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Wild pigs and their widespread threat to biodiversity conservation in South America

Luciano F. La Sala, Julián M. Burgos, Nicolas Caruso, Camilo E. Bagnato, Sebastián A. Ballari, Demetrio L. Guadagnin, Andreas Kindel, Matheus Etges, Mariano Merino, Andrea Marcos, Oscar Skewes, Daniella Schettino, Andrés Pérez, Ezequiel Condori, Agostina Tammone, Bruno Carpinetti, Sergio M. Zalba

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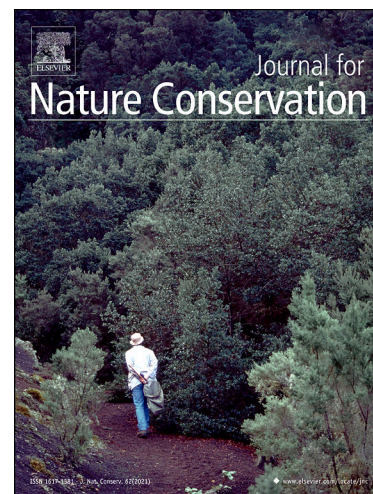
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1 Wild pigs and their widespread threat to biodiversity conservation in South America

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3 Luciano F. La Sala ^{a,*}, Julián M. Burgos ^b, Nicolas Caruso ^a, Camilo E. Bagnato ^c, Sebastián
4 A. Ballari ^d, Demetrio L. Guadagnin ^e, Andreas Kindel ^e, Matheus Etges ^e, Mariano Merino
5 ^f, Andrea Marcos ^g, Oscar Skewes ^h, Daniella Schettino ⁱ, Andrés Pérez ^j, Ezequiel Condori ^k,
6 Agostina Tammone ^k, Bruno Carpinetti ^l, Sergio M. Zalba ^m

7
8 ^a Instituto de Ciencias Biológicas y Biomédicas del Sur (CONICET – Universidad Nacional
9 del Sur), B 8000 ICN Bahía Blanca, Argentina

10 ^b Marine and Freshwater Research Institute, Reykjavík, Iceland

11 ^c Instituto de Investigaciones en Recursos Naturales, Agroecología y Desarrollo Rural
12 (INRAD) (UNRN-CONICET), Río Negro, Argentina

13 ^d Parque Nacional Nahuel Huapi (CENAC-APN). Consejo Nacional de Investigaciones
14 Científicas y Técnicas (CONICET), San Carlos de Bariloche, Río Negro, Argentina.

15 ^e Departamento de Ecología, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS,
16 Brazil

17 ^f Comisión de Investigaciones Científicas de la Provincia de Buenos Aires, Universidad
18 Nacional del Noroeste de la Provincia de Buenos Aires (UNNOBA)

19 ^g Dirección Nacional de Sanidad Animal, Servicio Nacional de Sanidad y Calidad
20 Agroalimentaria (SENASA), Argentina

21 ^h Departamento de Ciencias Pecuarias, Facultad de Medicina Veterinaria, Universidad de
22 Concepción, Chile

23 ⁱ Animal Health Coordination, Instituto de Defesa Agropecuária de Mato Grosso (INDEA-
24 MT), Mato Grosso, Cuiabá, Brazil

25 ^j Department of Veterinary Population Medicine, Center for Animal Health and Food
26 Safety, College of Veterinary Medicine, University of Minnesota, United States

27 ^k Centro de Investigación Veterinaria de Tandil (CIVETAN), Facultad de Ciencias
28 Veterinarias, Universidad Nacional del Centro de la Provincia de Buenos Aires, Argentina

29 ^l Cátedra de Ecología y Recursos Naturales, Universidad Nacional Arturo Jauretche,
30 Argentina

31 ^m GEKKO – Grupo de Estudios en Conservación y Manejo, Departamento de Biología
32 Bioquímica y Farmacia, Universidad Nacional del Sur, Argentina

33
34
35 * Corresponding author at: Instituto de Ciencias Biológicas y Biomédicas del Sur
36 (CONICET – Universidad Nacional del Sur). Phone: +54 9 291 4612445. Postal address:
37 San Juan 670 (B 8000 ICN), Bahía Blanca, Argentina.

38
39 E-mail addresses: lucianolasala@conicet.gov.ar (L. F. La Sala),
40 julian.burgos@hafogvatn.is (J. M. Burgos), nccaruso@gmail.com (N. Caruso),
41 bagnato@agro.uba.ar (C. E. Bagnato), sebastianballari@gmail.com (S. A. Ballari),
42 dlguadagnin@gmail.com (D. L. Guadagnin), andreaskindel@gmail.com (A. Kindel),
43 matheus.etges@gmail.com (M. Etges), mariano.merino@nexo.unnoba.edu.ar (M. Merino),
44 amarcos@senasa.gob.ar (A. Marcos), oskewes@udec.cl (O. Skewes), donas001@umn.edu
45 (D. Schettino), aperez@umn.edu (A. Pérez), ezequielcondori92@gmail.com (E. Condori),
46 agostinatammone@gmail.com (A. Tammone), brunoelcarpincho@hotmail.com (B.
47 Carpinetti), szalba@criba.edu.ar (S. M. Zalba)

Highlights

- Wild boars produce negative impacts in South America.
- Ecological niche modelling was used to predict potential wild boar distribution in South America.
- Most ecoregions in South America have suitable conditions to sustain wild boar populations.
- Suitable area occupied 85% of Atlantic Forest and 61.3% of Cerrado biodiversity hotspots.
- An alarming large number of protected areas are currently or potentially affected by the species.
- Control measures should be adopted to control wild boar impacts on biodiversity.

Abstract

Wild pigs, including wild boar (*Sus scrofa*) and feral domestic pig (*Sus scrofa domestica*), are associated with negative impacts in their native and introduced ranges. We compiled wild pig occurrence reports and utilized Maximum Entropy modelling to predict their potential distribution in ecoregions overlaying Argentina, Brazil, Bolivia, Chile, Uruguay and Paraguay. An analysis of their observed and potential distributions was carried out in relation to four biodiversity hotspots and 3766 protected areas to estimate the number of units and percent area currently and potentially invaded. Among biodiversity hotspots, Atlantic Forest, Cerrado, and Chilean Winter Rainfall-Valdivian Forests included 44.7% of wild pig records. The proportion of suitable area was 85% in Atlantic Forest, 61.3% in Cerrado, 37.5% in Chilean Winter Rainfall-Valdivian Forests, and 5.6% in Tropical Andes. The number of protected areas with wild pig presence was led by Uruguay (100%), followed by Chile (20.3%), Argentina (15.8%), Paraguay (9.5%), Bolivia (6.5%), and Brazil (4.7%). Potential distribution was highest in protected areas of Uruguay (100%), followed by Paraguay (72.6%), Brazil (58.0%), Argentina (57.4%), Chile (42.2%), and Bolivia (35.9%). Our work represents the first assessment of wild pig potential distribution in South America and highlights the potentially devastating impacts of wild pigs on the regional biodiversity and national conservation targets, especially at mega-diverse areas. We present a dynamic and web application that can be readily consulted by scientists, managers and decision makers to improve wild pig control and risk mitigation actions in the study region.

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Keywords: wild boar; wild pig; ecological niche modelling; potential distribution; protected areas; biodiversity.

1. Introduction

Wild boar (*Sus scrofa* Linnaeus, 1758) are native to large parts of Europe, Asia and North Africa, and are now present in all continents except Antarctica, as well as on many oceanic islands (Barrios-Garcia and Ballari, 2012) making it one of the world's most widely distributed mammals (Cuthbert et al., 2022). Similarly, since the early stages of European colonization, wild boar's domestic derivative, the domestic pig (*Sus scrofa domesticus*), has established naturalized populations in Australasia, the Americas, and Oceania, in addition to a large number of oceanic islands (Oliver et al., 1993). The success of wild pigs (from here on referring to wild boar and feral domestic pig) in colonizing a variety of habitats is partly due to their high reproductive potential (Beasley et al., 2018), highly plastic diet (Ballari and García-Barrios, 2014), wide climatic and topographic tolerance (Bosch et al., 2020), and behavioral adaptability under contrasting conditions of human pressure (Podgórski et al. 2013).

Worldwide, wild pigs are associated with strong negative effects (Barrios-Garcia and Ballari 2012) and large direct economic impacts (Anderson et al., 2016; FAO, 2020; Marcos, 2021; Cuthbert et al., 2022). In South America, pigs were introduced by Portuguese and Spanish explorers, and have established feral populations (Carpinetti et al., 2016; Salvador and Fernandez, 2017). Studies have shown the negative effects of wild pigs on ecosystem functioning in Brazil (Silveira de Oliveira et al., 2020), Argentina (Ballari et al., 2015), and Chile (Cuevas et al. 2021), and their impact on the biodiversity in protected areas has been widely documented (Cuevas et al., 2010; Ballari et al., 2015). The history of wild boar in the Neotropic goes back more than a century (Skewes and Jaksic, 2015), with their first introductions occurring in Argentina for hunting purposes during the early twentieth century and the following dispersion between 1906-1930 (Daciuk, 1978). More recent waves of introduction took place for hunting during the 1990s, followed by escape and cross-border dispersal (Pedrosa et al., 2015; Skewes and Jaksic, 2015; García et al., 2011), which led to explosive population growth in the Neotropics (Pedrosa et al., 2015). Hybridization with feral pigs has been suggested to be intense in southern South America (Figueroa et al., 2022) as well as Europe (Iacolina et al., 2018).

