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Modeling the spatial structure of the endemic mara (*Dolichotis patagonum*) across modified landscapes

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Across modified landscapes anthropic factors can affect habitat selection by animals and consequently their abundance and distribution patterns. The study of the spatial structure of wild populations is crucial to gain knowledge on species' response to habitat quality, and a key for the design and implementation of conservation actions. This is particularly important for a low-density and widely distributed species such as the mara (*Dolichotis patagonum*), a large rodent endemic of Argentina across the Monte and Patagonian drylands where extensive sheep ranching predominates. We aimed to assess the spatial variation in the abundance of maras and to identify the natural and anthropic factors influencing the observed patterns in Península Valdés, a representative landscape of Patagonia. We conducted ground surveys during the austral autumn from 2015 to 2017. We built density surface models to account for the variation in mara abundance, and obtained a map of mara density at a resolution of 4 km². We estimated an overall density of 0.93 maras.km⁻² for the prediction area of 3476 km². The location of ranch buildings, indicators of human presence, had a strong positive effect on the abundance of maras, while the significant contribution of the geographic longitude suggested that mara density increases with higher rainfall. Although human presence favored mara abundance, presumably by providing protection against predators, it is likely that the association could bring negative consequences for maras and other species. The use of spatial models allowed us to provide the first estimate of mara abundance at a landscape scale and its spatial variation at a high resolution. Our approach can contribute to the assessment of mara population abundance and the factors shaping its spatial structure elsewhere across the species range, all crucial attributes to identify and prioritize conservation actions.

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MODELING THE SPATIAL STRUCTURE OF THE ENDEMIC MARA (*DOLICHOTIS PATAGONUM*) ACROSS MODIFIED LANDSCAPES

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13 **ABSTRACT**

14 Across modified landscapes anthropic factors can affect habitat selection by animals and
15 consequently their abundance and distribution patterns. The study of the spatial structure of wild
16 populations is crucial to gain knowledge on species' response to habitat quality, and a key for the
17 design and implementation of conservation actions. This is particularly important for a low-
18 density and widely distributed species such as the mara (*Dolichotis patagonum*), a large rodent
19 endemic of Argentina across the Monte and Patagonian drylands where extensive sheep ranching
20 predominates. We aimed to assess the spatial variation in the abundance of maras and to identify
21 the natural and anthropic factors influencing the observed patterns in Península Valdés, a
22 representative landscape of Patagonia. We conducted ground surveys during the austral autumn
23 from 2015 to 2017. We built density surface models to account for the variation in mara
24 abundance, and obtained a map of mara density at a resolution of 4 km². We estimated an overall

25 density of 0.93 maras.km⁻² for the prediction area of 3476 km². The location of ranch buildings,
26 indicators of human presence, had a strong positive effect on the abundance of maras, while the
27 significant contribution of the geographic longitude suggests that mara density increases with
28 higher rainfall. Although human presence favored mara abundance, presumably by providing
29 protection against predators, it is likely that the association could bring negative consequences
30 for maras and other species. The use of spatial models allowed us to provide the first estimate of
31 mara abundance at a landscape scale and its spatial variation at a high resolution. Our approach
32 can contribute to the assessment of mara population abundance and the factors shaping its spatial
33 structure elsewhere across the species range, all crucial attributes to identify and prioritize
34 conservation actions.

35 INTRODUCTION

36
37 Habitat selection has been defined as the process by which individuals use or occupy a non-
38 random set of available habitats, and depends on the particular requirements of a given species or
39 population, the availability of resources and the ability of individuals to exploit those resources
40 (Morris, 2003). In addition, the patterns of habitat selection influence population dynamics
41 through differences in survival and breeding success across habitats types (Pulliam and
42 Danielson, 1991). Thus, variation in habitat quality (i.e the different combinations of physical
43 and biotic conditions affecting individual fitness) will be reflected in the variation in population
44 density (Bradshaw et al., 1995; Mayor et al., 2009). Across modified landscapes, both natural
45 and human-related factors are known to influence the abundance and distribution of wild species,
46 as changes imposed by human activities can favor or limit species' presence and subsequently
47 affect biodiversity at a given area (Hansson et al., 1995). Therefore, reliable models accounting
48 for the spatial variation in the abundance of wild populations are crucial to gain knowledge on

49 species' response to habitat quality, and subsequently to the implementation of conservation
50 actions (Fischer and Lindenmayer, 2006).

51 The Mara (*Dolichotis patagonum*) is a large caviomorph rodent endemic of Argentina, widely
52 distributed across the arid lands of the Monte and Patagonian steppe ecoregions (Taber, 1987;
53 Kufner and Chambouleyron, 1991; Campos et al., 2001). In Patagonia, pioneering work
54 conducted by Taber (1987), Taber and MacDonald (1992a, 1992b) showed that maras are
55 monogamous and breed communally, an unusual combination among mammals. Maras dig
56 breeding dens which are occupied exclusively by the young until they are 6 - 8 weeks old (Taber
57 and MacDonald, 1992a; Baldi, 2007). Although there are studies suggesting that open sites (i.e.
58 dominated by grasses and herbs or bare soil) and the proximity to ranch buildings would favor
59 the presence of maras, the research was focused on the location of breeding warrens, in particular
60 the occurrence of communal dens (Taber and MacDonald, 1992a; Baldi, 2007; Alonso Roldán
61 and Baldi, 2016) and habitat use by individuals around the breeding sites (Taber and MacDonald,
62 1992b; Rodríguez, 2009; Alonso Roldán et al., 2017). The mara has been assessed as a "Near
63 Threatened" species by the International Union for the Conservation of Nature (Roach, 2016), as
64 its global population has been reported to be dwindling due to habitat loss. Although estimates of
65 population abundance and distribution were identified as the main research priorities (Roach,
66 2016), the available estimates of abundance are restricted to particular dens surveyed intensively
67 during the breeding season (Taber and MacDonald, 1992a; Baldi, 2007; Alonso Roldán et al.,
68 2015), while estimates of abundance and distribution at a population scale in relation to habitat
69 variables are lacking.

