 40 seconds long with a  
172 1-min delay between exposures. Locations of the cameras were chosen based on visibility, but

173 we did not seek animal trails (Rowcliffe et al. 2008). After 2-5 weeks, videos were downloaded  
174 and cameras were relocated along transects at new sites. The overall effort was of 1253 camera  
175 days (minimum camera days per transect=86; maximum=289; average=156.6).

176

177 In addition to camera-trapping, direct census of animals was conducted through a distance-  
178 sampling approach. The sampling was conducted using the same eight transects as with the  
179 camera traps, plus two extra transects (N=10) located in low-disturbance areas (Fig. 1). We  
180 walked the transects 3 to 5 times at an average speed of 2 km per hour recording all the terrestrial  
181 mammals and birds detected (sighted or heard), and their perpendicular distances to the transect.  
182 For further analyses, perpendicular distances were truncated at 0, 5, 10, 15, 20, 30, 50, 100 and  
183 150 m.

184

185 Data analysis

186

187 Study of habitat use

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189 To compare habitat use at high vs. low disturbance sites, for each of the most frequently captured  
190 animals (deer, pheasant, and boar) we calculated the relative abundance index (RAI). This index  
191 was calculated as the number of independent captures obtained through camera-trapping ( $C$ )  
192 divided by trapping effort (TE) and multiplied by 100 camera-days. We considered captures of  
193 the same species as independent only when there was a difference of at least one hour between  
194 captures of studied species.

195 
$$RAI = \frac{C}{TE * 100 \text{ camera - days}}$$

196

197 As the effective trapping area differs widely among species with different body size (Rowcliffe  
198 et al. 2011), RAI was not used to make comparisons between species.

199

200 Estimation of population density

201

202 Population density was estimated from distance sampling data (Buckland et al. 2007). The half-  
203 normal (HN), hazard-rate (HAZ) and exponential (EXP) key functions for detection probability  
204 were fitted to truncated data of distance. For species with over 30 sightings (*L. nycthemera* and  
205 *S. rubecula*), we used type of environment (plantation, forest and shrubland) as a covariate of  
206 detection probability and level of disturbance (high or low) as a covariate of density (Marques et  
207 al. 2007). For the other species we used no covariates. The Akaike Information Criterion (AIC)  
208 together with diagnostic plots were used to choose between models (Appendix 1).

209

210 For each species we conducted a regression of log observed cluster size vs. estimated detection  
211 probability to test for size bias (i.e. tendency to observe larger clusters at longer distances). In all  
212 cases, the regression slope was not significantly different from zero ( $P > 0.46$ ). We thus used  
213 mean observed cluster size as an estimate of expected cluster size to calculate animal densities.  
214 Cluster size data were obtained from camera trap videos.

215

## 216 **Results**

217

218 Habitat use

219

220 We obtained a total of 710 independent captures of 8 mammal and terrestrial bird species  
221 through camera trapping. The species detected included one native small mammal (*O.*  
222 *longicaudatus*), five non-native mammals (*C. elaphus*, *D. dama*, *S. scrofa*, *F. domesticus* and *N.*  
223 *vison*), one native bird (*S. rubecula*) and one non-native bird (*L. nycthemera*). The great majority  
224 of captures (99.7%) were of non-native animals (Fig. 2). The species detected most frequently  
225 were non-native deer (55.4% of captures including both species), *L. nycthemera* (31.2%), and *S.*  
226 *scrofa* (11.3%). We did not capture other native species reported in the island by Daciuk (1978b).  
227 Deer captures were identified at species level when possible (83% of captures; 65%  
228 corresponded to *C. elaphus* and 35% to *D. dama*).

229

230 At highly disturbed sites we detected seven species, while at low disturbance sites we observed  
231 five. The only species detected in low disturbance sites but not in highly disturbed regions was  
232 *N. vison*. Three species were detected only in highly disturbed regions: *F. domesticus*, *S.*  
233 *rubecula* and *O. longicaudatus* (but the last two had only one capture each). *Lophura*  
234 *nycthemera* was relatively more abundant in highly disturbed areas than in low disturbance areas  
235 (Pearson's chi-squared test,  $p=0.001$ ; Fig. 3), while relative abundance indices of deer and *S.*  
236 *scrofa* did not vary among sites.

237

238 Population density

239

240 We detected five terrestrial animals through direct censuses: *L. nycthemera*, *C. elaphus*, *D.*  
241 *dama*, *S. scrofa* and *S. rubecula*. For *L. nycthemera*, the best model fit was achieved by the

242 exponential key function, with type of environment as a covariate for detection and level of  
243 disturbance as a covariate for density. *Lophura nycthemera* density was nearly twice as high  
244 ( $1.79 \pm 0.52$  ind/ha) in highly disturbed areas than in low disturbance areas ( $0.99 \pm 0.42$  ind/ha).  
245 For *S. rubecula*, best fit model used the hazard rate key function and level of disturbance as a  
246 covariate for density. *S. rubecula* density was more than twice as high in low disturbance areas  
247 ( $0.73 \pm 0.19$  ind/ha) than in highly disturbed areas ( $0.32 \pm 0.12$  ind/ha). For deer, the best fit model  
248 used the hazard rate key function, and estimated density was  $0.12 \pm 0.05$  ind/hectare. For *S.*  
249 *scrofa*, the best fit model used the exponential key function and estimated density at  $0.27 \pm 0.16$   
250 ind/hectare.

251

## 252 Discussion

253

254 Our results show that at least six non-native species have successfully established on Isla  
255 Victoria and become dominant. By contrast, we found very few native species detections. Non-  
256 native deer (*C. elaphus* and *D. dama*), *S. scrofa*, and *L. nycthemera* were among the most  
257 abundant species on Isla Victoria, and only *L. nycthemera* showed greater abundance in highly  
258 disturbed areas than in low disturbance areas. While it is difficult to assess whether non-native  
259 species are displacing native species (because there is no quantitative information of native  
260 populations before non-native species introductions), it is likely that the successful establishment  
261 of the non-natives could have contributed to their decline.

262

263 The current assemblage of non-native animals on the island results from a combination of  
264 intentional and unintentional introductions of species and range expansions of invasive species

265 from the continent. Old World deer and pheasants, for example, were intentionally introduced.  
266 Non-native rodents present on the island may have been introduced unintentionally through  
267 transport in the hold of ships. Some species that are believed to have reached the island by  
268 expansion of their invading ranges are *S. scrofa* and *Neovison vison*.