137 Despite their considerable impacts on agricultural, ecological systems functioning and
138 animal health (García-Barríos and Ballari, 2012), little is known about their broad-scale
139 potential distribution in South America, where published information is either outdated
140 (e.g., Bonino, 1995; Novillo and Ojeda, 2008) or limited to a specific countries such as
141 Argentina (Pescador et al., 2009, Ballari et al., 2019; Cuevas et al., 2021), Brazil (Pedrosa,
142 et al. 2015; Deberdt and Scherer, 2007) and Chile (Skewes and Jaksic, 2015). In the latter
143 countries, wild pig populations are currently growing and expanding their ranges at
144 alarming rates (Ballari et al., 2019; Skewes and Jaksic, 2015; Hegel et al., 2022).

145 Historical or current distributional information is more scarce in Bolivia (Tejeda et al.
146 2021), Paraguay, and Uruguay, even when in the latter country wild pigs are suggested to
147 have invaded the entire territory (Altuna et al., 2020; CEEI and Dinama, 2022). To this
148 date, the work by Salvador and Fernandez (2017) is the most comprehensive review of wild
149 pig global distribution in South America. Similarly, information about their current and
150 potential distribution in biodiversity hotspots and protected areas is incomplete and
151 scattered, with only a handful of studies conducted in South American countries (Ballari et
152 al. 2015; Salvador and Fernandez, 2017). This gap of knowledge raises concerns about
153 impacts that may not have been evaluated in their proper dimension, thus leading to
154 deficient prevention planning, control and mitigation strategies.

155 Management and control strategies are being developed throughout the world to
156 minimize the impacts of wild pigs and to control or eradicate their populations (e.g., Croft
157 et al., 2020; Bengsen et al., 2014). In addition to the actual observations, predictions of the
158 potential distribution of wild pigs derived from ecological niche models (ENMs) can
159 support these efforts. For example, information of the potential distribution of wild pigs in
160 areas of high conservation priority such as protected areas and biodiversity hotspots can be
161 used to improve the surveillance and prevention in still uninvaded but suitable areas,
162 efficiently allocate resources, and prioritize management practices on the most vulnerable
163 ecosystems. In this sense, ENMs have benefited biodiversity conservation through the
164 linkage between science and decision processes. ENMs have strengthened conservation
165 efforts worldwide by allowing more efficient planning for the management of invasive
166 species (Peterson, 2003), and they can reach their full potential when scientists, public
167 stakeholders and policy makers are brought together and used them as adaptive
168 management tools (McShea, 2014).

169 This study aimed to assess the current and potential spatial distribution of wild pigs in
170 southern South America, and to analyze their potential impact on biodiversity hotspots and
171 protected areas in the study region.

172 173 **2. Methods**

174 *2.1. Modeling workflow and reproducibility*

175 We followed a structured format consisting of five modelling steps to provide
176 transparency and comparability following best-practice standards (Guisan et al., 2017;
177 Araújo et al., 2019). These steps are (i) Overview/Conceptualization, (ii) Data, (iii) Model
178 fitting, (iv) Assessment and (v) Prediction. This approach, henceforth referenced as
179 ODMAP, assures the technical details needed to reproduce the methods (Feng et al., 2019)
180 and to assess their appropriateness for different purposes. Here, we used the ODMAP
181 protocol proposed by Zurrell et al. (2020), which was completed using the Shiny web
182 application ODMAP v1.0 (ODMAP Protocol, Supplementary Information).

183 All the analyses were performed using the open source programming language R (R
184 Core Team 2022). The packages “sf” (Pebesma, 2018) and “stars” (Pebesma, 2021) were
185 used for manipulation of spatial data. Graphics and maps were done using the package
186 “ggplot2” (Wickham, 2016). The scripts used to perform the analysis and a list of packages
187 used are available in a GitHub repository
188 (https://github.com/lucianolasala/Wild_boar_ENM). To allow better exploration of results,
189 a dynamic application was developed using Google Earth Engine through its JavaScript
190 API (<https://lucianolasala.users.earthengine.app/view/wild-pigs-south-america>), which
191 incorporates exploration capabilities for ENMs as continuous (suitability index) and binary
192 (presence/absence) outputs in single or multiple areas of specific interest (hotspots,
193 ecoregions, PAs), and offers a graphics interface that summarizes habitat suitability metrics
194 for the selected areas, such as average and range for the continuous ENM and
195 presence/absence area (sq. km).

196

197 2.2. *Occurrence records, data curation and sampling bias control*

198 Presence-only data were used, and included both direct (field observation) and indirect
199 (camera trapping, tracks) observations of wild boar and feral pigs reported by
200 knowledgeable collaborators (hunters, field researchers, park rangers, farmers). A complete
201 list of data sources is provided (Sources of Information, Supplementary Information).
202 Considering the strong hybridization that exists between wild boar and feral pigs in the
203 study region, the occurrence records of both taxa were combined in the analyses and are
204 jointly regarded as “wild pigs”.

205 Records from uncertain sources or with large locational uncertainty (>10 km) were
206 removed from analysis, including offset locations (e.g. “10 miles N of”). Records reported
207 as the centroid of a spatial polygon (e.g., states, protected areas) were also removed, given
208 the pervasive of this kind of data in ENMs (Park and Davis, 2017; Cheng et al., 2021).

209 Occurrence data were not collected via a standardized sampling scheme, which may
210 lead to modelling biases (Yackulic et al. 2013). The effects of these biases were minimized
211 via spatial thinning of records, which can improve model performance (Boria et al., 2014;
212 Fourcade et al., 2014). Spatial thinning was implemented using the R package “spThin”
213 (Aiello-Lammens et al. 2015), setting a thinning distance of 10 km and performing 100
214 iterations. The dataset including the maximum number of records (compared across all
215 iterations) was used for modeling purposes.

216

217 2.3. *Environmental variables*

218 When modelling niches and predicting species distributions, remote sensing products
219 can provide standardized measurements of environmental variables that are spatially
220 continuous, and have a quasi-global coverage at high temporal and spatial resolutions (He
221 et al. 2015; Pinto-Ledezma and Cavender-Bares 2021). We used remote sensing products,
222 including precipitation, temperature, biophysical and topographic variables representing
223 different components of vegetation and ecosystems. After an extensive literature review
224 (e.g., Park and Lee, 2003; Bosch et al., 2014; McClure et al., 2015; Froese et al., 2017;
225 Khwarahm et al., 2022), 24 variables were selected on the basis of their potential biological
226 association with the species’ distribution and their availability through remote sensing. A
227 list of data sources including the most relevant attributes is provided in the Supplementary
228 Information (Table S1). All remote imagery was processed using the Google Earth Engine

229 (Gorelick et al., 2017) through its JavaScript API. All layers were exported at the default
230 resolution of 1000 m.

231 A principal component analysis (PCA) approach was used to reduce multicollinearity
232 among variables. Because including redundant variables can cause the PCA to
233 overemphasize their contribution, highly correlated variables (Spearman correlation $|r| >$
234 80%) (Dormann et al., 2007) were removed, after which 11 variables remained in the final
235 set. Following, a PCA was performed on the remaining variables. The first six PCA axes
236 explained 91.3% of variability and were used as final explanatory variables in the model.
237 The spatial resolution of analysis was defined by fitting spherical variograms on the PCA
238 axes, and evaluating each raster's variance range to identify the autocorrelation
239 distance and. Based on the results a final resolution of 10 km² was selected for modeling
240 purposes.

241

242 2.4. *Study region, calibration and projection areas*

243 Our study region comprised ecoregions totally or partially overlapping Argentina,
244 Chile, Brazil, Uruguay, Bolivia and Paraguay. These countries cover 84.1% of South
245 America (ca. 15,001,900 km²), and include 68 unique ecoregions of which 50 lie
246 completely inside, and 18 extend into neighboring countries (Olson et al., 2001).
247 Ecoregions are defined as areas containing distinct sets of biological communities and
248 species associated to specific geographic and environmental phenomena (Omernik, 2004).
249 As such, they approximate areas where ecological processes most strongly interact (Orsini
250 1993), and reflect the distribution of species and communities more accurately than do units
251 based on other global and regional models (Olson et al., 2001). This may be informative
252 about barriers that have historically constrained the distributional potential of species.

253 A total of 41 (60.3%) ecoregions had wild pig occurrence records and were used as a
254 hypothesis of areas that have been accessible to the species over relevant time periods
255 (Barve et al., 2011; Soberón, 2010), and therefore as calibration area. Based on ecological
256 criteria (e.g., animal dispersion), the entire area of each of these ecoregions was considered
257 for model calibration, regardless of their extension beyond administrative boundaries of the
258 region of interest. Ecoregions without records were used for model projection, also
259 regardless of their extension beyond the region of interest. Ecoregions spatial data were
260 downloaded from a database maintained by the World Wildlife Fund (Olson et al. 2001,
261 <https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world>).