70 Our aim in this work was to account for the spatial variation in the abundance of maras at a
71 population scale in Península Valdés, a representative area of the arid Patagonia where wild

72 species share the range with human activities. We used density surface models (DSM, Miller et
73 al., 2013) which combine survey methodologies with mathematical models to obtain reliable
74 estimates of abundance, while identifying the main factors related to its spatial variation. We
75 hypothesize that both natural and human-related variables shape the spatial variation in the
76 abundance of maras throughout the area. We predict that higher plant productivity, heterogeneity
77 in vegetation structure, and flat terrain will all positively affect the number of maras. Regarding
78 human-related factors, the proximity to infrastructure such as ranch buildings will favor the
79 occurrence of maras and affect their spatial structure at the population scale, while high sheep
80 stocking rates are a disturbance which will result in decreased numbers of maras.

81 **MATERIALS AND METHODS**

82 The present work is a non-invasive study, conducted through the observation of animals by
83 means of binoculars. Permission for the research was given by the Direction of Conservation and
84 Protected Areas, and the Direction of Wildlife of the Province Chubut (DF & FS-SSG, Permits
85 71/2014, 73/2015, and 69/2016).

86 **Study site**

87 The study was conducted at Peninsula Valdés (PV), located in the Argentine Patagonia (Fig. 1), a
88 provincial protected area and also a UNESCO World Heritage Site since 1999. The climate of
89 PV is temperate semi-arid with a mean annual temperature of 13.6 °C, while annual precipitation
90 averages 230 mm with a high interannual variation (Coronato et al., 2017). The vegetation is
91 characteristic of the southern Monte Phytogeographic Province, but sharing plant species with
92 the northern Patagonian Province (León et al., 1998). Shrubs and grass-shrubs steppes dominate
93 northern and central PV with a vegetation cover that varies between 40 and 60 %, while grass
94 steppes predominate in the southern part of the area with an average cover of 70 % (Fig. 1;

95 Bertiller et al., 2017). The most common shrub species are *Chuquiraga avellanedae* and
96 *Chuquiraga erinacea*, while the most abundant perennial grasses are *Nassella tenuis*,
97 *Piptochaetium napostaence* and *Sporobolus rigens* (Bertiller et al., 2017).
98 Extensive sheep ranching for wool production occupies most of the land, which is divided by
99 fences into more than 60 properties. Each ranch is subsequently fenced into paddocks of 1000 -
100 2500 ha where the sheep graze on the native vegetation. There is usually one building per ranch
101 permanently occupied by a rural worker, and occasionally an outstation which may be inhabited
102 temporarily.

103 **Field surveys**

104 We conducted ground, line transect surveys (Buckland et al., 1993; Laake et al., 1993) of maras
105 during the austral autumn of 2015, 2016 and 2017 totaling 1085.4 km surveyed along secondary
106 dirt-roads and tracks, spaced by at least 1 km among contiguous tracks. Surveys were conducted
107 during the non-breeding period in order to maximize the number of observations, as maras tend
108 to be aggregated around communal dens during the breeding season (Taber, 1987; Baldi, 2007);
109 and to prevent possible biases in the abundance estimates due to pup mortality associated to the
110 breeding season (estimated around 55% of the pups born between August and December; Baldi,
111 2007). All surveys were conducted from an open pick-up vehicle, traveling at a maximum speed
112 of 25 km.h⁻¹, with two observers standing in the back. For every group of maras detected (one or
113 more individuals) we stopped the vehicle, counted the number of animals by means of
114 binoculars, recorded the perpendicular distance from the transect line to the location where the
115 group was standing at the time it was detected, using a laser rangefinder (Bushnell Yardage Pro
116 1000), and recorded our location and the angle relative to the group of animals using a portable
117 GPS (Garmin Oregon 550, Garmin, Olathe, KS, USA).

118 **Estimating the detection function**

119 Using standard distance sampling methodology (Buckland et al., 1993), we fitted a detection
120 function $g(y)$ to account for the probability of detecting maras. The detection model assumes that
121 all groups were detected at zero distance from the transect line, with detectability decreasing
122 with increasing distance from the line (Buckland et al., 2001). We evaluated the half-normal and
123 hazard-rate functions as candidate detection functions. The effect of data truncation (removal of
124 the 10% of the sightings corresponding to the most extreme distance values; Thomas et al., 2010)
125 was evaluated by analyzing the Q-Q plots and the Cramer-von Mises test for both candidates.
126 Then, we analyzed the effect of the group size as a covariate, and chose the best model by using
127 the Akaike Information Criterion (AIC, Burnham and Anderson, 2002), the Q-Q plots and the
128 Cramer-von Mises test. All analyses were performed using the ‘Distance’ package version 0.9.7
129 (Miller, 2017) for R.

130 **Predictor selection**

131 According to our hypothesis, we identified natural and anthropic variables as potential predictors
132 of mara abundance (Table 1). Additionally, we included the geographic latitude and longitude as
133 proxy variables to account for possible remaining variation (Table 1). As a correlate of primary
134 productivity, we calculated the mean values of the Normalized Difference Vegetation Index
135 (NDVI) for the spring-summer seasons (from September 21st to March 21st) of the years 2014-
136 2015, 2015-2016 and 2016-2017 according to the field surveys. As some areas of PV are a
137 mosaic of vegetation types, we found that a continuous variable such as the coefficient of
138 variation (CV) of the NDVI was better to represent changes in vegetation physiognomy than a
139 categorical variable. Thus, we calculated the CV of the NDVI between 2010 and 2014 to account
140 for variation in vegetation physiognomy, and found that it was larger across shrub steppes than in

