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Invasive wild boar's distribution overlap with threatened native ungulate in Patagonia

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Wild boar (*Sus scrofa*) is one of the most damaging invasive species in the world and can have a profound impact on the distribution of native species. Nevertheless, there still are limitations on the species' current fine-scale spatial information, which is needed to develop effective management measures. Here, we used Species Distribution Models (SDMs) and niche overlap analysis to estimate potential conflict areas between the wild boar and the native southern pudu (*Pudu puda*), which is a bioindicator of the forest conservation status within the Nahuel Huapi National Park (NHNP), Argentina. The two species' environmental niche overlaps by 40%, which results in a wide geographical overlap between wild boar and pudu distributions. The distribution model predicted that the wild boar potential distribution occupies 22% of the national park and overlaps up to 67% with the pudu distribution, which in turn occupies 20% of the park. Based on our models, we classified 12% of the park as extreme management priority areas, because both species are present. High priority areas, where wild boars have the potential to invade but will not overlap with pudu populations, represent 10% of the park. Medium priority areas, where wild boars do not threaten pudu populations, and low priority areas, with no potential presence of either species, are 8% and 68%, respectively. The results of this study show how SDMs developed at local scales can support the management and monitoring of native and invasive species and help guide the allocation of efforts and resources for management actions focused on protected areas.

Key words: conservation, mammals, *Pudu puda*, *Sus scrofa*, species distribution modeling, wildlife management

El jabalí (*Sus scrofa*) es una de las especies invasoras más dañinas del mundo, pudiendo ocasionar un profundo impacto en la distribución de numerosas especies nativas. Sin embargo, todavía existen limitaciones en la información espacial a pequeña escala de la especie que es clave para el desarrollo de medidas de manejo eficaces. En este estudio, utilizamos Modelos de Distribución de Especies (MDE) y análisis de superposición de nichos basados en variables climáticas y de paisaje para estimar las potenciales áreas de conflicto entre el jabalí y una especie indicadora del estado de conservación del bosque, el ciervo pudu (*Pudu puda*), dentro del Parque Nacional Nahuel Huapi (PNNH), Patagonia, Argentina. El nicho ambiental de las dos especies se solapa en un 40%, lo que se refleja en una superposición espacial entre las distribuciones potenciales de jabalí y pudu dentro del parque. Esta superposición es mucho mayor de lo esperado en una distribución aleatoria simulada para jabalí. Los modelos de distribución predicen que el jabalí y el pudu se pueden potencialmente distribuirse en un 22% y 20% del parque nacional, respectivamente. A pesar de estas limitadas distribuciones en el parque, se observa que las dos especies se superponen en 67% de sus potenciales áreas de distribución. Basándonos en nuestros modelos, clasificamos el 12% del parque como áreas de extrema prioridad de manejo, debido a la presencia de ambas especies. Áreas de alta prioridad representan el 10% del área del parque, donde los jabalíes tienen potencial de invadir, pero no se superponen con las poblaciones de pudu. Las áreas de prioridad media, donde las poblaciones de pudu no están amenazadas por el jabalí, y las áreas de prioridad baja, sin potencial presencia de las dos especies, representan 8% y 68% del área del parque, respectivamente. Los resultados de este estudio evidencian como los MDEs desarrollados a escalas locales pueden apoyar al manejo y monitoreo de especies nativas e invasoras, ayudando a orientar la asignación de esfuerzos y recursos para acciones de manejo focalizadas en áreas protegidas.

Palabras clave: conservación, mamíferos, manejo de vida silvestre, modelos de distribución de especie, *Pudu puda*, *Sus scrofa*

Wild boar (*Sus scrofa*) is considered as one of the most harmful and widely distributed invasive species in the world (Lowe et al. 2000). Originally from Eurasia, wild boars now are present on all continents except Antarctica (Long 2003). This extraordinary invasive potential is the result of two factors: (i) the species' naturally high behavioral plasticity (Graves et al.1984; Caruso et al. 2018) and (ii) dispersion facilitation due to human activities (Sales et al. 2017; Hernández et al. 2018). Humans frequently transport wild boars as livestock to new territories due to their appreciated meat and sometimes promote hybridization with its domestic forms (the domestic pigs) to increase the growth rate (Lowe et al. 2000; Long 2003). When accidentally or purposefully introduced in new territories, wild boars quickly spread due to high reproductive rates, generalist omnivorous diet, and high behavioral plasticity (Coblentz and Baber 1987; Podgórski et al. 2013; Ballari and Barrios-García 2014; Senior et al. 2016). Moreover, changes in land use and global climate in recent decades also are contributing to the expansion of wild boars and other invasive species (Hellman et al. 2008; Bellard et al. 2014; Morelle and Lejeune 2016; Sales et al. 2017).