269

270 Several factors can influence the likelihood that an introduced species will become established.

271 On Isla Victoria many factors such as species traits, propagule pressure, and climatic matching

272 have helped non-native species invasions. *Cervus elaphus*, *D. dama*, *S. scrofa*, *P. colchicus*, and

273 *N. vison* are known to have specific traits that make them good invaders in many regions (Table

274 3). In addition, the introduction of species bred in the zoological station was not a unique event,

275 but animals were released continuously for several years, increasing propagule pressure and

276 therefore increasing the likelihood of successful establishment (Lockwood et al. 2005).

277 Moreover, the area possibly offered an empty niche for some species (Azzurro et al. 2014). The

278 absence of big predators, for example, may have aided naturalization by non-native vertebrates.

279 Similarly, land birds in Patagonian forests are small in relation to non-native pheasants, which

280 may have different requirements. All these factors made Isla Victoria an ideal site for species

281 naturalization. As result of these multiple invasions, together with inadequate management, the

282 current assemblage of terrestrial mammals and birds on the island is highly dominated by non-

283 native species, in both composition and abundance.

284

285 Disturbance has long been cited as a factor that helps non-native species colonization and

286 invasion (Hobbs & Huenneke 1992). Thus, the association of non-native animals with highly-

287 disturbed areas such as conifer plantations could be facilitating the invasion of natural areas by

288 non-native herbivores (Lantschner et al. 2012). Our results showed that the only non-native  
289 animal that consistently associated with highly disturbed areas was *L. nycthemera*. *Cervus*  
290 *elaphus*, *D. dama* and *S. scrofa*, instead, made a similar use of low and high disturbance areas.  
291 Previous studies in the area showed that *C. elaphus* and *S. scrofa* prefer pine plantations instead  
292 of native vegetation at the landscape scale (Lantschner et al. 2012) and revealed a positive  
293 association of *S. scrofa* with roads (Gantchoff & Belant 2015). These results and our study thus  
294 suggest that deer, *S. scrofa*, and *L. nycthemera* are highly capable of using human-disturbed  
295 habitats. While deer and *S. scrofa* can also reach high abundances in native environments, and  
296 for instance have large impacts on native species inhabiting them, *L. nycthemera* may remain  
297 strongly associated with human-disturbed environments and scarce in native environments. *S.*  
298 *rubecula*, the only native land bird detected, was strongly associated with low disturbed  
299 environments. This could simply be due to the preference for native habitats (Lantschner &  
300 Rusch 2007), but it is also possible that the pheasant is displacing it from plantations.  
301 *Pteroptochos tarnii* coexists with *S. rubecula* in all areas surrounding Isla Victoria (Amico et al.  
302 2008), but it was not detected in this study. We hypothesize that both human disturbance and the  
303 presence of non-native species may be affecting *P. tarnii* abundance (Lantschner & Rusch 2007;  
304 Skewes et al. 2007).

305

306 One fact that can have a big impact on native biodiversity is the naturalization of non-native  
307 terrestrial carnivores, *N. vison* and *F. domesticus*, because the original assemblage of vertebrates  
308 on isla Victoria had no terrestrial carnivores (see Table 2). Thus, these species can have an  
309 important role as predators of birds and small mammals. A species that can be seriously affected  
310 by the naturalization of *N. vison* is imperial shag, *Phalacrocorax atriceps*, a species that nests at

311 steep rocky cliffs of the island and that is considered of special value by the National Park  
312 Service (Pozzi & Ramilo 2011). *Neovison vison* and *F. domesticus* can also be involved in the  
313 apparent local extinction of *P. tarnii* and can threat populations of other native ground-nesting  
314 birds such as *S. rubecula*.

315

316 We must take into account that the low number of native species detections may be partially  
317 explained by the low body mass of some species (*Dromiciops gliroides*, *Oligoryzomys*  
318 *longicaudatus*, *S. rubecula* and *P. tarnii*). Trap cameras have a bigger effective trapping area for  
319 species of higher body mass; for example in Barro Colorado Island studies found that effective  
320 detection distance is about 1.3m for species of low body mass (mouse unknown species, body  
321 mass=0.1kg) and about 3.5m for species of higher body mass (Collared peccary *Tayassu tajacu*,  
322 body mass=25.2kg) (Rowcliffe et al. 2011). However, camera-trapping has been used  
323 successfully for the study of small birds and mammals (Kays et al. 2011). In our study, through  
324 direct census *S. rubecula* was much more frequently detected -usually by its song - than big  
325 mammals, and estimated densities exceeded those of deer and *S. scrofa*. *P. tarnii*, however, also  
326 has an identifiable song but was never detected in direct censuses. Some evidence derived from  
327 mouse-trapping campaigns also suggests that small mammals are scarcer on Isla Victoria than on  
328 nearby continental areas of the National Park (Nuñez et al. 2013). We also understand that we  
329 are considering a snapshot of the abundance of terrestrial birds and mammals, although we  
330 believe this pattern is likely to be consistent in time.

331

332 It has been suggested that invasive species with no negative impacts on native biodiversity, can  
333 be beneficial because they can increase local biodiversity (Thomas & Palmer 2015) or supply



334 benefits such as habitat or food to native species (Davis et al. 2011). Some invasive species can  
335 also have an important role as dispersers of seeds of native species in their introduced range  
336 (Chimera & Drake 2010). On Isla Victoria *C. elaphus*, *S. scrofa* and *L. nycthemera* are  
337 consumers of fleshy fruits and might be contributing to seed dispersal of native plants. However,  
338 in our study site non-native species have reached such high proportions (see Fig. 2) that we can  
339 hypothesize they are displacing native fauna. The replacement of native fauna by non-native  
340 animals can have other important consequences for the functioning of local ecosystems. For  
341 example, on Isla Victoria, it has been demonstrated that non-native deer prefer native plants  
342 rather than non-natives, a fact that could promote the invasion by non-native conifers (Nuñez et  
343 al. 2008). The consumption of fruits of invasive shrubs by non-native animals, for example fruits  
344 of *Juniperus communis*, *Rosa rubiginosa* or *Rubus ulmifolius*, can be promoting plant invasions.  
345 Furthermore, soil disturbance by *S. scrofa* can facilitate invasive plant establishment (Barrios-  
346 Garcia & Simberloff 2013). Lastly, both *S. scrofa* and deer are involved in the dispersal of  
347 mycorrhizal fungi that allow colonization by non-native conifers (Nuñez et al. 2013).