141 mixed and grass steppes (see Supplemental Information SI1). The variables derived from the
142 NDVI were based on MODIS MOD13Q1 satellite images of 250 m spatial resolution available at
143 <https://lpdaac.usgs.gov>. Values of CV of altitude were obtained from the Digital Elevation
144 Model for South America (resolution of about 220 m) at <https://lta.cr.usgs.gov/SRTM1Arc>.
145 Updated numbers of sheep per paddock were obtained by asking owners and workers of the
146 ranches during the field surveys. Data on the location of ranch buildings was available at our
147 institute but it was also checked and updated in the field while working across PV between 2015
148 and 2017. We obtained the values for each variable using the QGIS Open Source Geographic
149 Information System (QGIS, version 2.16 Development Team 2016) and packages rshape2
150 version 1.4.2 (Wickham, 2007), raster version 2.5.8 (Hijmans et al., 2016) and ggplot2
151 version 2.2.1 (Wickham and Chang 2016; R software, version 3.2.1, Development Core Team
152 2015). The range of values of each variable across the study area was included as far as possible
153 in the surveyed tracks. Multicollinearity in predictor variables could make difficult to separate
154 the effects on the response variable and to compare alternative models (Lennon, 1999), so we
155 evaluated the collinearity between pairs of covariates taking the values measured at each
156 segment (see below, “*Density surface model (DSM)*”). We considered two predictors not to be
157 collinear when Pearson’s correlation coefficients were < 0.7 .

158 **Density surface model (DSM)**

159 Following Miller et al., (2013) and DSM methodology, each transect line was divided into
160 smaller segments of 1.8 km in length, totaling 603 segments. Subsequently, each observation
161 was assigned to its segment according to its location. Given that there were no covariates other
162 than distance in the detection function, the probability of detection (p) was constant for all
163 segments. Therefore, we estimated mara abundance per segment (n) by the ‘count method’

164 (Hedley and Buckland, 2004). In this way, the number of maras seen in each segment was
165 described by a generalized additive model (e.g., Wood, 2006) as the sum of smooth functions of
166 uncorrelated predictor variables measured at the segment.

$$167 \quad E(\hat{n}_j) = \hat{p} A_j \exp \left[\beta_0 + \sum_k f_k(z_{jk}) \right]$$

168 Where $E(\hat{n}_j)$ is the expected number of maras in the j th segment, \hat{p} is the estimated probability of
169 detection of maras, A is the segment area, z_{jk} is the value of covariate k in segment j , while f_k
170 represents the smooth function of the spatial covariate k and β_0 is an intercept term. We used
171 Restricted Maximum Likelihood (REML) for smoothness selection (Reiss and Ogden, 2009;
172 Wood, 2011). The concurvity of the smooth term (Wood, 2006) was evaluated to guarantee that
173 any smooth term could be approximated by one or more of the other smooth terms in the model.
174 We tested three response distributions including: Tweedie, negative binomial, and quasi-Poisson.
175 For each distribution we built a “base model” considered all the covariates as univariate smooths.
176 We performed the covariate selection in each base model by removing the non significant
177 covariates (with P approximate < 0.01 ; Marra and Wood, 2011), and included an additional
178 penalty for each smooth term, which allowed to decreased their degrees of freedom below 1
179 (Wood, 2006; section 4.1.6; Wood, 2011). Therefore we obtained three models as final
180 candidates (Table 2) and subsequently we selected the best-fit model based on the inspection of
181 residual plots. Models were fitted using the ‘dsm’ package version 2.2.12 (Miller et al., 2017) for
182 R. Residual autocorrelation was checked by inspecting the correlogram, which showed the
183 behaviour of the correlation between segments at a series of lags. Models were fitted using
184 the ‘dsm’ package version 2.2.12 (Miller et al., 2017) for R.

185 **Abundance and variance estimation**

186 We overlaid a grid of 4 km² cells to our study area, obtaining a prediction area of 3476 km².
187 Based on the cell covariates values we predicted the number of maras for each cell resulting from
188 the selected DSM, and subsequently obtained an overall estimate of abundance for PV. The
189 uncertainty associated to the estimation was calculated by using the variation propagation
190 method (Williams et al., 2011). Thus, we obtained the variance in the abundance of maras for
191 each 4 km² cell.

192 RESULTS

193 We recorded 119 sightings of maras (0.11 observations.km⁻¹) comprising a total of 316
194 individuals, averaging 2.65 ± 0.28 individuals per observation ($\bar{X} \pm SE$). The detection function
195 selected was the half normal (Fig. 2) with a truncation distance at 304 m from the transect line in
196 order to remove the extreme 10% of the sightings and improve data fitting (Thomas et al., 2010).
197 After truncation 107 sightings were kept, a higher number than the minimum of 80 observations
198 recommended for modeling clustered objects (Buckland et al., 2001).

199 The variables CV of NDVI and geographic latitude showed collinearity ($|r| > 0.7$), thus we kept
200 the former due to its ecological significance. The concurvity measures were very small
201 suggesting negligible concurvity (Wood, 2006; available as Supplemental Information SI2).

202 Overall population density estimated by the DSM was 0.93 maras.km⁻² (CV = 15%, Table 2) for
203 the 3476 km² prediction area (Fig. 3). Lowest densities (< 0.45 ind.km⁻²) were mainly
204 concentrated in the central and western areas of the Peninsula (Fig. 3), while the highest densities
205 (> 0.93 ind.km⁻²) were estimated for the eastern zone. The coefficient of variation associated
206 with the abundance estimation per cell showed a heterogeneous pattern (Fig. 4).

207 Statistically significant variables ($p < 0.01$) of the selected DSM were the distance to the nearest
208 ranch building ($p = 5.96 \times 10^{-9}$) and the geographic longitude ($p = 0.001$; Table 2). The

209 abundance of maras had non linear relationship with the significant predictors. The confidence
210 intervals of the smooth function of the predictor variables tended to be wider where the range of
211 the variables had reduced survey coverage (Fig. 5). Increasing distance to the nearest ranch
212 building showed a marked decrease in mara abundance within the range of 4000 m (Fig. 5A),
213 while the geographic longitude showed a positive effect from the central area of the PV to the
214 eastern coast. (Fig. 5B). A small amount of unmodelled correlation in residuals was observed
215 between adjacent segments in the fitted model (see Supplemental Information SI3).