262

263 2.5. *Model calibration and evaluation*

264 A maximum entropy modeling algorithm was used for estimating an environmental
265 niche and the potential area of distribution after projecting the first on geographical space.
266 The Maxent software (version 3.3.3 k; Phillips et al., 2006) was used via the R package
267 “kuenm” (Cobos et al., 2019). The complete occurrence dataset was randomly split into
268 calibration (75%) and testing (25%) sets, and background sampling of the calibration area
269 included 100 000 random samples. Initial candidate models were built using five
270 combinations of feature classes of increasing complexity, with the simplest model including
271 only the linear feature class, and subsequent models adding the quadratic, product,
272 threshold and hinge feature classes. Each combination of feature classes was fitted with
273 seven regularization multiplier values (0.1, 0.25, 0.5, 0.75, 1, 2.5, 5). For better computing
274 performance, the modeling process was implemented using the “sample with data” (SWD)
275 format.

276

277 2.6. *Evaluation and selection of best models*

278 The performance of candidate models was evaluated in terms of statistical significance
279 (partial ROC), prediction ability (omission rate; Peterson et al., 2008), and model
280 complexity (Warren and Seifert, 2011) following the Akaike information criterion
281 corrected for small sample sizes (AICc; Burnham and Anderson, 2002). Among the models
282 that were statistically significant and presented omission rates below a defined threshold
283 (5%), those with ΔAIC_c up to two units were selected as best models (Burnham and
284 Anderson, 2002). The “cloglog” output format was used, and posterior binary
285 transformations were also performed. For further details, the model workflow is described
286 in the ODMAP protocol.

287

288 2.7. *Final model evaluation, projection and extrapolation risk analysis*

289 A final model evaluation was conducted using an independent set of occurrences ($n =$
290 370) not used for model calibration, that were collected through a survey distributed among
291 SENASA’s (National Service for Agrifood, Health and Quality of Argentina) 14 regional
292 centers and their 370 local offices across the country’s territory. The evaluation was done in
293 terms of AUC ratio (ratio of observed to null expectations), statistical significance (partial
294 ROC) and omission rates (5%).

295 The final model was projected to ecoregions not included in model calibration (i.e.,
296 ecoregions without occurrence records). The process was replicated 10 times via
297 bootstrapping. Extrapolation types used were (a) “free extrapolation”, where responses in
298 areas environmentally different from the calibration area follow trends in the calibration
299 environmental data; (b) “extrapolation and clamping”, where the response in areas with
300 environments distinct from those in the calibration area is clamped to levels present at the
301 periphery of the calibration region in environmental space; and (c) “no extrapolation”,
302 where the response is set to zero if the environments in transfer areas are more extreme than
303 those in areas across which the models were calibrated. A final model prediction was
304 produced by averaging across all model bootstrap repetitions for each extrapolation type.

305 The mobility-oriented parity (MOP) (MOP; Owens et al., 2013) metric was used to
306 analyze the novelty of climate conditions in the projection area relative to the calibration
307 area. This analysis helps determine areas where strict extrapolation occurs (i.e., transfer
308 areas with values outside the range of climates in the calibration area). Areas with higher
309 extrapolative values indicate higher uncertainty, and caution is required when interpreting
310 likelihood of species presence in such areas. Finally, models representing the standard
311 deviation and range of suitability values were produced for evaluation.

312

313 2.8. *Threshold selection*

314 When applied to ecological problems, such as the potential impact of invasive alien
315 species, ENM often require a threshold to transform continuous models into binary outputs.
316 Several methods have been proposed for use with presence-only data (Phillips et al., 2006;
317 Pearson et al., 2007; Li and Guo, 2013; Liu et al., 2013). Here, we selected a threshold that
318 maximized the sum of sensitivity and specificity (maxSSS) (Liu et al. 2005, 2013, 2016),
319 which has good performance in presence-only data scenarios. This approach minimizes
320 omission errors, which are generally costlier in conservation applications such as
321 identifying areas under risk for biological invasion (Liu et al., 2005; Jiménez-Valverde and
322 Lobo, 2007). Then, the mean value of maxSSS was calculated across all 10 replicates of the

323 final model, including the calibration and projection areas, and this value was used as
324 optimum threshold to produce binary models.

325

326 2.9. *Biodiversity hotspots, ecoregions and protected areas*

327 Based on the built model, we evaluated habitat suitability at three different spatial
328 levels, which are relevant in terms of biodiversity conservation and ecosystem functioning:
329 these were biodiversity hotspots (henceforth denoted as hotspots), ecoregions, and
330 protected areas (PAs).

331 Hotspots are regions which meet two criteria: they contain at least 1500 species of
332 vascular plants (>0.5% of the world's total) as endemics, and have 30% or less of its
333 original vegetation (extent of historical habitat cover) remaining (Mittermeier et al., 2004).
334 Threats to hotspots are similar to, although more intense than, the threats facing
335 biodiversity worldwide (Brooks et al., 2002). Spatial data of hotspots overlapping total or
336 partially with the study region were downloaded from the Data Basin database (Hoffman et
337 al., 2016). For the purpose of our analysis, only the area of each hotspot overlapping our
338 calibration or projection areas was considered. The presence of wild pig records within
339 each hotspot was assessed, and the total and percentage of suitable and unsuitable areas
340 within each hotspot were calculated.

341 Ecoregions are defined as areas containing distinct sets of biological communities and
342 species associated to specific geographic and environmental phenomena (Omernik, 2004).
343 These units approximate the areas where ecological processes interact most strongly
344 (Orians 1993), and reflect the distribution of species and communities more accurately than
345 do units based on other global and regional models (Olson et al., 2001). This may be
346 informative about barriers that have historically constrained the distributional potential of
347 species. The presence of wild pigs was assessed within each ecoregion. Since ecoregions
348 reflect the history of the changing distributions of species, if the species was detected in one
349 or more sites inside an ecoregion, it was assumed that it could potentially find suitable
350 habitats across a large proportion of the area. Under this rationale, ecoregions were
351 classified as “invaded” if the presence of wild pigs was confirmed, or “unknown (UNK)”
352 otherwise. Also, ecoregions were classified as suitable if they overlapped (totally or
353 partially) with suitable areas for wild pigs, or unsuitable otherwise. Finally, the continuous
354 niche model was used to derive summary statistics (mean, minimum, maximum, standard
355 deviation) of suitability in each ecoregion.

356 Data on protected areas were downloaded and processed from the Protected Planet
357 database (UNEP-WCMC and IUCN, 2022) using the R package “wdpar” (Hanson, 2021).
358 We also included additional PAs considered relevant for biodiversity conservation but not
359 included in this database. Relevant sources of information from each country were
360 consulted with regards to the presence of wild pigs within PAs (see Sources of Information
361 in Supplementary Information). For the purpose of PAs analyses, these data were
362 complemented with the wild pig presence records in PAs used in the modeling process.

363 The analysis was performed at two levels by selecting PAs where: (i) wild pig
364 occurrences have been reported within their boundaries, and (ii) the binary model shows
365 spatial overlap between PAs and suitable areas. Firstly, PAs were classified as “invaded”
366 under the assumption that if the presence of wild pigs was confirmed within their
367 boundaries, the whole PA could potentially be invaded. Secondly, the total number of PAs
368 overlapping (totally or partially) with suitable areas was calculated in each country, and

369 PAs were classified with regards to their risk status as “at risk” if they overlapped suitable
370 areas, or “not at risk” otherwise.

371 Finally, we estimated the binary model’s capacity to correctly classify PAs with
372 regards to their risk status. The following performance metrics were calculated: accuracy
373 (model’s ability to correctly classify PAs’ status), sensitivity (proportion of correctly
374 classified PAs at risk), specificity (proportion of correctly classified PAs not at risk),
375 omission (type I) and commission (type II) errors.

376 The PAs included in the analyses have been categorized by the International Union for
377 Conservation of Nature (IUCN) into the following management categories (Dudley, 2008):
378 “strict nature reserve” (Ia), “wilderness area” (Ib), “national park” (II), “natural monument
379 or feature” (III), “habitat or species management area” (IV), “protected landscape or
380 seascape” (V), and “protected area with sustainable use of natural resources” (VI). The
381 frequency distribution of PAs among IUCN management categories was analyzed for PAs
382 predicted to be at risk according to our binary model.

383

384 **3. Results**

385 3.1. *Wild pig occurrences*

386 Occurrence records covered a temporal range of 116 yrs. (1906-2022) and consisted of
387 6502 records with acceptable levels of precision (≤ 10 km), which were distributed as
388 follows: Argentina (2479), Bolivia (36), Brazil (3931), Chile (155), Paraguay (69), and
389 Uruguay (202). Additionally, information on wild pig occurrences were collected from 278
390 PAs in these countries.

391

392 3.2. *Niche modelling and suitable areas*

393 After spatial thinning of occurrence data, 2511 wild pig records were retained for
394 modeling purposes. A total of 35 candidate models were produced. One model passed pre-
395 defined criteria (statistically significant model meeting omission rate and AICc criteria) and
396 was selected as the best model. This model was parameterized using a regularization
397 multiplier of 1 and linear, quadratic and product features.