In areas where it was introduced, the wild boar is extremely damaging, mainly due to its rooting behavior (the act of excavating the ground to consume underground plant tissues, invertebrates, and fungi), turning extensive areas of forest soil, which disturbs the structure and composition of plant communities (Barrios-García and Ballari 2012; Ballari and Barrios-García 2014). Beyond the rooting behavior and habitat modification, wild boars also prey upon small vertebrates, such as frogs and ground nesting bird, compete for resources with the local species, transmit diseases (Barrios-García and Ballari 2012; Ballari and Barrios-García 2014), and even interfere in the efforts to protect threatened and endangered species (Bevins et al. 2014). Some native ungulate species, such as the Pampas deer (*Ozotoceros bezoarticus*), are particularly susceptible to wild boar activity, presenting reduced activities and detection rates in areas where wild boars are active (Pérez et al. 2009). The drivers behind the negative effects of wild boars on native ungulate populations most probably are related to resource competition, but other antagonistic interactions, including predation, also are possible causes because wild boars are known to prey upon young lambs (Choquenot et al. 1997, for Australia).

In Argentina, the wild boar first was introduced in its domestic form by the Spanish colonizers in the 16th century (Carpinetti et al. 2016). Later, at the beginning of the 20th century, it was introduced a second time from Europe, in its wild form, for hunting purposes (Navas 1987). Since these introductions, continuous translocations, and reintroduction in hunting grounds and game reserves, the species has expanded rapidly throughout Argentina, already being present in at least 10 of the 16 terrestrial ecoregions, with the potential to invade and disperse effectively to novel areas, including protected areas (Ballari et al. 2015; Sanguinetti and Pastore 2016, Ballari et al. 2019a). In some protected areas, such as the Nahuel Huapi National Park (NHNP), the wild boar has been recorded for almost a century (Daciuk 1978; Ballari et al. 2015) and is reported to negatively affect the local biodiversity and ecosystem processes (Nuñez et al. 2013; Barrios-García et al. 2014; Ballari et al. 2020). Despite the extensive damage caused, the spatial distribution and potential pathways of dispersion of the wild boar within the NHNP still are unknown.

The NHNP is an important conservation site, home of a valuable population of the endangered southern pudu (*Pudu puda*), a small deer endemic to the temperate and coastal forests of Argentina and Chile. In Argentina, the southern pudu only occurs within a very limited distribution, inhabiting humid, temperate, and cold forests with a dense shrub layer (Jimenez 2010; Ballari et al. 2019b). The pudu is herbivorous and consumes leaves, fruits, buds, and flowers, of several native shrubs and trees. This emblematic deer could play a key role in the seed dispersion of several species in Patagonian forest (Jimenez 2010; Pavez-Fox and Estay 2016). The species is classified as vulnerable for Argentina and Chile (Meier and Merino 2007; Silva-Rodríguez et al. 2016; Ballari et al. 2019b); major threats to its populations include the impact of invasive species, habitat loss and fragmentation, road fatalities, and illegal hunting (Silva-Rodríguez et al. 2009). Within the NHNP, wild boar distribution is expected largely to overlap areas inhabited by southern pudu (Meier and Merino 2007), and the presence of pudu is reported to be scarce or nonexistent in areas heavily used by invasive mammals such as red deer (*Cervus elaphus*) and wild boar (Meier and Merino 2007; Gantchoff et al. 2013).

Considering available data regarding the invasion of wild boar and the vulnerability of pudu within the NHNP, this study had three objectives: (i) identify the niche overlap of wild boar and southern pudu populations in NHNP; (ii) predict at a fine spatial scale the potential distribution of the wild boar and pudu, as well as their overlap within the park; and (iii) use the potential distribution and overlap of these species as a criterion to define priority areas for wild boar management to guide the allocation of resources for species conservation to the more cost-effective sites in NHNP.