216 **DISCUSSION**

217 Human dwellings are key in habitat selection by maras and strongly related to the species'
218 abundance in Península Valdés. Also, it is the only human-related factor explaining the spatial
219 structure of the mara population. Although the main results do not contradict our hypothesis
220 about natural and anthropic factors involved in mara habitat selection, only the geographic
221 longitude could reflect some variation in environmental conditions, while predictive variables
222 related to plant productivity, vegetation physiognomy and topography did not show significant
223 effects in the abundance of maras.

224 Human presence – represented by the distance to inhabited ranch buildings – favored the
225 increase in mara abundance throughout the modified landscape of Península Valdés. Previous
226 studies conducted at a local scale, focused on particular warrens during the breeding season,
227 suggested that maras would gain protection from predators as the ranchers usually kill carnivores
228 like the puma (*Puma concolor*), grey and culpeo foxes (*Lycalopex gymnocercus* and *Lycalopex*
229 *culpaeus*), and smaller cats (*Leopardus geoffroyi* and *Leopardus colocolo*) in order to protect
230 their sheep (Taber and McDonald, 1992a; Rodríguez, 2009; Rivas et al., 2015; Alonso Roldán
231 and Baldi, 2016). Therefore, the proximity to inhabited ranch buildings could represent safe

232 areas with low risk of predation for *Dolichotis patagonum* and likely this is reflected at a
233 population scale.

234 It is known that human activity can alter the interactions between mammalian carnivores and
235 their prey species (Berger et al., 2001; Schuette et al., 2013), leading to numerous consequences
236 such as local irruptions of native and domestic herbivores (Sinclair, 1998), site-specific changes
237 in prey behavior (Berger, 1999), and disease propagation (Wilson and Childs, 1997). For
238 example, predator displacement by humans was found to result in a positive, indirect effect on
239 prey species abundances such as elk (*Cervus elaphus*) and white-tailed deer (*Odocoileus*
240 *virginianus*) in the drylands of southwestern Canada, where pumas and wolves (*Canis lupus*) are
241 actively persecuted (Hebblewhite et al., 2005; Muhly et al., 2011). It is likely that human
242 activities related to sheep ranching in Península Valdés are disruptive of predator-prey
243 interactions and hence favor the local abundance of maras in the vicinity of ranch buildings. In
244 Patagonia, carnivores are perceived by ranchers as a threat to their livestock (Sillero-Zubiri et al.,
245 2004; Travaini et al., 2000; Walker and Novaro, 2010), and this led to high hunting rates in areas
246 frequented by humans or where the ranchers live (Novaro et al., 2005). As the mara is an
247 important prey species across the Patagonian drylands (Walker and Novaro, 2010), different
248 hunting pressure on carnivores resulting in differences in predation rates throughout the
249 landscape (Novaro et al., 2005) could be reflected in mara distribution and abundance patterns.

250 Also, it is likely that the abundance of maras is positively influenced by the availability of food
251 in the vicinity of human dwellings. Usually, ranch buildings are close to temporary lagoons
252 which provide single, resource-rich patches of nutritive food items where maras tend to feed all
253 year round (Taber and MacDonald, 1992b).

254 Although our work showed a positive effect of human presence on the abundance of maras, it is
255 necessary to investigate what are the possible costs associated to this interaction. For example,
256 there is evidence showing that maras are exposed to infectious disease like Johnes's disease and
257 toxoplasmosis, common to the domestic sheep and the invasive European hare (*Lepus*
258 *europaeus*) in Península Valdés (Marull et al., 2004). Therefore the proximity to ranch buildings,
259 which are next to shearing sheds and corrals where the sheep are gathered, could bring negative
260 consequences for mara's health. Regarding the abundance of sheep, we did not find effects on
261 the abundance of maras in this study. It is known that livestock grazing and trampling drive
262 changes in the vegetation structure (Bisigato and Bertiller, 1997; Van de Koppel et al., 1997;
263 Bisigato et al., 2005) that subsequently affect the abundance and distribution of wild species
264 (Longland and Young, 1995; Keesing, 1998; Campos et al., 2001; Tabeni and Ojeda, 2003). On
265 the other hand, there is evidence that the diets of maras and sheep do not show a high overlap
266 which could lead to potential competition for food resources (Bonino et al., 1986, Kufner and
267 Pelliza de Sbriller, 1987; Bonino et al., 1997; Campos et al., 2001; Sombra and Mangione, 2005;
268 Rodríguez and Dacar, 2008) although the decrease in cover of palatable grasses and the increase
269 of woody species and bare soil after overgrazing by the sheep, could affect habitat use by maras
270 (Kufner and Chambouleyron 1991; Taber and MacDonald 1992b; Rodríguez, 2009).

271 Nevertheless, specific studies designed to investigate mara-sheep interactions are needed to
272 assess the effects of the abundant and widespread domestic species on the wild, low-density
273 populations of maras.

274 Although the correlates of plant productivity and vegetation physiognomy had no significant
275 effects on the spatial variation in the abundance of maras as we predicted, we cannot rule out
276 their possible effects. It is likely that both the NDVI and its coefficient of variation were not

277 sufficiently sensitive variables to account for the variation in the composition of different life -
278 forms affecting habitat selection by maras. However, the proxy variable "geographic longitude"
279 did have a significant effect on the variation in mara abundance. Broadly, this variable could be
280 interpreted as a good approximation to spatial variation in the rainfall regime, a crucial attribute
281 controlling the presence and abundance of grasses and herbs across the arid systems (Noy-Meir,
282 1973). In Península Valdés, the average annual rainfall increases from the west towards the
283 eastern coast (Coronato et al., 2017) where the model estimated the highest densities of maras
284 (Fig. 3), and the relationship between mara abundance and geographic longitude was positive
285 (Fig. 5B). This could be associated to the abundance of grasses and herbs which are important
286 food items for the mara, and their growth rates respond quickly to the rainfall regime (Kufner
287 and Pelliza de Sbriller, 1987; Campos, 1997). The pre-breeding period of the mara occurs
288 between May and August, when the precipitation tends to be higher and high-quality food items
289 are more abundant. However, this study was limited to the post-reproductive period. Future
290 research could incorporate the seasonal dynamics in abundance and distribution to analyze
291 variation in habitat selection by maras throughout the year.