398 The final model is presented in two forms; as continuous “cloglog” output and as
399 binary model classifying the study region as suitable or unsuitable (Figs. 1 and 2). County-
400 level results are presented for the continuous and binary models (Supplementary
401 Information, Figs. S1-S6). According to the binary model, 35.8% of the territory in the
402 studied countries was suitable, and country-level suitability was led by Uruguay (97.3%),
403 followed by Paraguay (48.3%), Argentina (43.6%), Brazil (35.9%), Chile (15.3%) and
404 Bolivia (12.5%) (Table 1).

405

406 3.3. *Final model evaluation, projection and risk of extrapolation*

407 The independent evaluation showed that the final model performs well (mean AUC
408 ratio: 1.98; partial ROC: $p < 0.0001$; omission rate at 5%: 0.046). Based on these results,
409 the model was projected to ecoregions without wild pig records (projection area). The MOP
410 analysis identified only very small areas of extrapolation in projection region located in
411 northern Brazil, western Bolivia, northern and southern Chile (Supplementary Information,
412 Fig. S17). Only the model built using a “free extrapolation” algorithm was selected for
413 further analyses.

414

415 3.4. *Biodiversity hotspots, ecoregions and protected areas*

416 Three hotspots (Atlantic Forest, Cerrado, and Chilean Winter Rainfall-Valdivian
 417 Forests) laid completely inside the study region, and one (Tropical Andes) overlapped only
 418 partially (Fig. 3). A total of 3076 (44.8%) wild pig records were located within hotspots.
 419 The first three hotspots included 44.7% of all records, whereas Tropical Andes included
 420 0.1%. The proportion of suitable area inside each hotspot was led by the Atlantic Forest
 421 (85%), followed by Cerrado (61.3%), Chilean Winter Rainfall-Valdivian Forests (37.5%),
 422 and Tropical Andes (5.6%) (Table 2). The hotspot areas with highest habitat suitability
 423 were Atlantic Forest (mean: 0.706; SD: 0.142), followed by Cerrado (mean: 0.606; SD:
 424 0.192), Chilean Winter Rainfall-Valdivian Forests (mean: 0.457; SD: 0.267), and Tropical
 425 Andes (mean: 0.122; SD: 0.203) (Fig. 4 and Fig. S12-S15, Supplementary Information).
 426 Individual binary models for each hotspot are presented (Fig. S8-S11, Supplementary
 427 Information).

428 At the ecoregion level, suitability ranged between maximum values in Araucaria Moist
 429 Forests (mean: 0.772; range: 0.166-0.967; SD: 0.12) and lowest values in Atacama Desert
 430 (mean: 0.001; range: 0-0.066; SD: 0.004). Continuous models for individual ecoregions are
 431 presented (Fig. S18-S85, Supplementary Information). Of all 68 ecoregions, 41 (60.3%)
 432 were reported to have wild pigs, 64 (94.1%) overlapped totally or partially with suitable
 433 environmental conditions, and 18 (26.5%) had mean suitability values above the mean
 434 threshold suitability value of 0.579 (range = 0.503-0.599; SD = 0.03) (Table S2,
 435 Supplementary Information). Only Solimões-Japurá Moist Forests in northern Brazil, Lake
 436 on the border between western Bolivia and Perú, Central Andean Dry Puna between
 437 northwest Argentina, northeast Chile and southwest Bolivia, and Atacama Desert in
 438 northern Chile, were classified as completely unsuitable.

439 The number of protected areas (PAs) currently affected by wild pig presence was led
 440 by Uruguay (100%), followed by Chile (20.3%), Argentina (15.8%), Paraguay (9.5%),
 441 Bolivia (6.5%), and Brazil (4.7%). When analyzing the risk status of PAs, Uruguay (100%)
 442 also ranked first, followed by Paraguay (72.6%), Brazil (58.0%), Argentina (57.4%), Chile
 443 (42.2%), and Bolivia (35.9%) (Table 3). The complete dataset of PAs with their respective
 444 information is presented (Excel file Protected Areas, Supplementary Information).

445 Regarding the capacity of our binary model to correctly classify PAs in terms of their
 446 risk status, the overall accuracy was 48.1% (1,810/3,766), sensitivity was 82.8% (231/279),
 447 and specificity was 45.3% (1,579/3,487). Omission and commission errors were 17.1% and
 448 54.7%, respectively.

449 The distribution of PAs at risk among IUCN management categories varied by country
 450 (Table S3, Supplementary Information). When considering all six countries combined, the
 451 percentage of PAs at risk in each category was led by protected landscapes (73.3%),
 452 followed by national parks (63.9%), natural monuments or features (59.1%), habitat/species
 453 management areas (57.6%), wilderness areas (57.1%), strict nature reserves (55.7%), areas
 454 with undefined category (48.1%), and protected areas with sustainable use of natural
 455 resources (44.6%).

456

457 **4. Discussion**

458 *4.1. Wild pig potential distribution*

459 According to our model, the potential distribution of wild pigs occupies large
 460 percentages of each country's territory, being 97.3% in Uruguay, 48.3% in Paraguay,
 461 43.6% in Argentina, 35.9% in Brazil, and 15.3% in Chile. In Uruguay, the estimated
 462 suitable area occupied 97.3%, or 2.4% less than that reported by Salvador and Fernandez

463 (2017), who also reported the percentage of invaded area for Argentina (41.9%), Brazil
464 (7.5%), Chile (8.9%) and Paraguay (7.3%).

465 When comparing our results with other research in individual countries, the differences
466 are stark. For example, in Argentina, although we could confirm the current presence of
467 wild pigs in the same ecoregions and provinces reported by Ballari et al. (2019), our model
468 estimated a potential distribution area 2.2 times larger than the distribution reported by
469 these authors (43.6% vs. 13.6% of the total territory). Similarly, in Chile, our model
470 estimated a potential distribution area 4.4 (150 100 vs. 27 600 km²) times larger than the
471 distribution area reported by Skewes and Jaksic (2015). In Brazil, we confirmed wild pig
472 occurrences in 205 previously unreported municipalities compared with the most
473 exhaustive analysis (Hegel et al., 2022), where wild pigs were reported in 1152
474 municipalities across the country. Hence, our data expands the current range for wild pigs
475 in this country raising the total number of currently invaded municipalities by 17.8%. Also,
476 we found that nearly 36% of Brazil's territory was classified as suitable, with the southern
477 states of Santa Catarina, Paraná, São Paulo, Minas Gerais, Goiás and Mato Grosso do Sul
478 being the most vulnerable. Although this agrees broadly with the most severely affected
479 areas according to other research (Pedrosa et al., 2015; Salvador and Fernandez, 2017), the
480 distribution reported in the present work (which includes both occupied and potentially
481 invadable areas) was nearly 4 times larger (35.9% vs. 7.5%).

482 The broader distributions reported in our study compared with previous ones from
483 Argentina, Brazil, and Chile could be explained by the different methodological approach
484 used and by the inclusion of a large number of new records spanning a longer period of
485 time. In general, other studies estimated wild pig distributions based on mapping
486 occurrences at the level of administrative divisions (Pedrosa et al., 2015; Salvador and
487 Fernandez, 2017) or by drawing minimum convex polygons around occurrence records
488 (Ballari et al., 2019). Contrarily, with our approach, we identified not only effectively
489 occupied areas, but also areas where the species may be present but has not be detected, and
490 also regions with suitable conditions which have not been invaded as yet (Peterson et al.,
491 2011). The latter scenario could be explained by an unfilled niche in the study region
492 (Guisan et al., 2014), which is expected as a result of recent colonization and ongoing
493 dispersal processes and has been reported in wild pigs globally (Strubbe et al., 2014) and in
494 the Neotropics (Sáles et al., 2017). We are aware of the perils of training niche models in
495 regions undergoing invasion and not in distributional equilibrium (Peterson, 2005).
496 However, occurrence data from invaded regions offer additional insights of novel
497 environments and biotic contexts, and have been extensively used (e.g., Rouget et al., 2004;
498 Muñoz and Real, 2006).

499 Niche models must be evaluated rigorously prior to any use as management tools, in
500 forecasting or risk mapping (Peterson, 2005). In invasive species applications, model
501 validation should be conducted first within the training region to assure significant
502 predictive ability before model transfer to other regions. Such validation should ideally rely
503 on an independent dataset with different source of biases to efficiently validate the model
504 (e.g., different origin, collected with different sampling methods) to avoid incorrect or
505 incomplete results (Lobo et al., 2008; Peterson et al., 2008). Not surprisingly, as
506 independent datasets are seldom available, robust model assessments and predictive
507 performance are quite rare in ENM (Joppa et al., 2013). In our work, we highlight the
508 model validation performed prior to model projection, and that the results obtained
509 reinforce the reliability of the model.