Material and Methods

Study area

The study was carried out in the Nahuel Huapi National Park (41°00′ S, 71°30′ W), a protected area with 712,160 ha in southwest Argentina. The park hosts at least 282 vertebrate species, of which 21, including the southern pudu, are classified as "Vertebrate Species of Special Value" (VSSV) and at least 113 of the park's species are considered endangered. The park also includes areas of three major Argentine ecoregions: the Patagonian Steppe, Patagonian Forests, and High Andean Forest (SIB 2017).

Species occurrence records

We gathered occurrence records for wild boar and pudu in the NHNP. Records were obtained from online databases, personal interviews, and direct observations. Data from online databases were obtained from SIB (Biodiversity Information System, of National Parks Administration of Argentina; https://www.sib.gob.ar). Data from peer-reviewed journal papers were obtained searching in Web of Science, Google Scholar, and SciELO, using the keywords ("wild boar" OR "feral pig" OR "Sus scrofa" OR "jabali" OR "cerdo salvaje" OR "chancho salvaje") AND ("Nahuel Huapi National Park" OR "Parque Nacional Nahuel Huapi") for wild boars, and ("pudu" OR "Pudu puda") AND ("Nahuel Huapi National Park" OR "Parque Nacional Nahuel Huapi") for pudu. The personal interviews were undertaken with park rangers, national park technicians, researchers from CONICET (the National Scientific and Technical Research Council of Argentina), local landowners, local hunters, and tour guides. The interviews were informal meetings where the presence of wild boar and pudu was indicated in a map of NHNP according to the experience of each interviewed person. We also carried out fieldwork surveys in areas of the NHNP where there were no data as to the presence of wild boar or pudu within a radius of least 1 km. The fieldwork surveys consisted in following trails for ca. 500 m (exact distances were not measured precisely), looking for signs of wild boar presence. Locations of fieldwork were defined mostly by logistic considerations (see Supplementary Data SD1 and SD2 for records details, and Supplementary Data SD3 for the spatial distribution of the records). Despite the opportunistic and nonstandardized field work approach, data collected in the fieldwork remain reliable for the present study, because the statistics employed rely only on species occurrence records, allowing the usage of data from multiple and nonstandardized sources (Peterson et al. 2011). Finally, to reduce the environmental biases of occurrence points, we used a 1-km spatial rarefaction, dividing the park area in a 1-km^2 grid and considering only one record per grid cell.

Environmental variables

We used a set of 41 variables of climate, soil, land cover and topography, to characterize the environmental conditions of the study area at a fine spatial scale (1 km), because, with the exception of the climatic variables, remaining variables were generated from environmental conditions with great accuracy, thus characterizing the local habitat of the species. We obtained 19 bioclimatic variables from WorldClim v. 2.0 (Fick et al. 2017). For soil, we used "soil organic carbon stock" and "soil depth" variables from SoilGrids (Hengl et al. 2014), because the wild boar have the habit of overturning the soil. For land cover, we calculated 19 raster variables with the linear distance of each land cover class feature (see Supplementary Data SD4), creating a continuous surface representing at each pixel the distance from each land cover class categories defined by the National Park Administration (APN 2007), and multiplied by minus one to have an inverse effect of distance. Finally, we also added an elevation variable by using a digital elevation model (DEM), with elevation values in meters from Shuttle Radar Topography Mission—SRTM v. 4.1 (Farr et al. 2007). A complete description of the variables is available in Supplementary Data SD4. All variables were calculated or resampled at one km^2 using geographic coordinates, using Datum WGS 84. We used the NHNP borders as background limit because we only were interested in the detailed distribution of the species inside the study area, where the occurrence data were more available. We added this background limit because invasive species tend to adapt feeding habits and behavior according to very localized environmental features (Mooney and Cleland 2001; Clavero and Garcia-Berthou 2005). A careful selection of environmental variables is important to obtain realistic predictions of invader distributions, particularly when the distribution is projected into novel environments (Sheppard and Gonzalez-Andujar 2013). We carried out a Principal Component Analysis on all variable values from the whole background (PCA-env) to reduce collinearity, choosing 12 axes resulting from the PCA-env. These axes jointly explained 95.8% of the environment background variation (De Marco and Nóbrega Júnior 2018). We then obtained the score values from these axes and created 12 raster files that were used to create the Species Distribution models (SDM). The scree plot from the PCA-env can be visualized in Supplementary Data SD5 and Fig. 1. We computed two ellipses (95% from variation) for each species to visually explore occurrences in relation to the total variation of environmental conditions (Fox and Weisberg 2019).