292 Surveys and testimonies of ranchers and wildlife wardens suggest that mara abundance is
293 decreasing in PV (Nabte, 2010), while a declining global trend has also been reported for its
294 distributional area (Rodríguez, 2012). However, the available information is restricted to studies
295 limited to both spatial and temporal scale. Although research on local habitat use and occurrence
296 provided key knowledge on mara ecology, studies allowing to assess population trends are still
297 lacking. Using the DSM, we provided the first estimate of mara abundance and its spatial
298 variation at a high resolution, for a representative area of the species' distributional range. As for
299 other studies, our results showed that DSM are a very useful tool to study species distribution

300 and abundance (Katsanevakis, 2007; Herr et al., 2009; Katsanevakis and Thessalou-Legaki,
301 2009; Buckland et al., 2012; Winiarski et al., 2013, 2014; Schroeder et al., 2014; Schroeder et
302 al., 2018; Flores et al., 2018), even for species occurring at low population densities (Williams et
303 al., 2011; Harihar et al., 2014; Antún et al., 2018).

304 **CONCLUSIONS**

305 Natural and anthropic variables shape the spatial variation in the abundance of maras in
306 Península Valdés. The location of ranch buildings was key in habitat selection by maras across
307 the landscape, while the positive association between species' abundance and geographic
308 longitude could reflect the variation in the rainfall regime and ultimately in the abundance of
309 grasses and herbs. Our results showed that maras are heterogeneously distributed and their
310 population density is low across the modified landscape of Península Valdés, a representative
311 area of the arid Patagonia. The use of density surface models allowed us to (i) obtain the first
312 estimate of mara abundance at a population scale; (ii) describe its variation at a higher resolution;
313 and (iii) identify the main variables explaining the spatial structure of the population. This
314 approach can contribute to assess mara population abundance and distribution elsewhere across
315 its range, by combining the well-known distance sampling survey method with spatial modeling.
316 While the identification of the main variables explaining the variation in the abundance of maras
317 is a first step toward the design of conservation actions, future research should focus on the
318 mechanisms underlying the observed patterns and their effects on mara population dynamics.

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Figure 1

Location of the study area and vegetation units according to Bertiller et al. (2017).

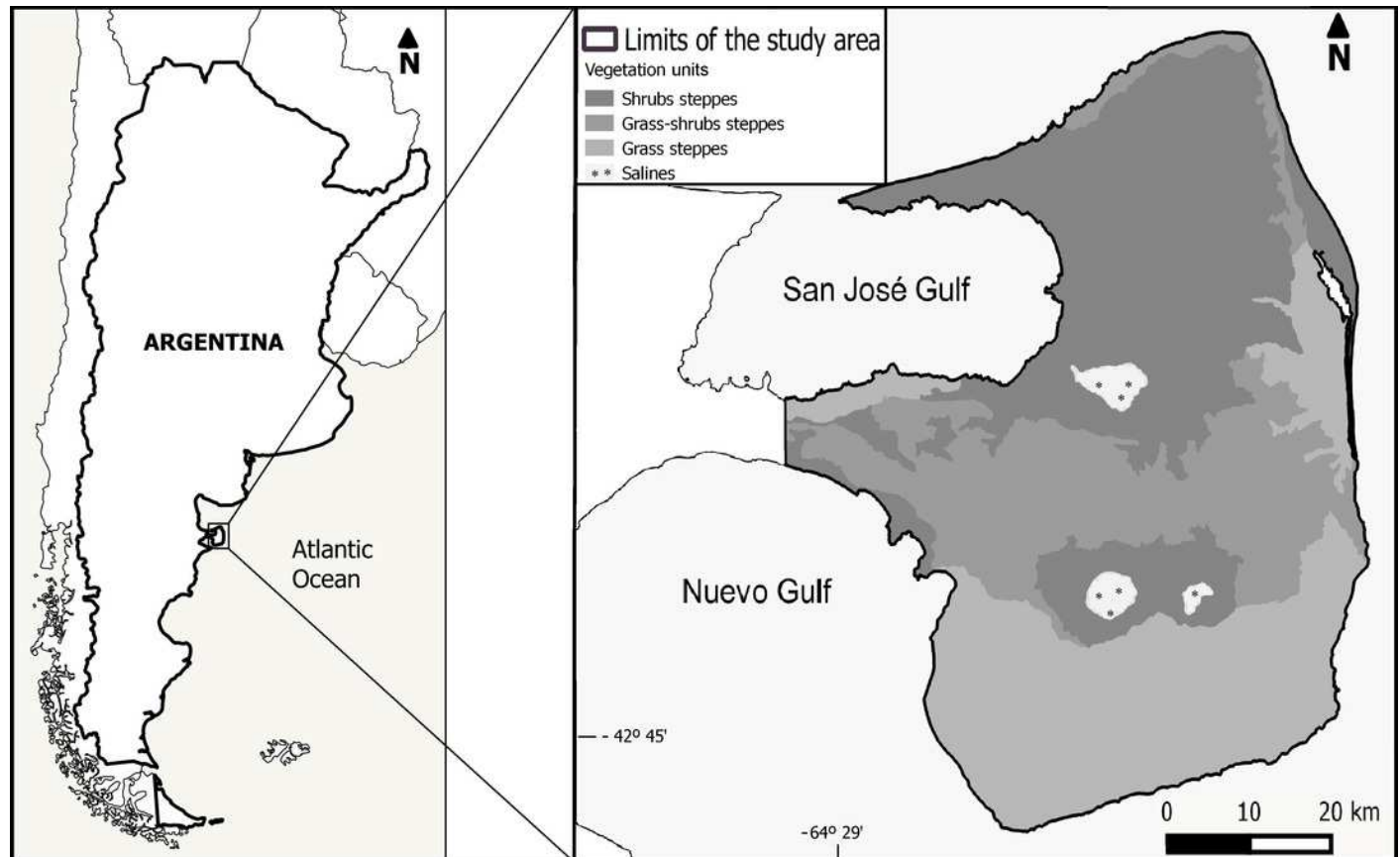


Figure 2 (on next page)

Distribution of perpendicular detection distances of *D. patagonum* sightings.