348

349 It is difficult to know whether the presence of non-native animals was the driver of native species  
350 decline, but based on previous evidence it is likely that at least the successful establishment of  
351 the non-natives could have contributed to the decline of the natives. We believe this is likely  
352 based on the extremely low capture rate of native vertebrates (0.3% of camera-trapping captures)  
353 and the presence of species known to have reduced populations or extinguished species  
354 elsewhere (Table 3).

355

356 Recently, Nahuel Huapi National Park has started implementing a management plan for invasive

357 non-native vertebrates (Disposition 422/2014, Mujica 2014). Specifically, this plan regulates the  
358 control through hunting of *C. elaphus*, *D. dama*, and *S. scrofa* on Isla Victoria, Nahuel Huapi  
359 National Park. This program allowed the removal of more than 150 individuals during its first  
360 year of implementation (unpublished data), and it could represent a first step towards the  
361 recovering of native biodiversity on Isla Victoria. We suggest that monitoring through camera  
362 trapping using a sampling design similar to ours could be an economic way to evaluate the  
363 results of this program. Also, we strongly recommend that a plan for the control and eradication  
364 of non-native species on the island should also contemplate *N. vison* and *F. domesticus*, because  
365 of their role as predators of native fauna. Together with the monitoring of terrestrial fauna using  
366 camera-trapping, we suggest conducting a monitoring focused on small mammals (rodents and  
367 marsupials) using some array of live traps. In addition, active efforts to reintroduce native deer  
368 species as *P. pudu* and *H. bisulcus* could be highly beneficial for their global conservation, given  
369 that Isla Victoria has proved to be an ideal place for the acclimatization of herbivores, and that  
370 these two species are categorized as vulnerable and endangered respectively by the IUCN.  
371 Administrators of protected areas should also take measures to prevent the expansion of invasive  
372 species and the entrance of new ones to other regions of Nahuel Huapi National Park.

374 **Acknowledgments**

375

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381

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538 **Table 1: Introduced and naturalized terrestrial vertebrates on Isla Victoria.** List of  
 539 introduced and naturalized terrestrial vertebrates on Isla Victoria, Nahuel Huapi National Park;  
 540 their estimated date of introduction and current status. *Pudu pudu* was the only native species  
 541 introduced to the island.

Species	Estimated date of introduction	Current status on the island
Birds		
<i>Pavo cristatus</i>	1951-1959 (Daciuk 1978a)	Extinct
<i>Chrysolophus pictus</i>	1951-1959 (Daciuk 1978a)	Extinct
<i>Chrysolophus amhersti</i>	1951-1959 (Daciuk 1978a)	Extinct
<i>Lophura nycthemera</i>	1951-1959 (Daciuk 1978a)	Naturalized
<i>Phasianus colchicus</i>	1951-1959 (Daciuk 1978a)	Extinct
<i>Phasianus</i> sp.	1951-1959 (Daciuk 1978a)	Extinct
<i>Numida meleagris</i>	1951-1959 (Daciuk 1978a)	Extinct
Mammals		
<i>Rattus</i> sp.	Unknown (Daciuk 1978a)	Unknown
<i>Mus</i> sp.	Unknown (Daciuk 1978a)	Unknown
<i>Cervus elaphus</i>	1917-1922 (Daciuk 1978a)	Naturalized
<i>Cervus axis</i>	1917-1922 (Daciuk 1978a)	Extinct
<i>Dama dama</i>	1917-1922 (Daciuk 1978a)	Naturalized
<i>Pudu pudu</i> (native)	1951-1959 (Daciuk 1978a)	Extinct
<i>Sus scrofa</i>	~1999, natural spread from continent (Simberloff et al. 2003)	Naturalized
<i>Neovison vison</i>	Unknown, natural spread from continent (Pozzi & Ramilo 2011)	Naturalized
<i>Felis domesticus</i>	Unknown (Daciuk 1978a)	Naturalized (feral)

542

544 **Table 2: Original assemblage of native terrestrial vertebrates on Isla Victoria.** List of  
 545 species of the original assemblage of native terrestrial vertebrates on Isla Victoria, Nahuel Huapi  
 546 National Park according to historical records and their current status.

Species	Reference of historical records	Current status on Isla Victoria
Reptiles		
<i>Liolaemus spp.</i>	(Daciuk 1978b)	Present (personal observation)
<i>Tachymenis chilensis</i>	Not available	Present (personal observation)
Birds		
<i>Scelorchilus rubecula</i>	(Daciuk 1978b)	Present (this study)
<i>Pteroptochos tarnii</i>	(Daciuk 1978b)	Probably Extinct
Mammals		
<i>Dromiciops gliroides</i>	(Daciuk 1978b)	Present (D. Rivarola, personal communication)
<i>Oryzomys longicaudatus</i>	(Contreras 1973)	Present (this study)
<i>Irenomys tarsalis</i>	Not available	Present (D. Rivarola, personal communication)
<i>Hippocamelus bisulcus</i>	(Koutché 1942)	Extinct