510

511 *4.2. Wild pigs in ecoregions, biodiversity hotspots, and protected areas*

512 Our results show that wild pigs are currently present in 60.3% of the ecoregions under
513 analysis, suggesting that established populations are highly likely. This scenario represents
514 a 1.5-fold increase compared with the 39.7% reported in previous research conducted in the
515 same countries, except Bolivia (Salvador and Fernandez, 2017). Also, in our study, most
516 (94.1%) ecoregions overlapped totally or partially with suitable environmental conditions,
517 and only four ecoregions (Solimões-Japurá Moist Forests, Lake, Central Andean Dry Puna,
518 Atacama Desert) were classified as completely unsuitable. Among these, the last three are
519 cold deserts with extreme weather conditions, of which extremely low precipitation most
520 likely explains their unsuitability for wild pig occurrence.

521 In terms of relevant areas for biological conservation, results are at least concerning.
522 Hotspots harbor half of the world's plant species and more than a third of mammal, bird,
523 reptile, and amphibian species in 2.3% of Earth's land surface. Moreover, the introduction
524 of exotic species is having a huge impact on the native communities of many hotspots
525 (Mittermeier et al., 2004). Here, we identified four hotspots which are currently invaded by
526 wild pigs, each encompassing variable areas of suitable habitat for wild pigs, ranging
527 between 5.6% and 85% of their total area within the study region. Together, these hotspots
528 harbor an important number of threatened (vulnerable, endangered and critically
529 endangered) endemic and non-endemic mammal (42 and 136), bird (177 and 267), and
530 amphibian (326 and 394) species (see Table 11 in Mittermeier et al., 2004,).

531 At the PAs level, the number of PAs in the study region that are invaded or at risk is
532 worrying. As the impact of wild pigs on ecosystems is increasingly acknowledged
533 worldwide, assessing their potential effects on these areas becomes of paramount
534 importance for policy-making and management (Ballari et al., 2015). Whereas other
535 authors have reported great geographical expansion (Pescador et al., 2009) and increased
536 wild pig abundances (Carpinetti and Merino, 2003; Pérez Carusi et al., 2009) in PAs of
537 Argentina, impact assessments on PAs from Chile have been less systematic (Skewes and
538 Jaksic, 2015). In Brazil, according to Salvador and Fernandez (2017), either wild pig
539 presence has not been evaluated in most PAs due to the recent onset of the invasion, or the
540 available assessments have been biased with only a few of the IUCN's categories of PAs (I
541 and II) being considered (Sampaio and Schmidt, 2013; Ziller and Dechoum, 2013). Lastly,
542 to our knowledge, this is the first systematic review of currently and potentially invaded
543 PAs in Uruguay, Bolivia and Paraguay which hinders any comparisons based on previous
544 reports.

545 The sensitivity of our binary model was nearly 83%, and showed a relatively small
546 omission error which makes this model a useful tool for the identification of invaded PAs.
547 Contrarily, the commission error was relatively high. We should note that, in the context of
548 ENM, this error can have a twofold contribution from true and apparent commission errors
549 (Anderson et al., 2003). Firstly, true commission error is represented by the proportion of
550 truly negative PAs falsely classified as suitable, which can lead to model overprediction.
551 Although this error has been cited as a problem (Brotons et al., 2004; Stockman et al.,
552 2006) in terms of potential distribution, we stress that this caveat should not be seen as a
553 shortcoming but rather as a desirable trait in the identification of areas susceptible to
554 colonization by an invasive species, as was suggested by Peterson et al., (2011). Also,
555 considering the invasiveness of wild pigs and their negative impacts on ecosystem, this
556 overprediction adheres to a "precautionary principle" weighing in favor of environmental

557 protection in the case of uncertainty (Cooney, 2004). Secondly, apparent commission error
558 derives from suitable regions correctly predicted as presence, but that cannot be
559 demonstrated as such because the species exists but has not yet been reported. This may be
560 the case when inadequate sampling exists (Karl et al. 2002) and could explain part of the
561 commission error detected in our results. Also, PAs located in suitable areas which have not
562 yet been invaded might explain part of this error, which should lead to a swift
563 improvement of active surveillance inside and near those PAs. It is expected that these
564 frequencies will change in the future as new wild pig reports become available from
565 previously unoccupied PAs or previously occupied PAs where detections had failed. In any
566 case, this scenario is expected considering that wild pigs seem to be in the process of
567 expansion in the study region.

568 In comparison with the most comprehensive and updated study in the region (Salvador
569 and Fernandez, 2017), we found higher proportions of PAs that are already invaded or at
570 risk in every country, except Uruguay, where all PAs are reported to be affected. The
571 notable increases in the proportion of PAs with confirmed presence of wild pigs was led by
572 Chile (16.7%) and followed Paraguay (9.5%), Argentina (3.6%), and Brazil (2.3%). These
573 rises could be accounted for by at least three factors, separately or in combination; namely a
574 different methodological approach as explained before, a more thorough and updated
575 compilation of wild pig records, or a true expansion of wild pig populations and their
576 establishment in previously uninvaded areas in recent years.

577 Our study is unique in at least three contributions, by (i) adding novel information
578 about invasion and habitat suitability in biodiversity hotspots; and (ii) providing an updated
579 list of PAs currently occupied or at risk for wild pig invasion where prompt allocation of
580 resources for management and control should be prioritized, and (iii) developing a dynamic
581 web application that offers interested parties such as scientists, managers and decision
582 makers, access to relevant information that can be used as a conservation tool, either alone
583 or in combination with other resources. Finally, our work raises yet another alert about the
584 current and potential impacts of wild pigs on the regional biodiversity, especially at mega-
585 diverse areas and on national conservation targets, if rapid and stringent measures are not
586 adopted.

587

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1064 Table 1. Results of threshold-based model that classifies the calibration and projection
 1065 areas as suitable or unsuitable. The total area (km²) of each country and suitable/unsuitable
 1066 area is presented, followed by their corresponding percentages between parentheses.

1067

Country	Total area	Suitable area	Unsuitable area
Argentina	3 447 500	1 504 300 (43.6%)	1 943 200 (56.4%)

Bolivia	1 139 200	142 200 (12.5%)	997 000 (87.5%)
Brazil	8 784 900	3 155 800 (35.9%)	5 629 100 (64.1%)
Chile	980 800	150 100 (15.3%)	830 700 (84.7%)
Paraguay	437 900	211 600 (48.3%)	226 300 (51.7%)
Uruguay	211 600	205 900 (97.3%)	5700 (2.7%)
Total	15 001 900	5 369 900 (35.8%)	9 632 000 (64.2%)

1069 Table 2. Biodiversity hotspots in the study region. The estimated area inside the study region is presented, followed by suitable and
1070 unsuitable areas and their respective percentages. The number of wild pig records inside each hotspot is presented followed by its
1071 percentage.

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Hotspot	Total area	Suitable (%)	Unsuitable (%)	Records (%)
Atlantic Forest	1 337 900	1 137 900 (85)	200 000 (15)	1174 (17.1)
Cerrado	2 114 200	1 296 700 (61.3)	817 500 (38.7)	1263 (18.4)
Chilean Winter Rainfall- Valdivian Forests	507 300	190 500 (37.5)	316 800 (62.5)	635 (9.2)
Tropical Andes	841 200	50 000 (5.6)	836 200 (94.4)	4 (0.1)
Total	4 800 600	2 675 100 (55.7)	2 170 500 (44.3)	3076 (44.8)

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1086 Table 3. Country-level summary of (a) total number of protected areas (PAs) and their accumulated area, (b) total number and
 1087 percentage of PAs with reports of wild boar followed by the total and percent area comprised, and (c) total number and percentage of
 1088 PAs that partially or completely overlap with the area suitable for the establishment of wild boar according to our model. Areas are
 1089 reported in km².
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Country	(a) Protected areas		(b) Reports		(c) Model predictions	
	Total	Area	PAs invaded	Area invaded	PAs at risk	Area at risk
Argentina	408	267 521	64 (15.7%)	123 465 (46.1%)	233 (57.1%)	157 184 (58.8%)
Bolivia	153	401 089	10 (6.5%)	126 593 (28.2%)	55 (35.9%)	311 486 (77.7%)
Brasil	2899	2 951 455	135 (4.7%)	348 438 (11.8%)	1682 (58.0%)	1 610 810 (54.6%)
Chile	192	171 062	39 (20.3%)	40 372 (23.6%)	81 (42.2%)	93 296 (54.5%)
Paraguay	95	27 677	9 (9.5%)	6117 (22.1%)	69 (72.6%)	8476 (30.6%)
Uruguay	19	7851	19 (100%)	7851 (100%)	19 (100%)	7851 (100%)
Total	3766	3 826 654	278 (7.4%)	652 835 (17.1%)	2139 (56.8%)	2 189 103 (57.2%)

1092 **Legends for figures**

1093

1094 Figure 1. Continuous ecological niche model for wild pigs in southern South America.
1095 Habitat suitability is shown for ecoregions completely or partially overlaying Argentina
1096 (AR), Bolivia (BO), Brazil (BR), Chile (CL), Paraguay (PY), and Uruguay (UY).

1097

1098 Figure 2. Binary-response ecological niche model for wild pigs in southern South America.
1099 Habitat suitability is presented as presence/absence areas in ecoregions completely or
1100 partially overlaying Argentina (AR), Bolivia (BO), Brazil (BR), Chile (CL), Paraguay
1101 (PY), and Uruguay (UY).