Solid line represents the half-normal detection function selected after the data truncation of the 10% of the sightings. The circles represent the sightings of *D. patagonum*, while the bars represent the observed data grouped into distance intervals according to the perpendicular distance where they were detected.

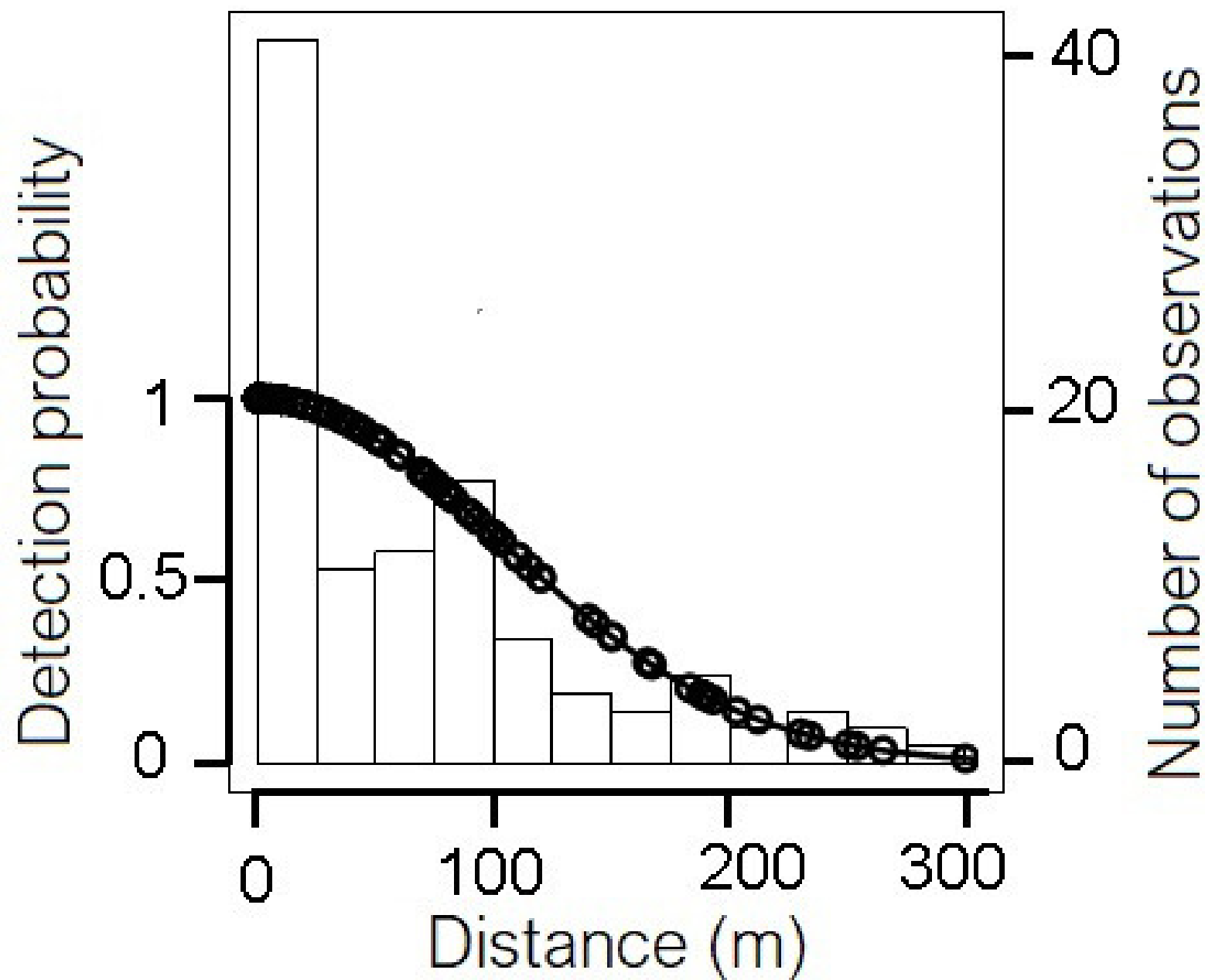


Figure 3

Spatial variation in the abundance of *D. patagonum*.

Abundance is expressed in terms of absolute density (maras.km⁻²) for each 4 km² cell, totaling a 3476 km² prediction area.