Environmental Niche overlap

We explored the overlap in the environmental niches of the two species using Schoener's *D* niche overlap metrics, which applies kernel smoothers to densities of species occurrence in a gridded environmental space (Broennimann et al. 2012). We used the same PCA-env described above, but using just the first and second axis of the PCA-env, which then were gridded into 100 × 100 cells covering the maximum and minimum values of the data. The first and second axis of the PCA-env captured about 37.9% and 26.84% of the data variation, respectively, totaling 64.74% of the environmental variability. We then calculated Schoener's D index, which ranges from 0 (complete discordance) to 1 (identical niches), to estimate the niche overlap of the two species. Finally, we tested if the similarity of niches (niche of wild

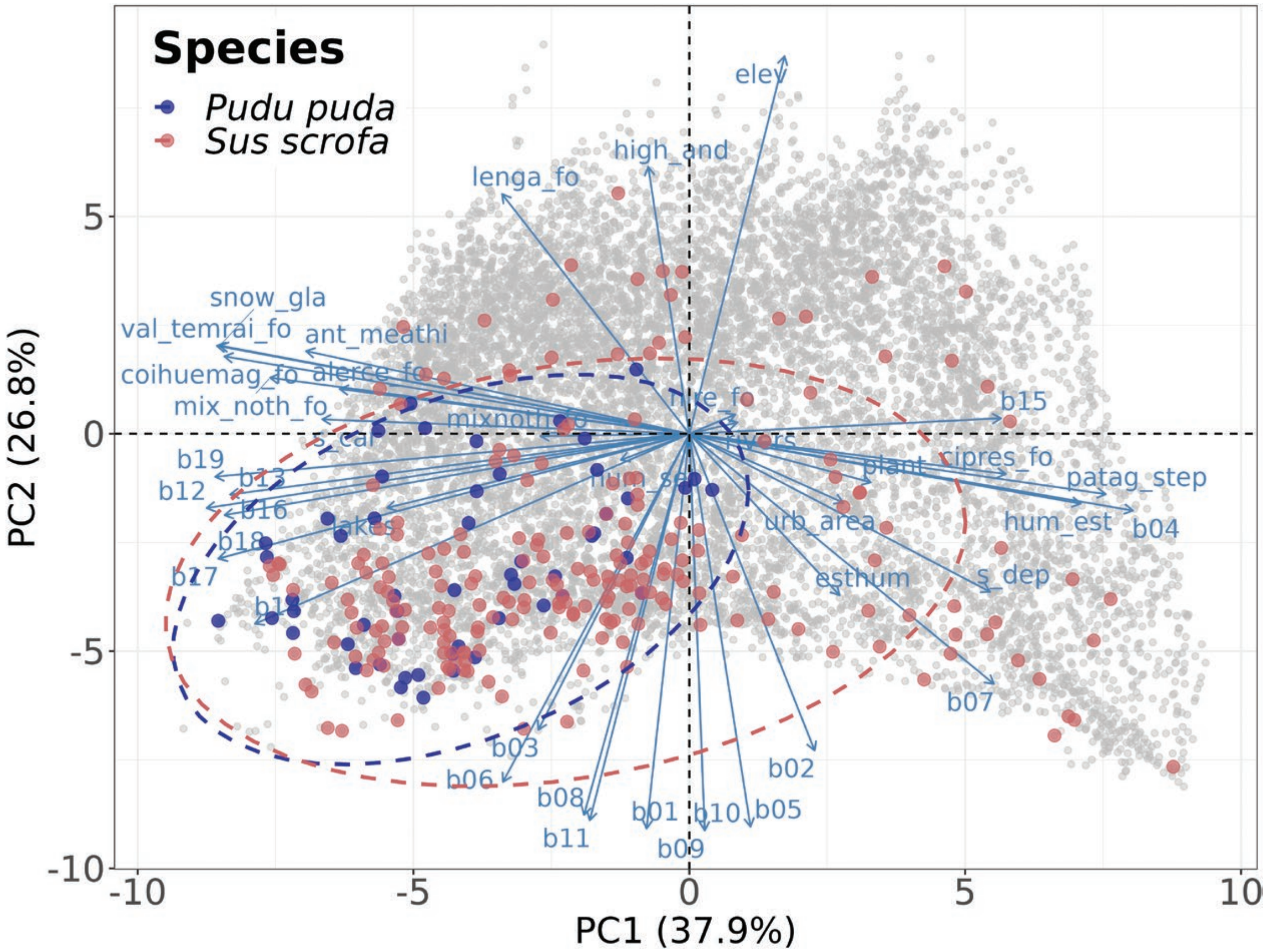

Fig. 1.—Biplot from the Principal Component Analysis (PCA-env) of the environmental variables related to all variable values from the whole background. The occurrence records of southern pudu are represented by blue points and from wild boar are represented by red points, in Nahuel Huapi National Park (NHNP), in Argentina. complete description of the variables is available in Supplementary Data SD4.

boar on pudu niches) was greater than expected from random points in the study area, with 999 iterations from a bootstrap test. All analyses were carried out using the ecospat package (Broennimann et al. 2018).

Species distribution modeling

Species distribution models (SDMs) are a common tool used to define suitability areas of a particular species, given a suite of environmental conditions. First, climatic tolerances of the species should be the main determinants of their distribution, neglecting dispersal limitations and biotic factors (e.g., competition, predation, or facilitation), which only seldom can be incorporated into SDMs (Rödder et al. 2008). The realized niche (i.e., the environmental conditions present within the geographical space occupied by the species) therefore is, under natural circumstances, only a subset of the fundamental niche (Hutchinson 1957; Soberón and Peterson 2005). Second, we assumed that the range of the species under study is in equilibrium with environmental variation (Pearson and Dawson 2003; Araújo and