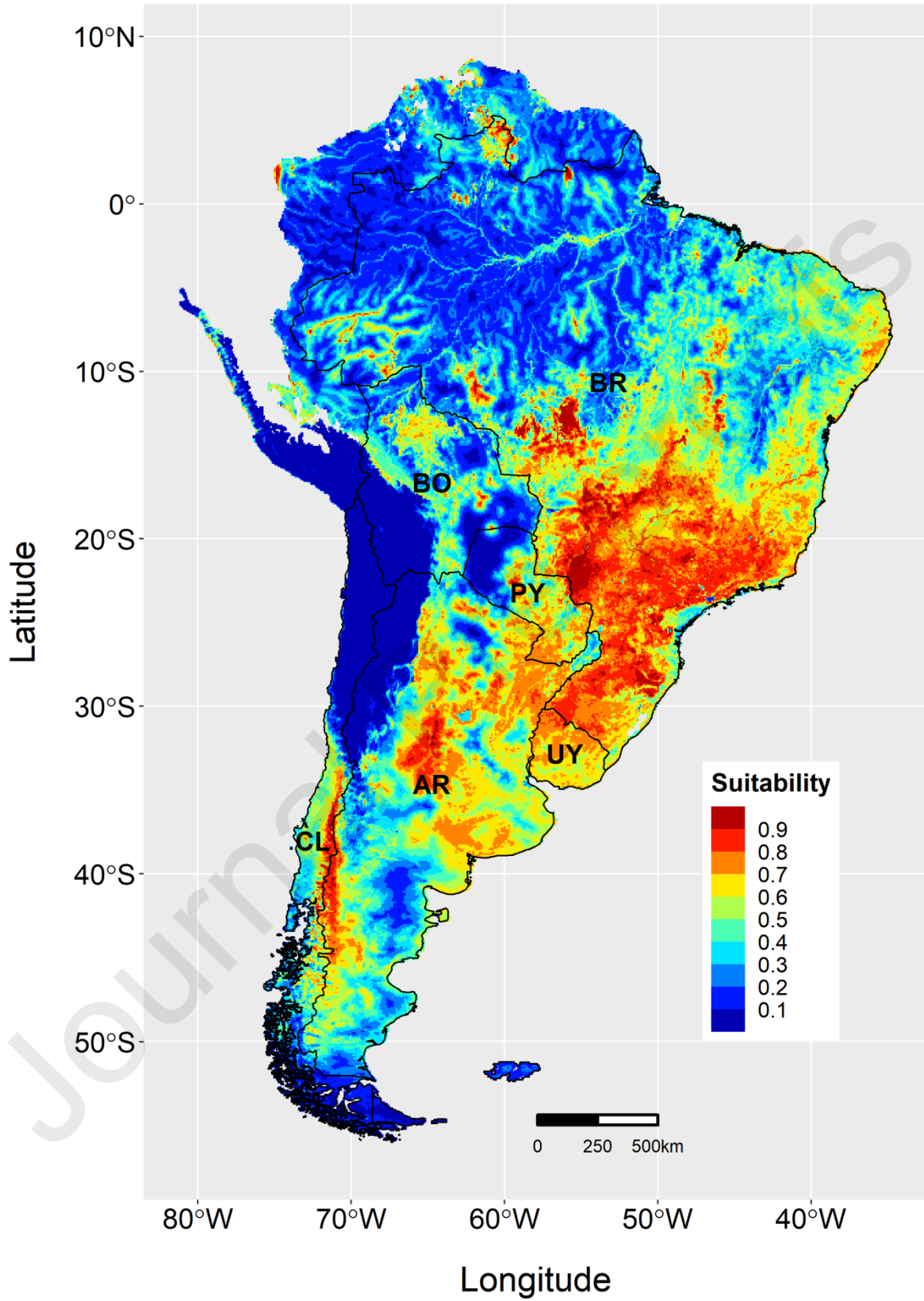
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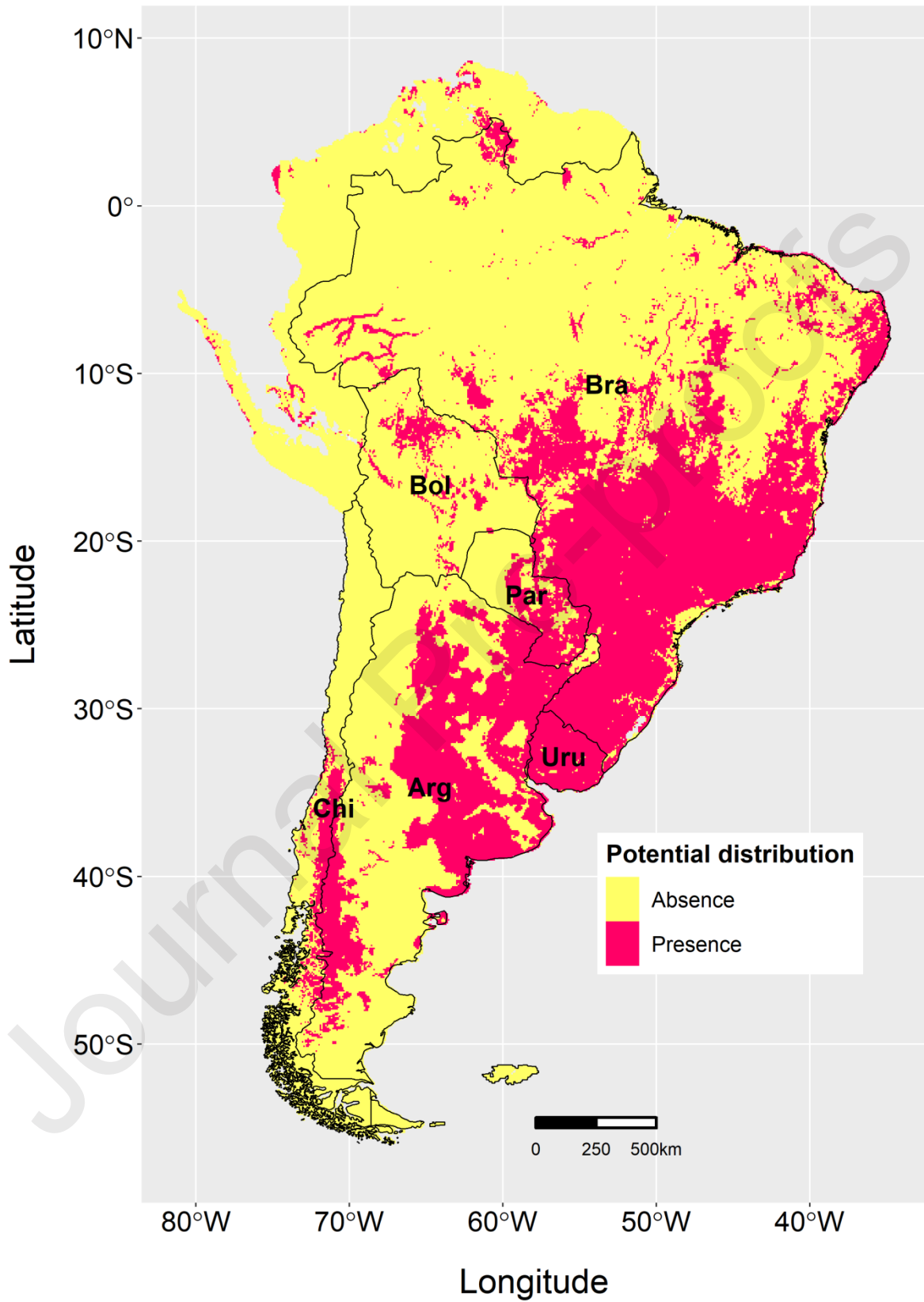
1103 Figure 3. Biodiversity hotspots of the study region: Atlantic Forest (AF), Cerrado (CE),
1104 Chilean Winter Rainfall-Valdivian Forests (CF), and Tropical Andes (TP).