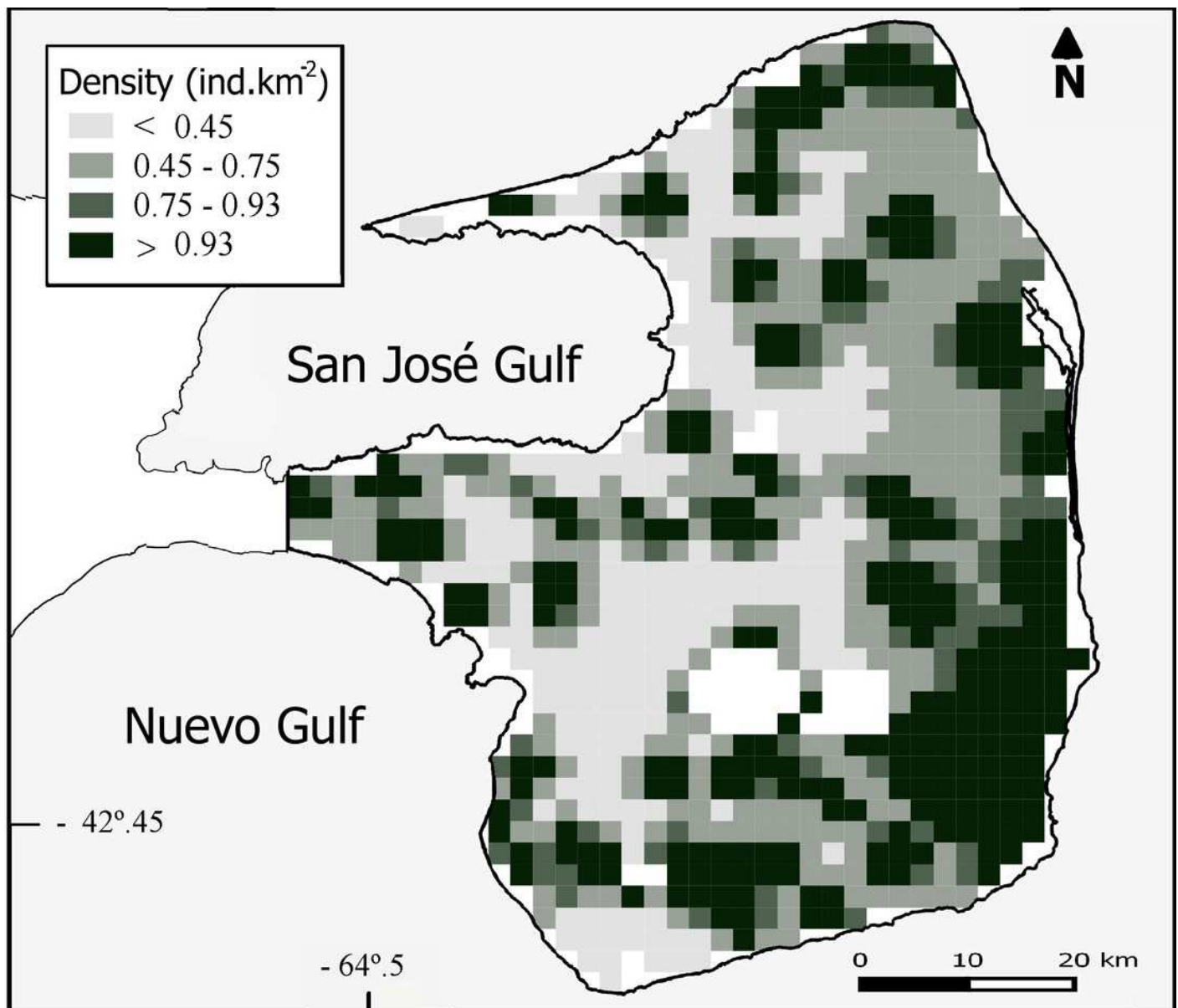


Figure 4

Uncertainty associated with the predicted abundance of *D. patagonum* per 4km² cell, in terms of the coefficient of variation of the estimate.

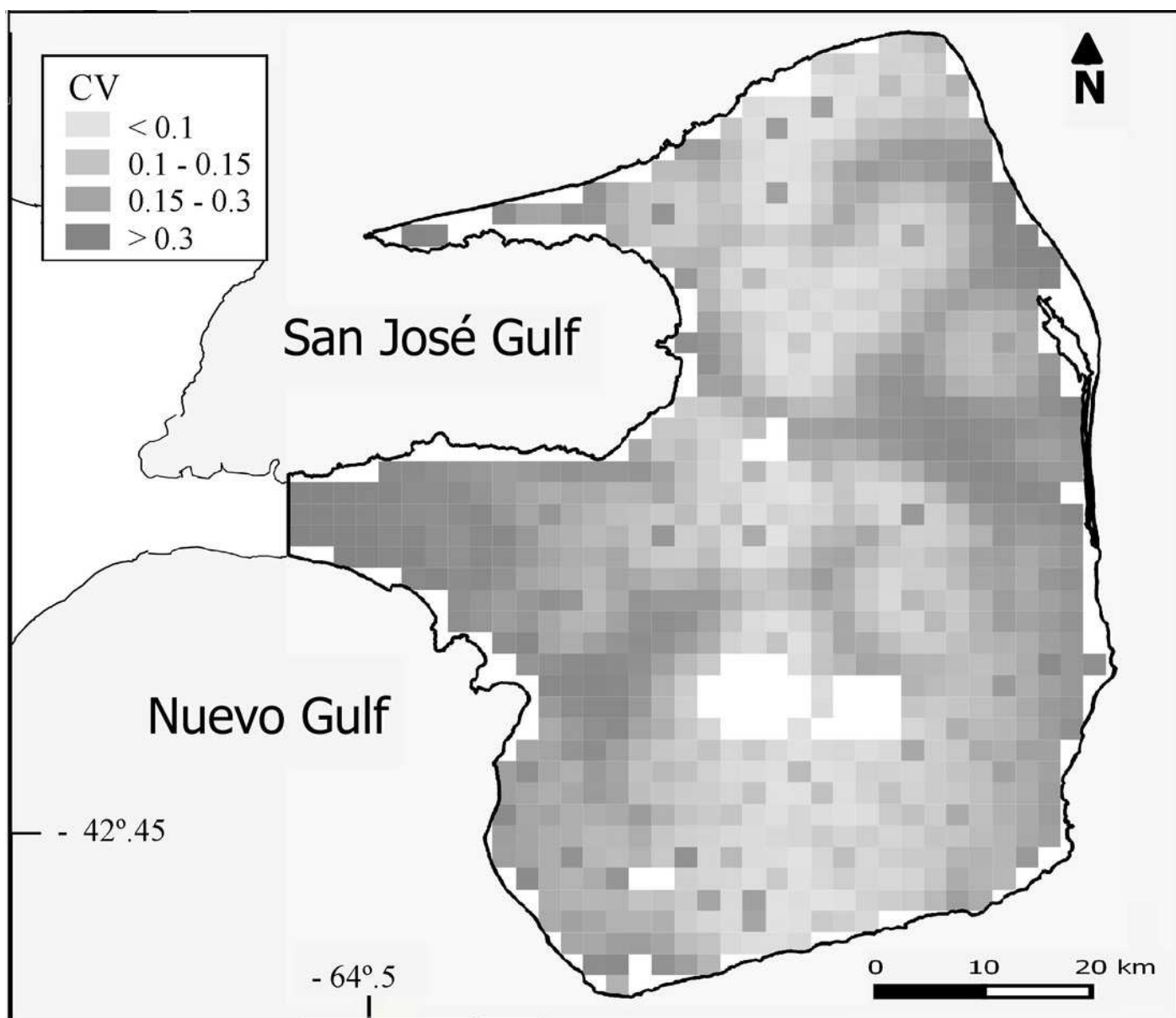


Figure 5(on next page)

Partial effects of the significant predictors on the abundance of *D. patagonum* according to the best fitting model.