Pearson 2005). Third, we assumed that the niche is conservative over time and space (Peterson et al. 1999). These are common assumptions adopted in SDM studies, and besides being rarely fully met in nature, models ensuing still result in high predictive power, being very useful for predicting habitat suitability for species in conservation efforts (Jeschke and Strayes 2008).

Because models using different mathematical algorithms can result in different predictions of species' distributions (Qiao et al. 2015), we used a forecast ensemble approach (Araújo and New 2007), which is a consensual combination of different algorithms. This way, despite variations in algorithms' premises and predictions, the ensemble result leads to more reliable predictions by considering the uncertainties of the predictions (Diniz-Filho et al. 2009). We used six algorithms: (i) BIOCLIM (Nix 1986); (ii) Domain (Carpenter et al. 1993); (iii) Generalized Linear Models (GLMs; Guisan et al. 2002); (iv) Random Forest (Breiman, 2001); (v) Support Vector Machine (SVM; Tax and Duin 2004); and (vi) Maximum Entropy (MaxEnt; Phillips et al. 2017). The algorithms were fitted using the R-packages "dismo," "randomForest," and "kernlab" (Karatzoglou and Feinerer 2010; Liaw and Wiener 2002; Hijmans et al. 2015; R Core Team 2019).

We modeled each species individually using bootstrap criteria of 70% and 30% of the records used for train and test, respectively. This occurrence-partitioned criterion was used to evaluated the performance of each model using the area under the curve (AUC) metric, considering values between 0.7 and 0.9 as a "reasonable" prediction, and values higher than 0.9 as a "very good" prediction (Elith et al. 2006; Peterson et al. 2011). We produced 30 replicates for each algorithm, obtaining 180 maps (6 algorithms × 30 replicates) for each species. For the consensus ensemble, we used only replicas with AUC values above 0.75 by weighted mean (Elith et al. 2006; Peterson et al. 2011) using AUC metrics of single-models (Araújo and New 2007). Finally, we used the threshold that produces the Maximum True Skill Statistic (TSS) using the presence and pseudo-absence points (Liu et al. 2005) to reclassify the suitability map into presence-absence model, using the function "ecospat.max.tss" from *ecospat* package (Broennimann et al. 2018).