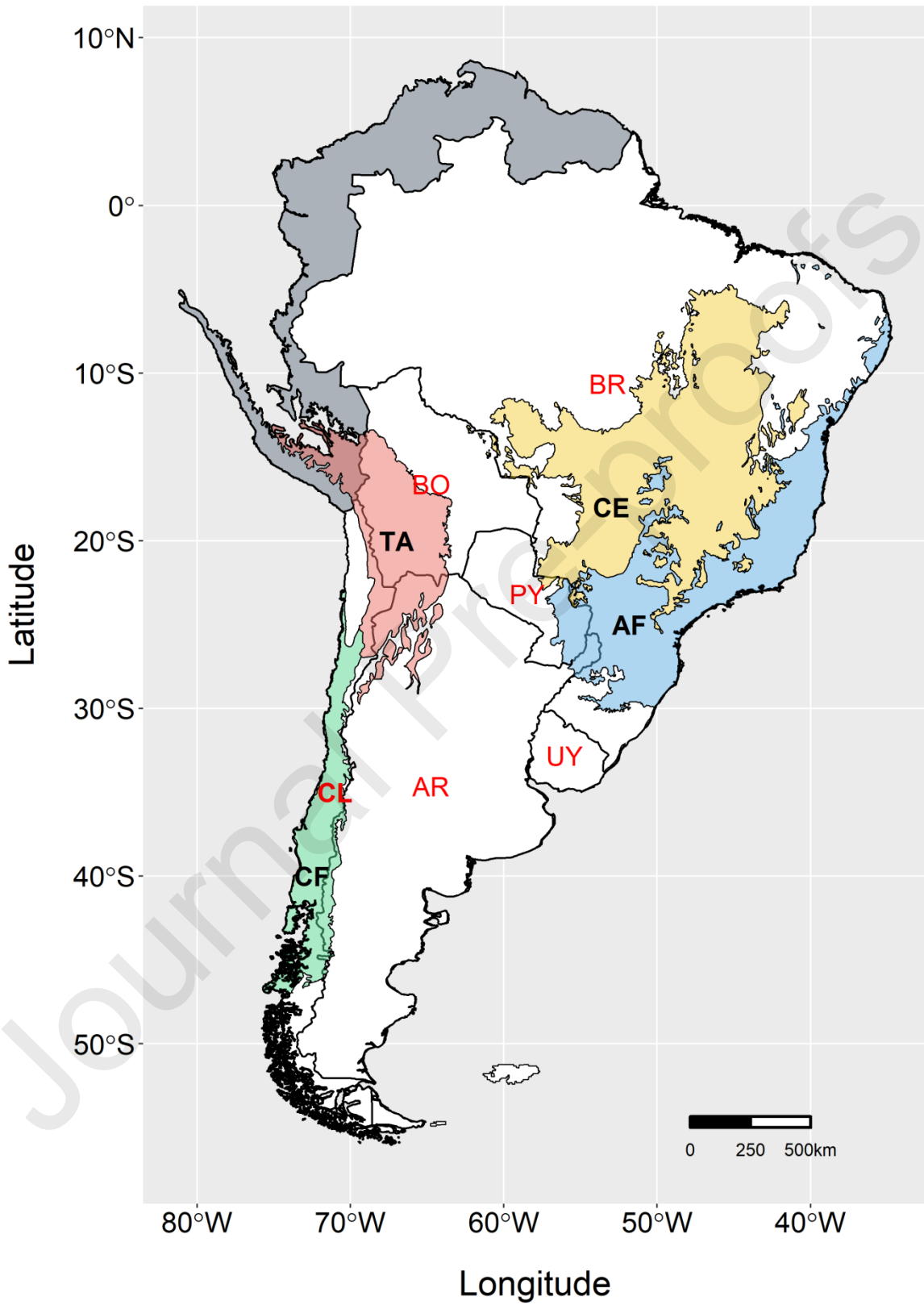
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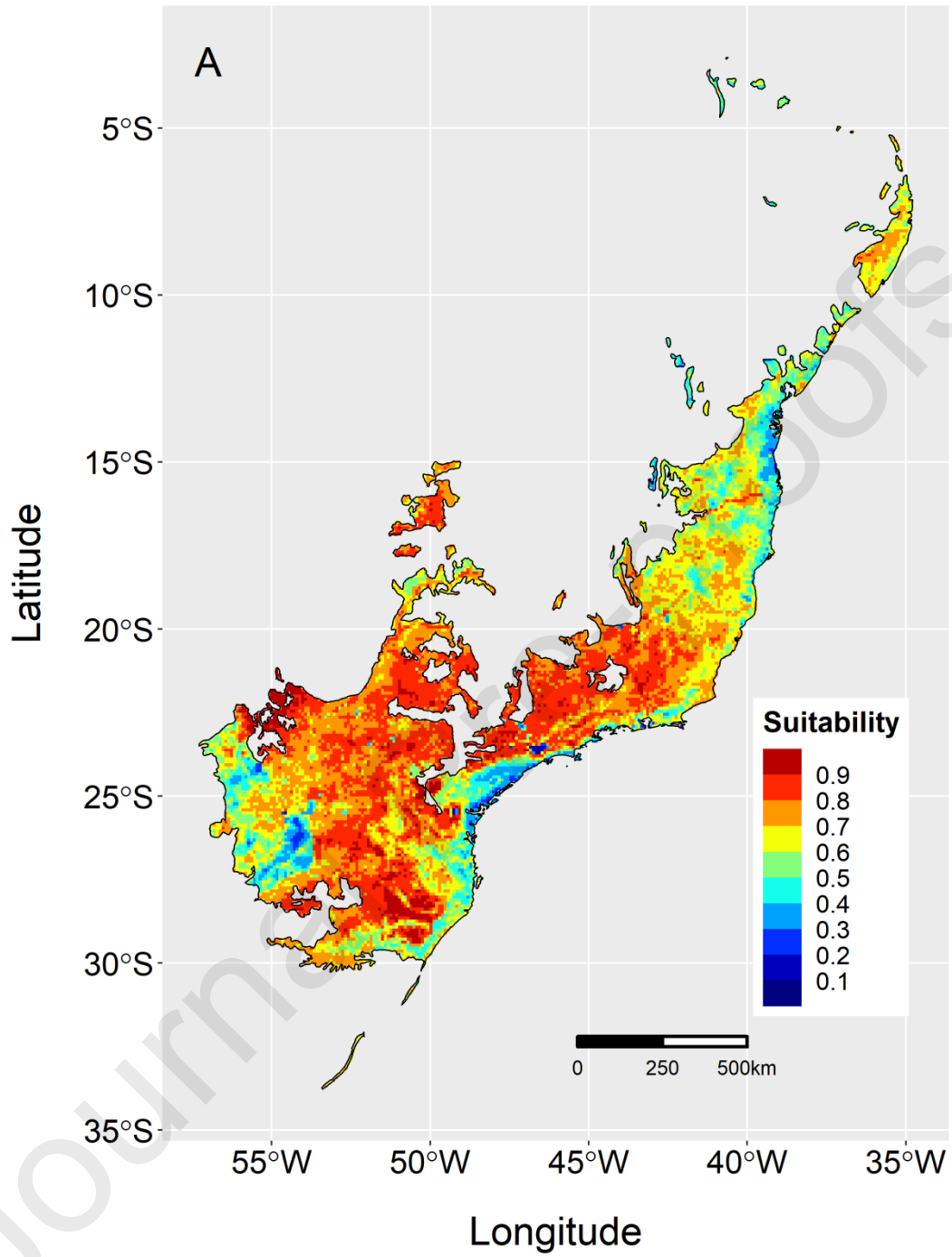
1106 Figure 4. Continuous models showing habitat suitability in biodiversity hotspots overlaying
1107 the study region: Atlantic Forest (A), Cerrado (B), Chilean Winter Rainfall-Valdivian
1108 Forests (C), and Tropical Andes (D).

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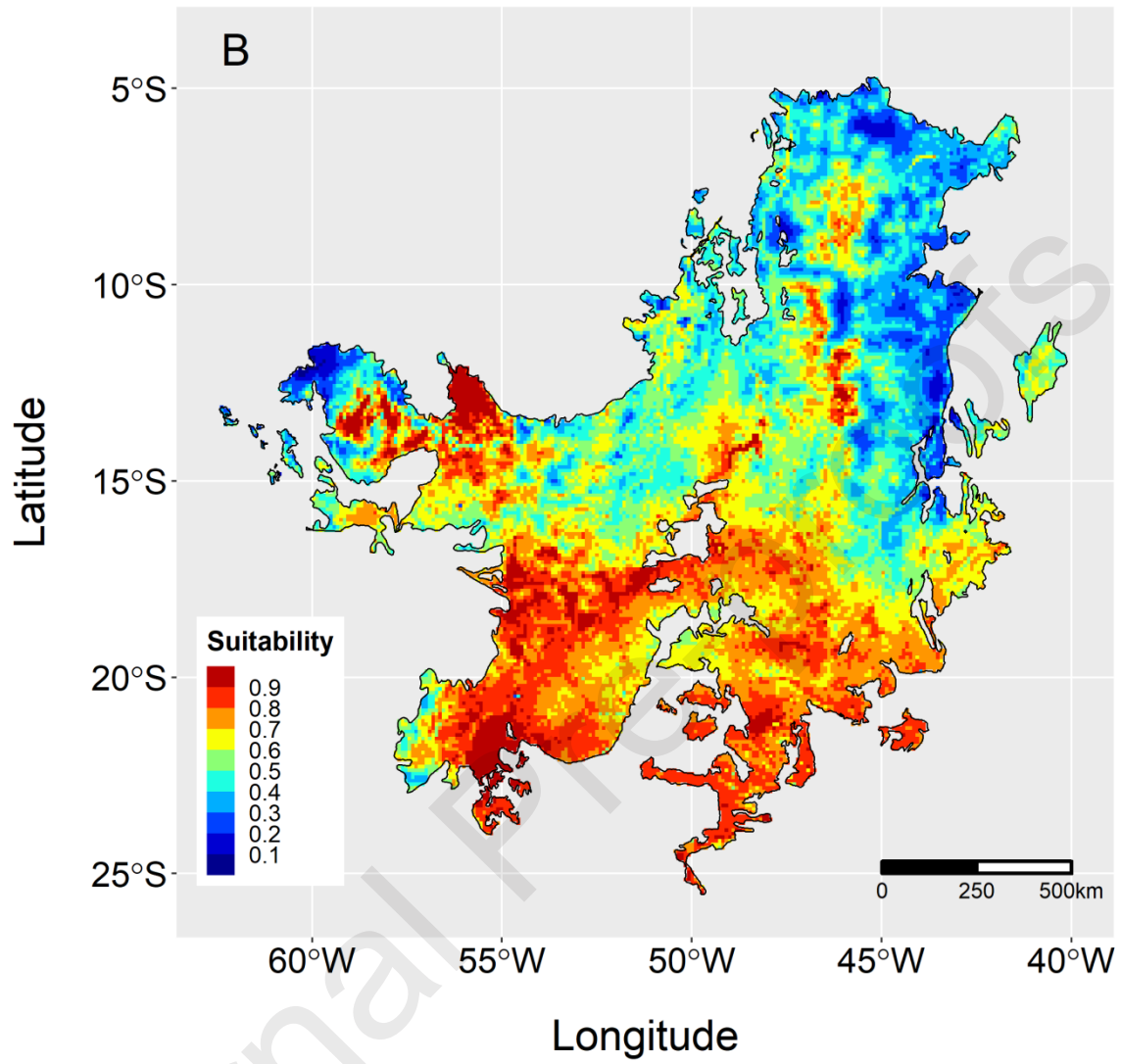