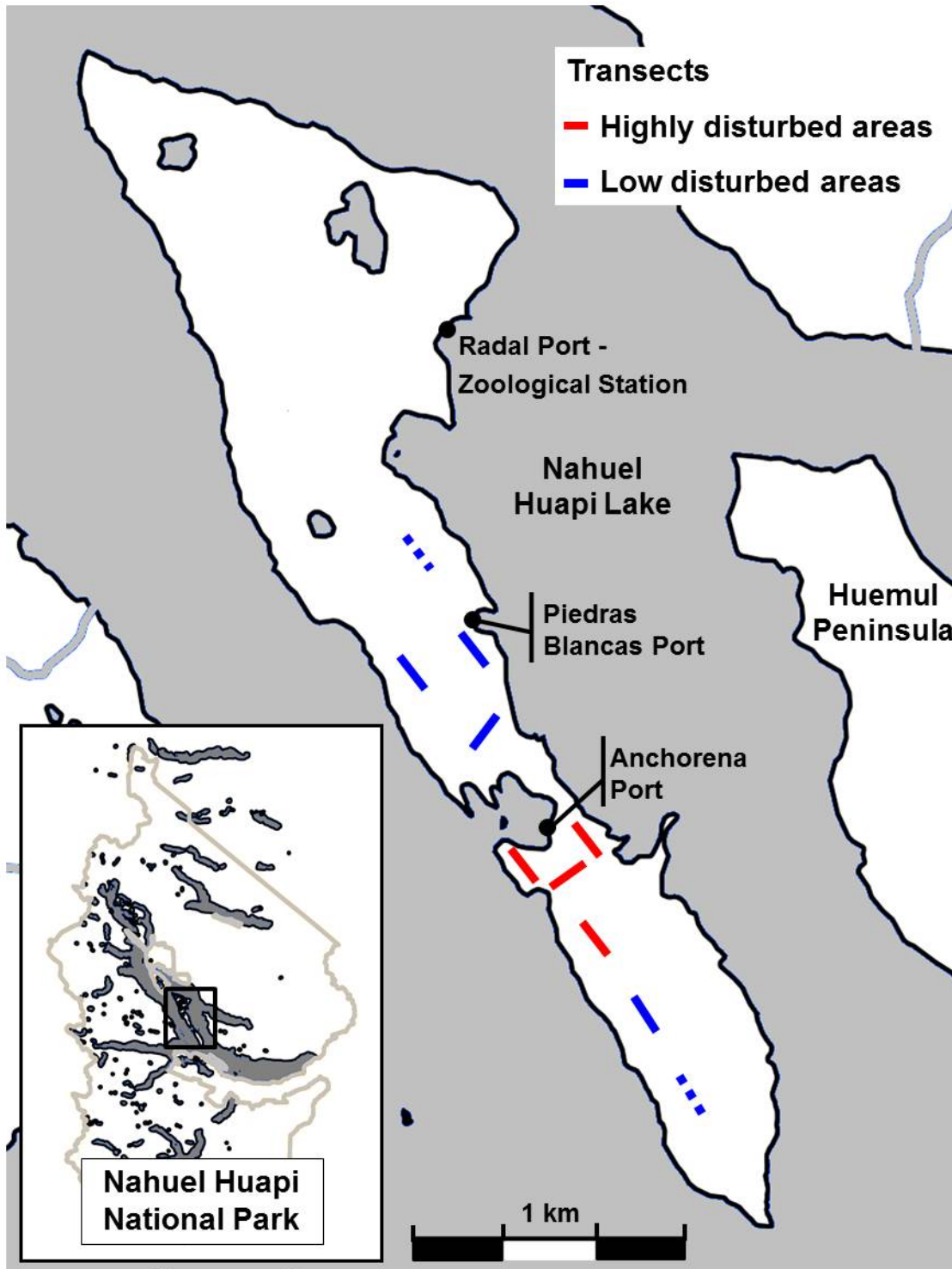
548 **Table 3: Antecedents of invasion of non-native species detected on Isla Victoria.** List of non-  
 549 native species detected on Isla Victoria and their known native range, invaded regions and  
 550 impacts reported.

Species	Native range	Invaded regions	Known impacts	Reference(s)
<i>Cervus elaphus</i>	Eurasia	North and South America, New Zealand and Australia	Impact on natural regeneration of the native forest and facilitation of non-native plant growth. Dispersal of non-native ectomycorrhizal fungi that promote Pinaceae invasions. Competitive displacement of native deer.	(Barrios-Garcia et al. 2012; Coomes et al. 2003; Nuñez et al. 2013; Nuñez et al. 2008; Relva et al. 2010; Wood et al. 2015)
<i>Dama dama</i>	Eurasia	North and South America, South Africa, New Zealand and Australia.	Impact on natural regeneration of the native forest and facilitation of non-native plant growth. Dispersal of non-native ectomycorrhizal fungi that promote Pinaceae invasions.	(Barrios-Garcia et al. 2012; Nuñez et al. 2013; Nuñez et al. 2008; Relva et al. 2010)

			Competitive displacement of native deer.	
<i>Sus scrofa</i>	Eurasia, north of Africa	Widely distributed worldwide, it is present on all continents except Antarctica, and many oceanic islands	Change in soil structure and processes, reduction of plant cover, decreasing of plant species diversity, alteration of plant species composition, predation of seeds of native species, increase of non-native plants abundance. Predation, nest and habitat destruction, and resource competition with other animals. Dispersal of non-native ectomycorrhizal fungi that promote Pinaceae invasions. Alteration of water quality and	(Barrios-Garcia & Ballari 2012; Barrios-Garcia et al. 2014; Barrios-Garcia & Simberloff 2013; Massei & Genov 2004; Nuñez et al. 2013)

			chemistry.	
<i>Lophura nycthemera</i>	Southeast Asia	Argentina and Germany	Competition with native fauna, seed dispersal of non-native plants.	(Daciuk 1978a; Lever 2005)
<i>Felis domesticus</i>	Domesticated from the Wildcat ( <i>F.s. lybica</i> ), probably 9-10,000 years ago in the Fertile Crescent region of the Near East.	Widely distributed worldwide, it is present on all continents except Antarctica, and many oceanic islands	Predation on native fauna including reptiles, birds and mammals. Responsible for many extinctions on oceanic islands.	(Driscoll et al. 2007; Loss et al. 2013; Medina et al. 2011; Woinarski et al. 2015)
<i>Neovison vison</i>	North America	Argentina, Chile, widely distributed throughout Eurasia	Predation on native fauna including mammals, birds, amphibia and Crustacea. Competition with native minks.	(Bonesi & Palazon 2007; MacDonald & Harrington 2003)