Priority areas for wild boar management

Given the ongoing decline in southern pudu populations (Silva-Rodríguez et al. 2016), its requirement for highly preserved habitat (Silva-Rodríguez et al. 2013; Fox and Estay 2016), and the habitat degradation driven by the wild boars, we decided to use the potential presence of pudu and wild boar as a criterion to define priority management areas within the NHNP. We classified the NHNP area into four categories: (i) Extreme priority areas: areas where both species potentially are present, indicating urgency in management and control of wild boar population; (ii) High priority areas: areas of potential presence of wild boar but with no potential presence of southern pudu. Despite the absence of the pudu, these areas require management to avoid becoming sources for the wild boar population, which then migrate and colonize other managed areas; (iii) Medium priority areas: areas with potential presence of pudu populations but not threatened potential invasion by wild boar; and (iv) Low priority areas: areas with no potential presence of either species.

Results

We found 64 records of *P. puda* and 253 records of *S. scrofa* (Supplementary Data SD1 and SD2, respectively). After carrying out the spatial rarefaction (i.e., maintaining just one record per one km^2 grid cell), we retained 54 records of pudu and 220 records of wild boar. For both species, more than 50% of the records were from areas of extensive public use and more than 40% of the records occurred in regions of Mixed *Nothofagus* forest (Roble-Raulí-Coihue; see Supplementary Data SD6). Maps with the spatial distribution of occurrences in the study area are available in Supplementary Data SD3.

The exploration analysis of occurrences disposition in the first two axes of the PCA-env shows that wild boar has a wide tolerance to environmental variation, which is highlighted by the wide geographic dispersion of the occurrences and by the large estimated ellipse (95% confidence interval) around the plotted points (Fig. 1). In contrast, pudu occurrences are more grouped, with a smaller estimated ellipse, being entirely contained within the wild boar's estimated ellipse. We also observed that wild boar occurrence is not driven by a single major environment variable, but rather by a set of variables each with a relatively small individual effect. The pudu occurrence is driven mostly by precipitation and distance from forest formations and lakes (Fig. 1).

Results of the environmental niche overlap analysis demonstrated that the two species overlap by 40% ($D = 0.403$), which reflects the environmental conditions overlap between wild boar and pudu distributions. This value was much higher than the similarity test ($D\text{sim} = 0.11$, $p = 0.034$), indicating that overlap of the niches is greater than expected based on a simulated random distribution of wild boars in the study area (Fig. 2).

In the model evaluation process, most models provided reasonable predictions when applied to wild boar, obtaining AUC values above 0.75 for all the algorithms used, with the exception of two algorithms, BIOCLIM and Domain (Supplementary Data SD7). The SDM prediction, from the assembled models, indicates areas of high habitat suitability for wild boar in the southern and northern regions of the NHNP, with lesser suitability in central areas of the NHNP. However, areas near lakes present high habitat suitability for wild boar, even when located in the central portion of the park. For pudu, suitable areas are restricted to the western region of the park; as a corollary, areas of the eastern portion of the park have low habitat suitability for pudu (Fig. 3). Adopting the thresholds to binarize the models, the potential distribution for wild boar and pudu correspond to 22.48% and 20.14% of the park area, respectively (Supplementary data SD8). From these areas, 66.9% of the potential distribution for pudu overlaps with the potential distribution of wild boar (Fig. 4A). Based on the potential distribution maps and the geographical overlap between the two species, we categorized 11.73% of the park as areas of extreme management priority, 10.15% as areas of high management priority, and 7.87% as areas of medium priority. The remaining 67.59% was classified as low management priority areas (Fig. 4B). The extreme management priority areas are mostly located in the west of the NHNP, which is a less populated area (few human settlements) and more humid due to higher rainfall. In turn, the high management priority areas are located mostly to the east of the park, being areas with less rainfall and with a higher human population density.

Discussion

The wild boar and the pudu presented an environmental niche overlap of 40% ($D = 0.403$). The similarity test showed that wild boars have great overlap with the environmental niche of pudu, indicating that the invasive species can occupy the same environmental conditions as the native species. Indeed,