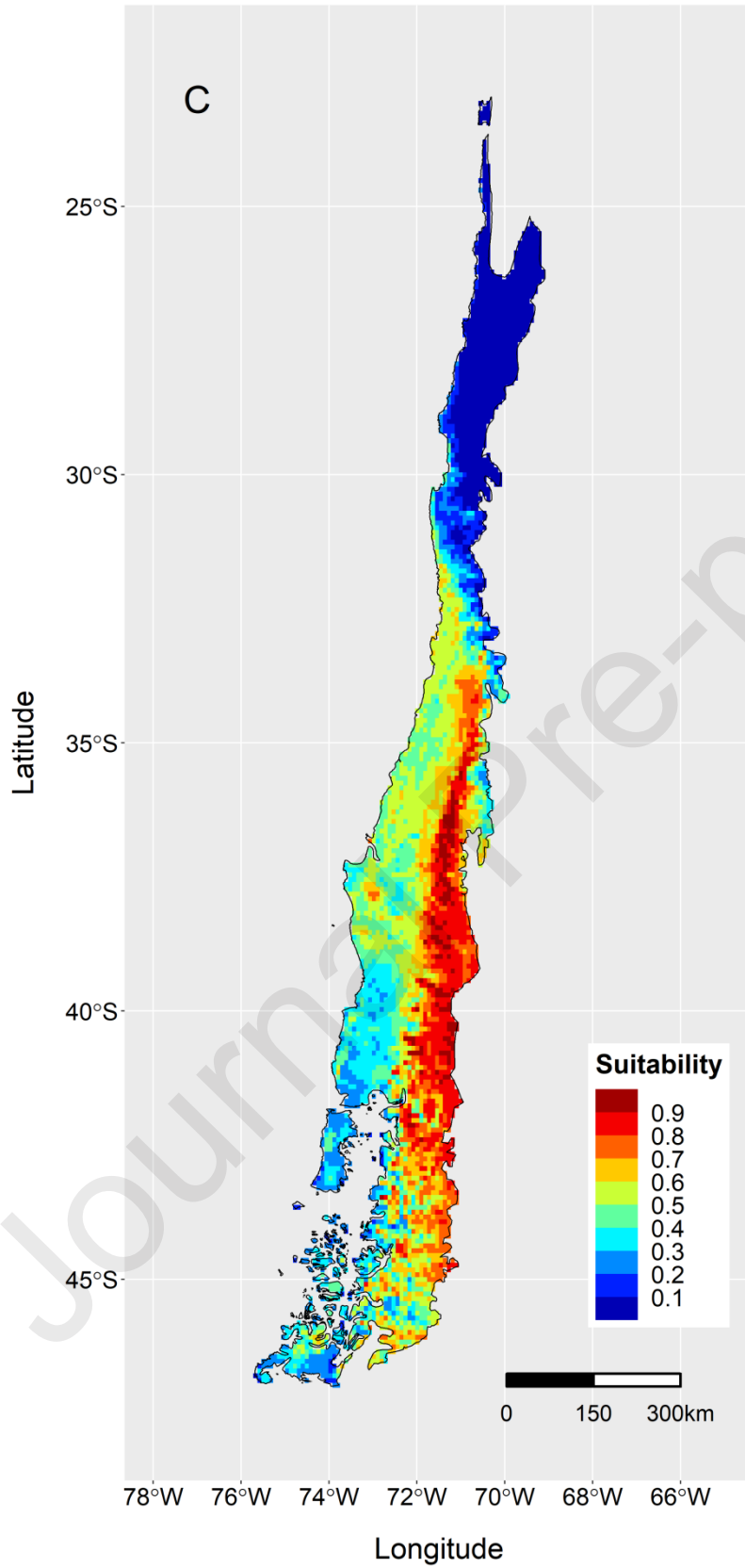


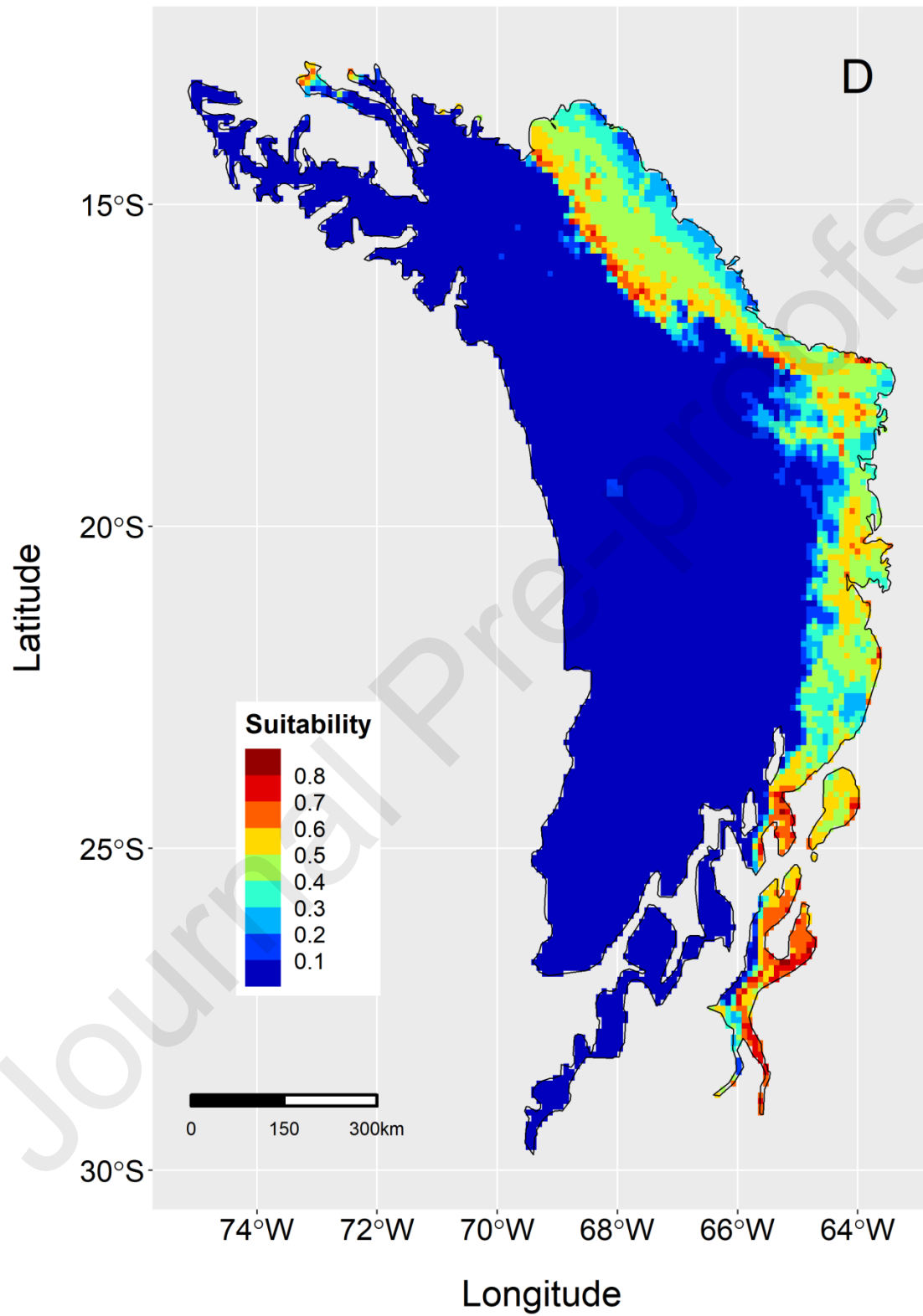


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1117 **Declaration of interests**

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1119 The authors declare that they have no known competing financial interests or personal
1120 relationships that could have appeared to influence the work reported in this paper.

1121

1122 The authors declare the following financial interests/personal relationships which may be
1123 considered as potential competing interests:

1124

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