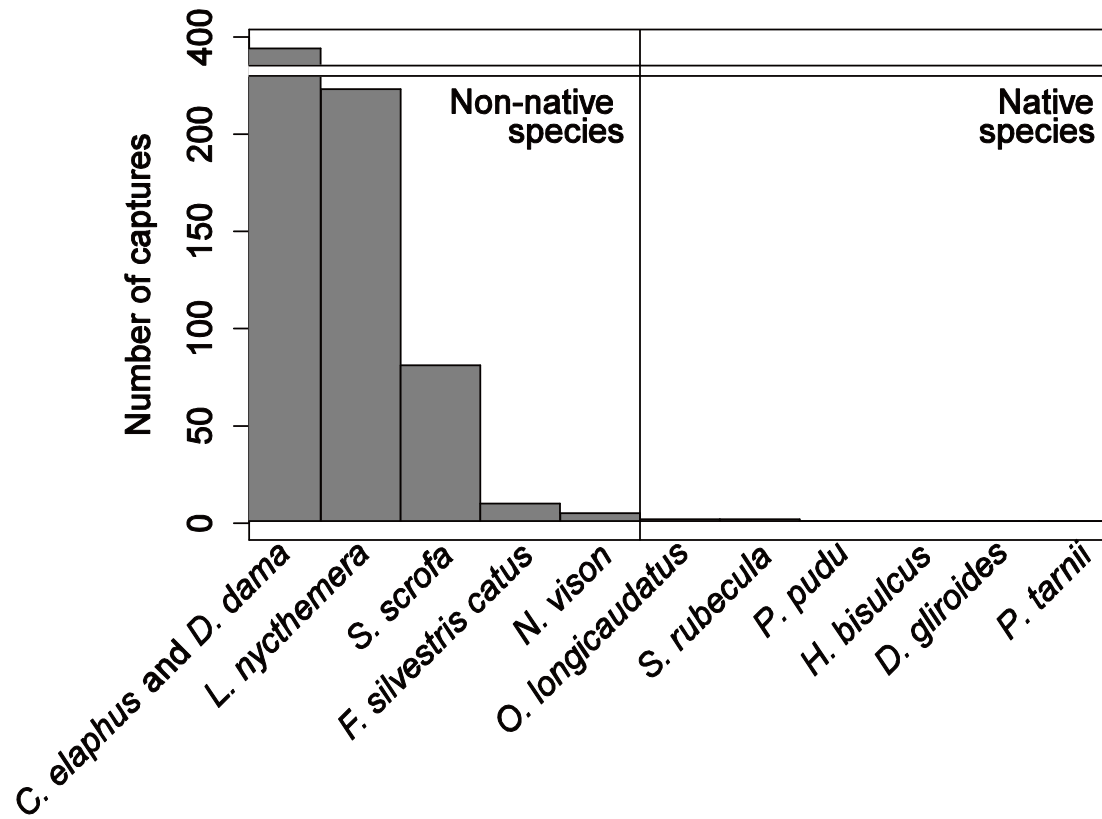
553 **Fig. 1: Study area.** Map of Isla Victoria showing the main ports and the transects for camera  
554 trapping and censuses. A solid line indicates that both camera trapping and censuses were  
555 conducted; a dashed line indicates that only direct censuses were conducted.



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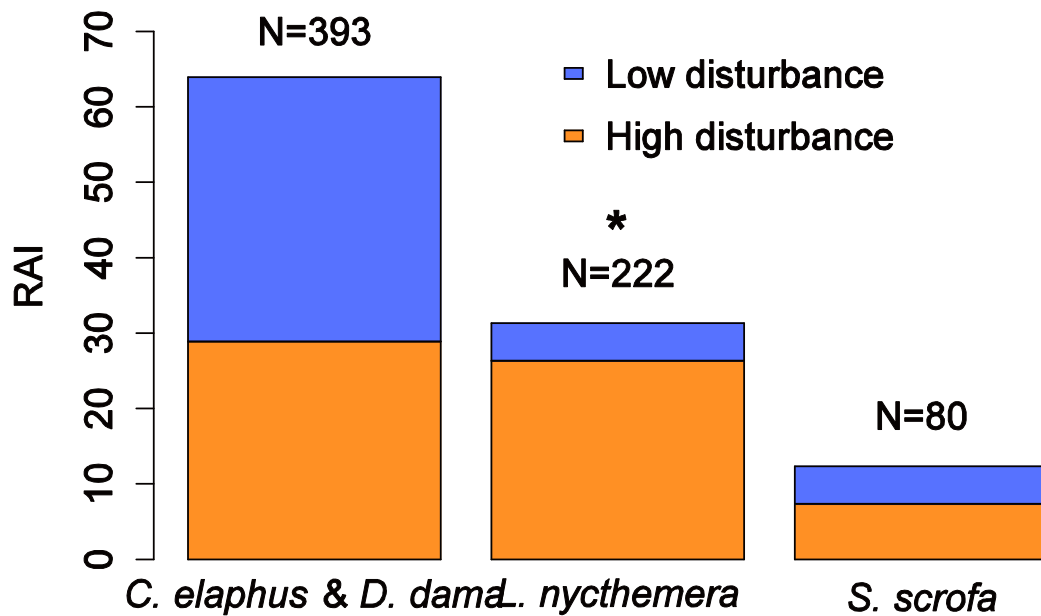


557 **Fig. 2: Camera trapping captures of terrestrial species.** Total number of captures  
558 obtained by camera trapping for each terrestrial species, including species reported for  
559 the island in Daciuk (1978b) and not detected in this study.



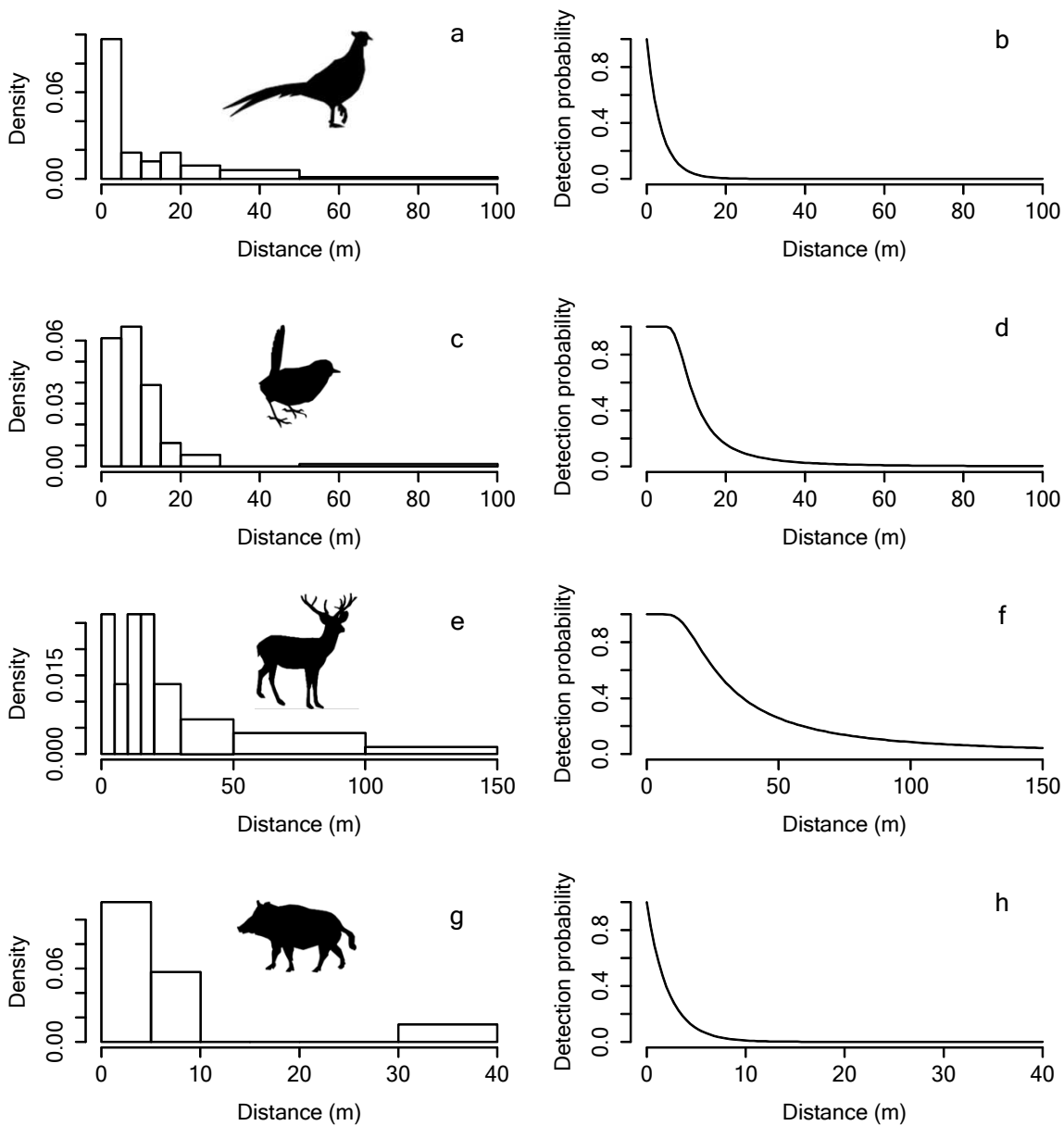
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562 **Fig. 3: Habitat use.** Relative abundance index (RAI) for the four species most frequently  
563 captured in areas with high and low levels of disturbance. Ns represent the total number of  
564 captures obtained for each species. An asterisk indicate species with differential use of low and  
565 high-disturbed habitats.