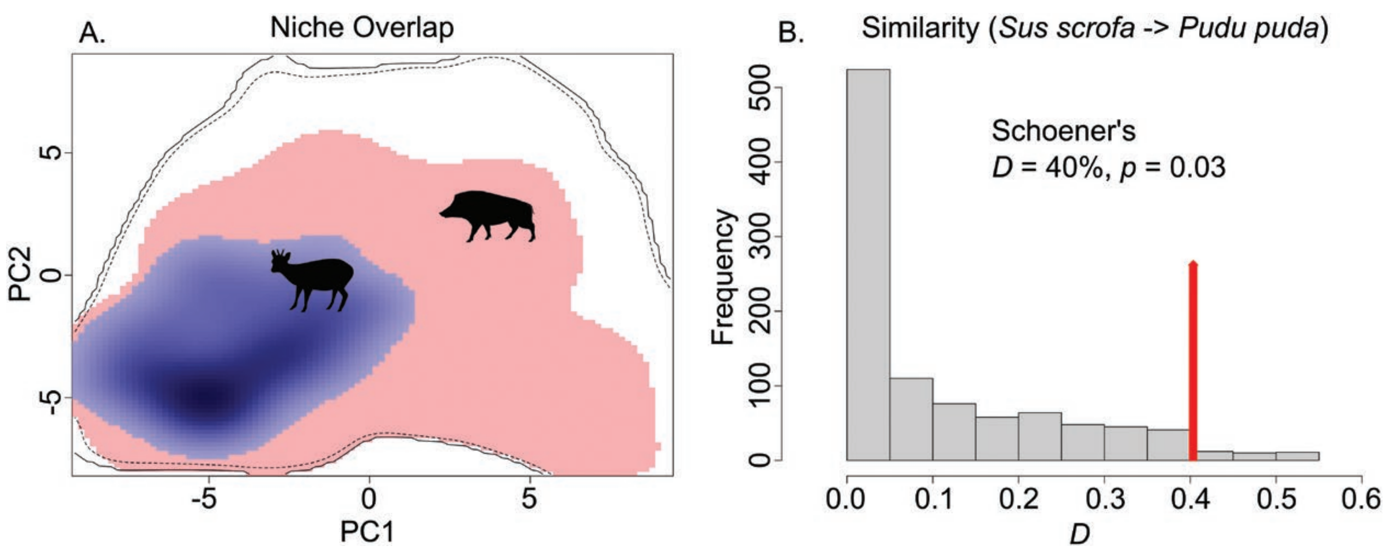

Fig. 2.—The niche overlap analysis of wild boar and southern pudu in Nahuel Huapi National Park (NHNP), Argentina: A) Niche overlap to two first PCA-env axis, the pudu in blue and the wild boar in pink; black lines represent all environmental variation (solid) and 95% from environmental variation (dashed); B) frequency distribution of Schoener's D values from bootstrap to similarity test, with the real value represented by the red line.

predictive maps of the SDMs showed that 66% of the suitable area within the NHNP for the endangered southern pudu also is suitable for wild boar. Considering the potential distribution of both species, up to 33% of the park area therefore requires some level of wild boar management to protect the pudu population.

The extensive distribution overlap between the pudu and wild boar within the NHNP is an especially concerning issue, considering that the southern pudu is very sensitive to disturbances caused by invasive mammals (Silva-Rodríguez and Sieving 2012; Meier and Merino 2007; Gantchoff et al. 2013). Wild boar can threaten pudu populations not only by resource competition, with the potential to cause competitive exclusion (Choquenot et al. 1997; Barrios-García and Ballari 2012), but also by being a vector of diseases. Wild boars are reservoirs of several viral, bacterial, and parasitic diseases, some of which are highly transmissible and damaging, such as brucellosis, tuberculosis, foot-and-mouth disease, and swine fever (Barrios-García and Ballari 2012; Miller et al. 2017). In addition, the fact that both species are ungulates increases the concern about their co-existence, given that ungulates share a large number of common pathogens (de la Fuente et al. 2004; Flueck and Flueck 2012). Nevertheless, we are aware that the mere presence or distribution overlap of wild boar with a native species does not exclusively imply competition. However, there is evidence that the population of pudu is lower in areas dominated by wild boar (Martin-Albarracin et al. 2015).