The gray shading represents 95% confidence intervals for the mean effect. The rug ticks at the bottom of the plot indicate the coverage of the range of values of each variable in the survey area. The number in brackets in each “s” gives the effective degrees of freedom (a measure of flexibility) of each term.

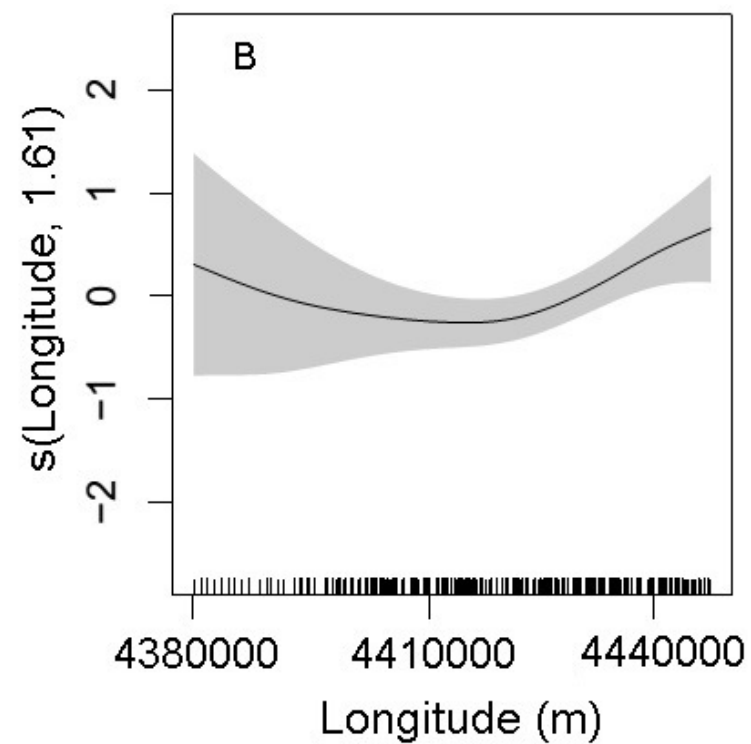
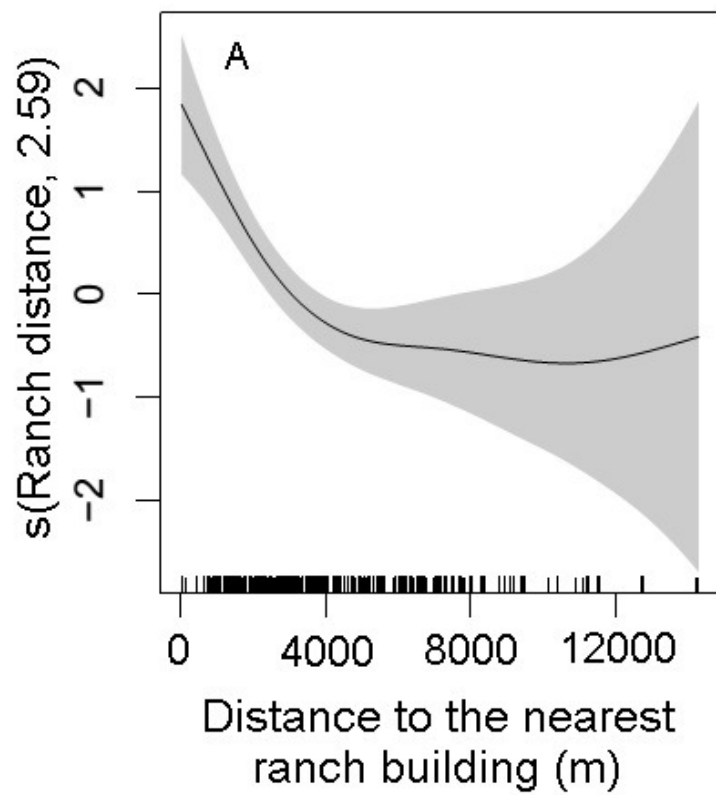


Table 1 (on next page)

List and description of all the variables proposed

1 List and description of all the variables tested

Variable type	Name of the Variable	Description
Natural	Mean NDVI	Mean Normalized Difference Vegetation Index for the spring-summer seasons of 2014-2015, 2015-2016 and 2016-2017 according to each field survey
	CV NDVI	Coefficient of variation of NDVI from 2010 to 2014
	CV altitude	Coefficient of variation of mean altitude
Anthropic	Ranch dist.	Distance to the nearest ranch building in metres
	Sheep stock.	Sheep stocking rate (sheep.km ⁻²) obtained per paddock
Proxy	Longitude	Longitude projected into metres using Universal Transverse Mercator zone 20
	Latitude	Latitude projected into metres using Universal Transverse Mercator zone 20

2

Table 2 (on next page)

Density surface models tested.

The best fitting model selected is shaded (Exp.Dev.: percentage of explained deviance; Ab.: total number of individuals of *D. patagonum* estimated for the study area; SE: standard error; CV: coefficient of variation).

1 **Density surface models tested.**

2 The best fitting model selected is shaded (Exp.Dev.: percentage of explained deviance; Ab.: total
 3 number of individuals of *D. patagonum* estimated for the study area; SE: standard error; CV:
 4 coefficient of variation).

Final Models	Response distribution	Significant variables	Exp.Dev.	Ab.	SE	CV
A	Tweedie	s(ranch dist.) s(longitude)	15.9	3261	494	0.15
B	Quasi-Poisson	s(ranch dist.) s(longitude)	24.1	3195	357	0.11
C	Negative binomial	s(ranch dist.) s(longitude)	9.18	3047	559	0.18

5

6