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568 **Fig. 4: Detectability of animals.** Histograms of observed distances and fitted detection functions  
569 for *L. nycthemera* (a and b respectively, N=33), *S. rubecula* (c and d, N=36), *C. elaphus* and *D.*  
570 *dama* (e and f, N=15), and *S. scrofa* (g and h, N=7).



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**Table 1** (on next page)

Introduced and naturalized terrestrial vertebrates on Isla Victoria

List of introduced and naturalized terrestrial vertebrates on Isla Victoria, Nahuel Huapi National Park; their estimated date of introduction and current status. *Pudu pudu* was the only native species introduced to the island.

Species	Estimated date of introduction	Current status on the island
Birds		
<i>Pavo cristatus</i>	1951-1959 (Daciuk 1978a)	Extinct
<i>Chrysolophus pictus</i>	1951-1959 (Daciuk 1978a)	Extinct
<i>Chrysolophus amhersti</i>	1951-1959 (Daciuk 1978a)	Extinct
<i>Lophura nycthemera</i>	1951-1959 (Daciuk 1978a)	Naturalized
<i>Phasianus colchicus</i>	1951-1959 (Daciuk 1978a)	Extinct
<i>Phasianus</i> sp.	1951-1959 (Daciuk 1978a)	Extinct
<i>Numida meleagris</i>	1951-1959 (Daciuk 1978a)	Extinct
Mammals		
<i>Rattus</i> sp.	Unknown (Daciuk 1978a)	Unknown
<i>Mus</i> sp.	Unknown (Daciuk 1978a)	Unknown
<i>Cervus elaphus</i>	1917-1922 (Daciuk 1978a)	Naturalized
<i>Cervus axis</i>	1917-1922 (Daciuk 1978a)	Extinct
<i>Dama dama</i>	1917-1922 (Daciuk 1978a)	Naturalized
<i>Pudu pudu</i> (native)	1951-1959 (Daciuk 1978a)	Extinct
<i>Sus scrofa</i>	~1999, natural spread from continent (Simberloff et al. 2003)	Naturalized
<i>Neovison vison</i>	Unknown, natural spread from continent (Pozzi & Ramilo 2011)	Naturalized
<i>Felis domesticus</i>	Unknown (Daciuk 1978a)	Naturalized (feral)

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**Table 2** (on next page)

Original assemblage of native terrestrial vertebrates on Isla Victoria

List of species of the original assemblage of native terrestrial vertebrates on Isla Victoria, Nahuel Huapi National Park according to historical records and their current status.

Species	Reference of historical records	Current status on Isla Victoria
Reptiles		
<i>Liolaemus spp.</i>	(Daciuk 1978b)	Present (personal observation)
<i>Tachymenis chilensis</i>	Not available	Present (personal observation)
Birds		
<i>Scelorchilus rubecula</i>	(Daciuk 1978b)	Present (this study)
<i>Pteroptochos tarnii</i>	(Daciuk 1978b)	Probably Extinct
Mammals		
<i>Dromiciops gliroides</i>	(Daciuk 1978b)	Present (D. Rivarola, personal communication)
<i>Oryzomys longicaudatus</i>	(Contreras 1973)	Present (this study)
<i>Irenomys tarsalis</i>	Not available	Present (D. Rivarola, personal communication)
<i>Hippocamelus bisulcus</i>	(Koutché 1942)	Extinct

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**Table 3** (on next page)

Antecedents of invasion of non-native species detected on Isla Victoria

List of non-native species detected on Isla Victoria and their known native range, invaded regions and impacts reported.



Species	Native range	Invaded regions	Known impacts	Reference(s)
<i>Cervus elaphus</i>	Eurasia	North and South America, New Zealand and Australia	Impact on natural regeneration of the native forest and facilitation of non-native plant growth. Dispersal of non-native ectomycorrhizal fungi that promote Pinaceae invasions. Competitive displacement of native deer.	(Barrios-Garcia et al. 2012; Coomes et al. 2003; Nuñez et al. 2013; Nuñez et al. 2008; Relva et al. 2010; Wood et al. 2015)
<i>Dama dama</i>	Eurasia	North and South America, South Africa, New Zealand and Australia.	Impact on natural regeneration of the native forest and facilitation of non-native plant growth. Dispersal of non-native ectomycorrhizal fungi that promote Pinaceae invasions. Competitive displacement of native deer.	(Barrios-Garcia et al. 2012; Nuñez et al. 2013; Nuñez et al. 2008; Relva et al. 2010)
<i>Sus scrofa</i>	Eurasia, north of	Widely distributed	Change in soil	(Barrios-Garcia &

	Africa	worldwide, it is present on all continents except Antarctica, and many oceanic islands	structure and processes, reduction of plant cover, decreasing of plant species diversity, alteration of plant species composition, predation of seeds of native species, increase of non-native plants abundance. Predation, nest and habitat destruction, and resource competition with other animals. Dispersal of non-native ectomycorrhizal fungi that promote Pinaceae invasions. Alteration of water quality and chemistry.	Ballari 2012; Barrios-Garcia et al. 2014; Barrios-Garcia & Simberloff 2013; Massei & Genov 2004; Nuñez et al. 2013)
<i>Lophura nycthemera</i>	Southeast Asia	Argentina and Germany	Competition with native fauna, seed dispersal of non-	(Daciuk 1978a; Lever 2005)

			native plants.	
<i>Felis domesticus</i>	Domesticated from the Wildcat ( <i>F.s. lybica</i> ), probably 9-10,000 years ago in the Fertile Crescent region of the Near East.	Widely distributed worldwide, it is present on all continents except Antarctica, and many oceanic islands	Predation on native fauna including reptiles, birds and mammals. Responsible for many extinctions on oceanic islands.	(Driscoll et al. 2007; Loss et al. 2013; Medina et al. 2011; Woinarski et al. 2015)
<i>Neovison vison</i>	North America	Argentina, Chile, widely distributed throughout Eurasia	Predation on native fauna including mammals, birds, amphibia and Crustacea. Competition with native minks.	(Bonesi & Palazon 2007; MaCdonald & Harrington 2003)

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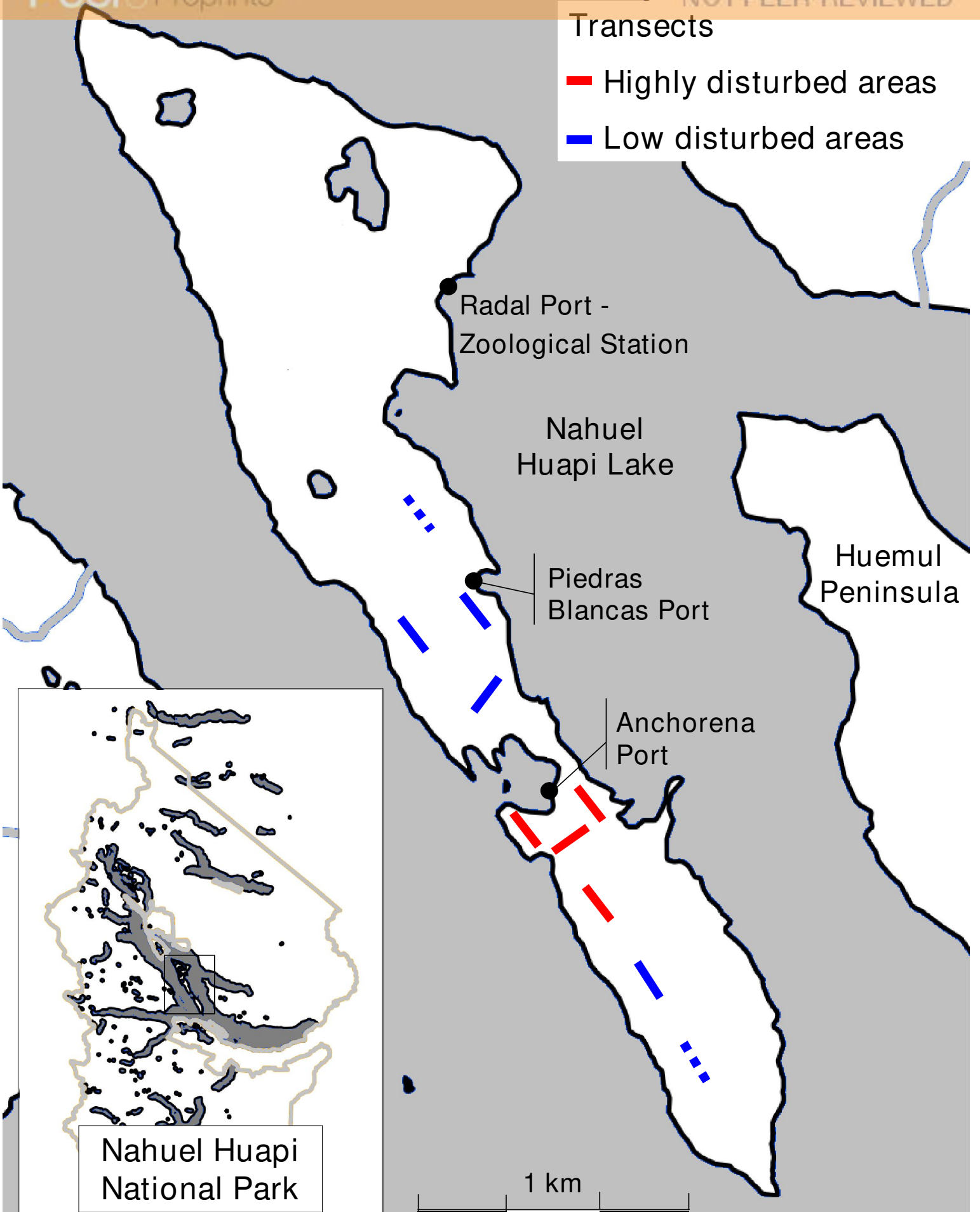
**Figure 1** (on next page)

## Study area

Map of Isla Victoria showing the main ports and the transects for camera trapping and censuses. A solid line indicates that both camera trapping and censuses were conducted; a dashed line indicates that only direct censuses were conducted.

Transects

- Highly disturbed areas
- Low disturbed areas



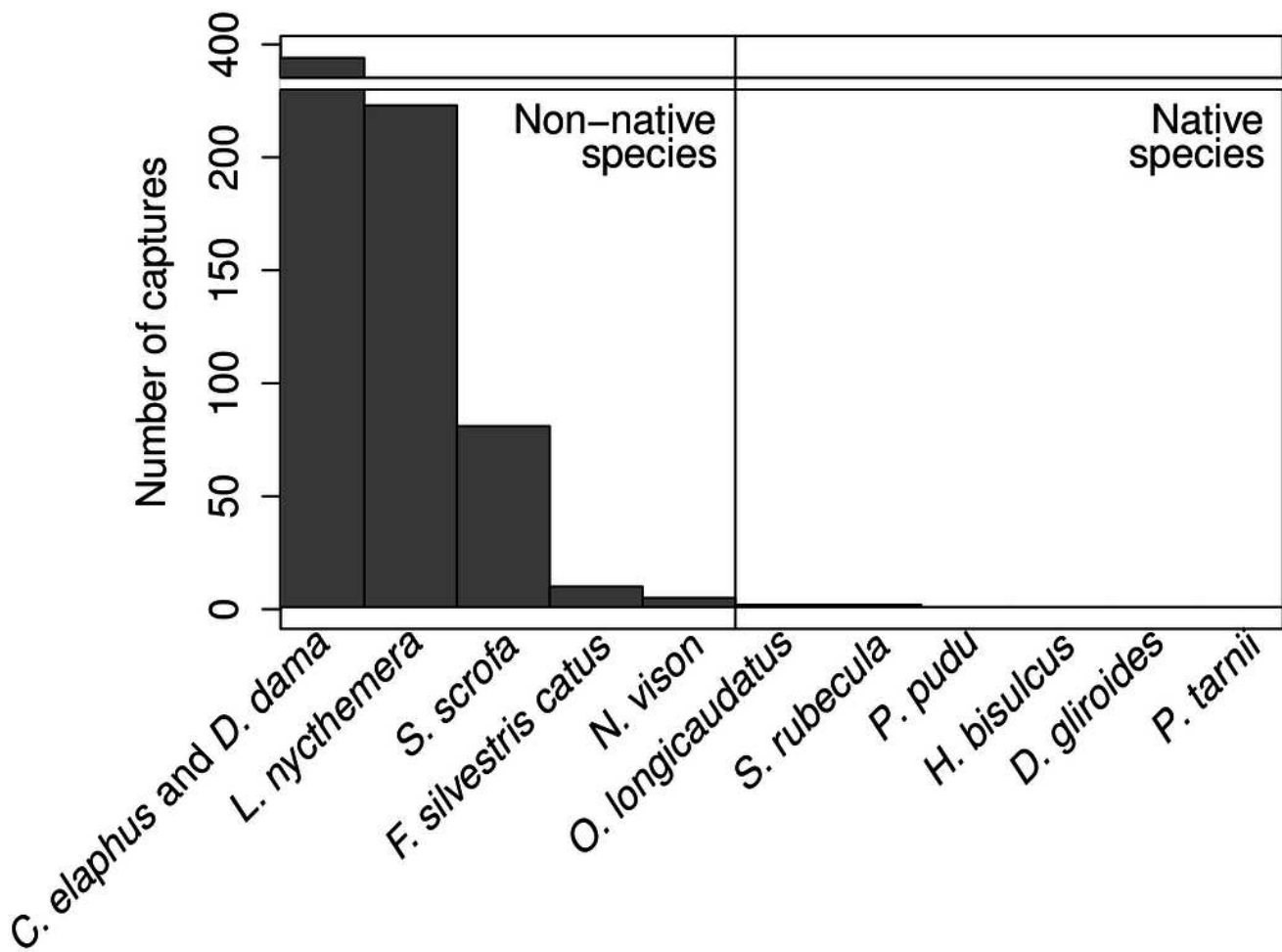
Nahuel Huapi National Park

1 km

## 2

## Camera trapping captures of terrestrial species

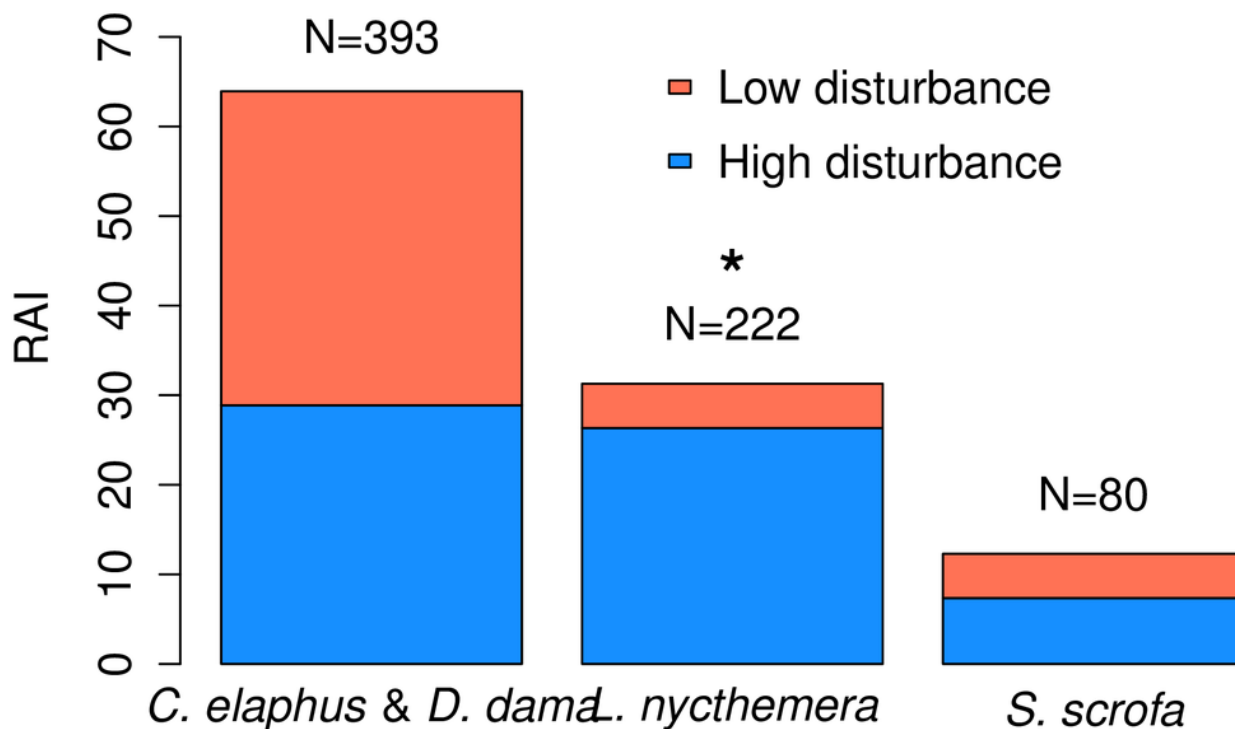
Total number of captures obtained by camera trapping for each terrestrial species, including species reported for the island in Daciuk (1978b) and not detected in this study.



## 3

## Habitat use

Relative abundance index (RAI) for the four species most frequently captured in areas with high and low levels of disturbance. Ns represent the total number of captures obtained for each species. An asterisk indicate species with differential use of low and high-disturbed habitats.



# 4

## Detectability of animals

Histograms of observed distances and fitted detection functions for *L. nycthemera* (a and b respectively, N=33), *S. rubecula* (c and d, N=36), *C. elaphus* and *D. dama* (e and f, N=15), and *S. scrofa* (g and h, N=7).