The precautionary principle for the management of invasive species in Argentina's national parks states that when an invasive exotic species, such as the wild boar, is considered to be potentially harmful, appropriate management measures must be applied to avoid, reduce, or mitigate, that invasive species' impacts on the natural values of the protected area (APN 2007). Here, the extensive distribution and overlap between the pudu and wild boar allow us to define priority areas for management efforts within the NHNP. The pudu occurrence is considered indicative of pristine areas with high conservation value (Fox and Estay 2016), and the wild boar is known to promote considerable changes in the habitat structure and is considered as nocuous ecosystem engineers (Barrios-García and Ballari 2012) that can jeopardize the native biodiversity of the park (Clavero and García-Berthou 2005). The pudu distribution therefore can be used as a proxy of pristine areas to be protected, and the wild boar distribution as a proxy of the distribution of a threat to the indigenous environment. This categorization of priority areas allows decision makers to optimize the local management strategy by allocating limited available resources and wild boar suppression efforts to an area of about a quarter of the park. In addition, the results also indicate areas that do not require efforts in terms of boar suppression, but that must be monitored to detect possible new invasion events and to follow the general population dynamics of the local species and ecosystems.

It is noteworthy that the potential high suitability areas for wild boar are not restricted to any specific vegetation type, and extends with confirmed records beyond the park's area, which may indicate a potential for new dispersion events to new areas. A further expansion of the wild boar distribution could lead to disastrous consequences, given that because of its omnivorous generalist diet, the boar would have access to several food sources, including several types of native plants, and terrestrial vertebrates and invertebrates (Wilcox et al. 2009; Barrios-García and Ballari 2012; Ballari and Barrios-García 2014). The rooting behavior of the wild boars would impact directly the ecosystem functions in these new areas, altering soil properties including soil microorganism communities and ecosystem processes such as decomposition and soil compaction (Barrios-García et al. 2014; Cuevas et al. 2010). The impacts caused by wild boar rooting also could affect the regeneration

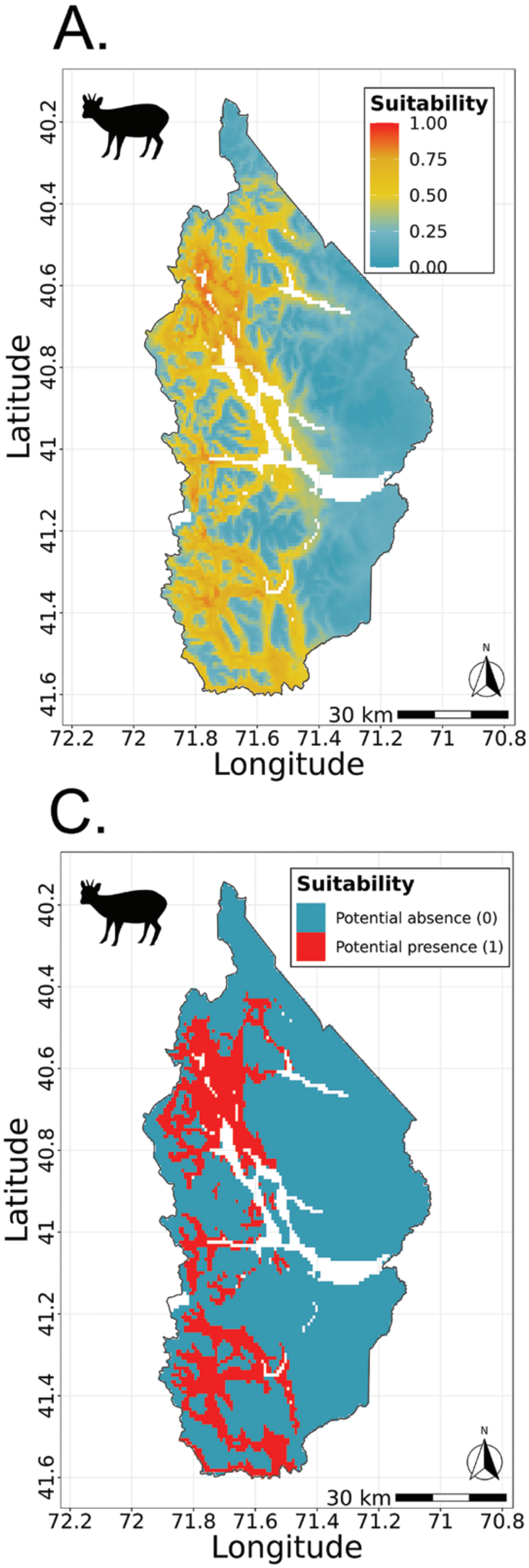

Fig. 3.—Potential distribution of wild boar (right panels) and southern pudu (left panels) in Nahuel Huapi National Park (NHNP), Argentina. The upper maps show the continuum suitability and lower maps show the binary potential distribution (potential presence and absence).

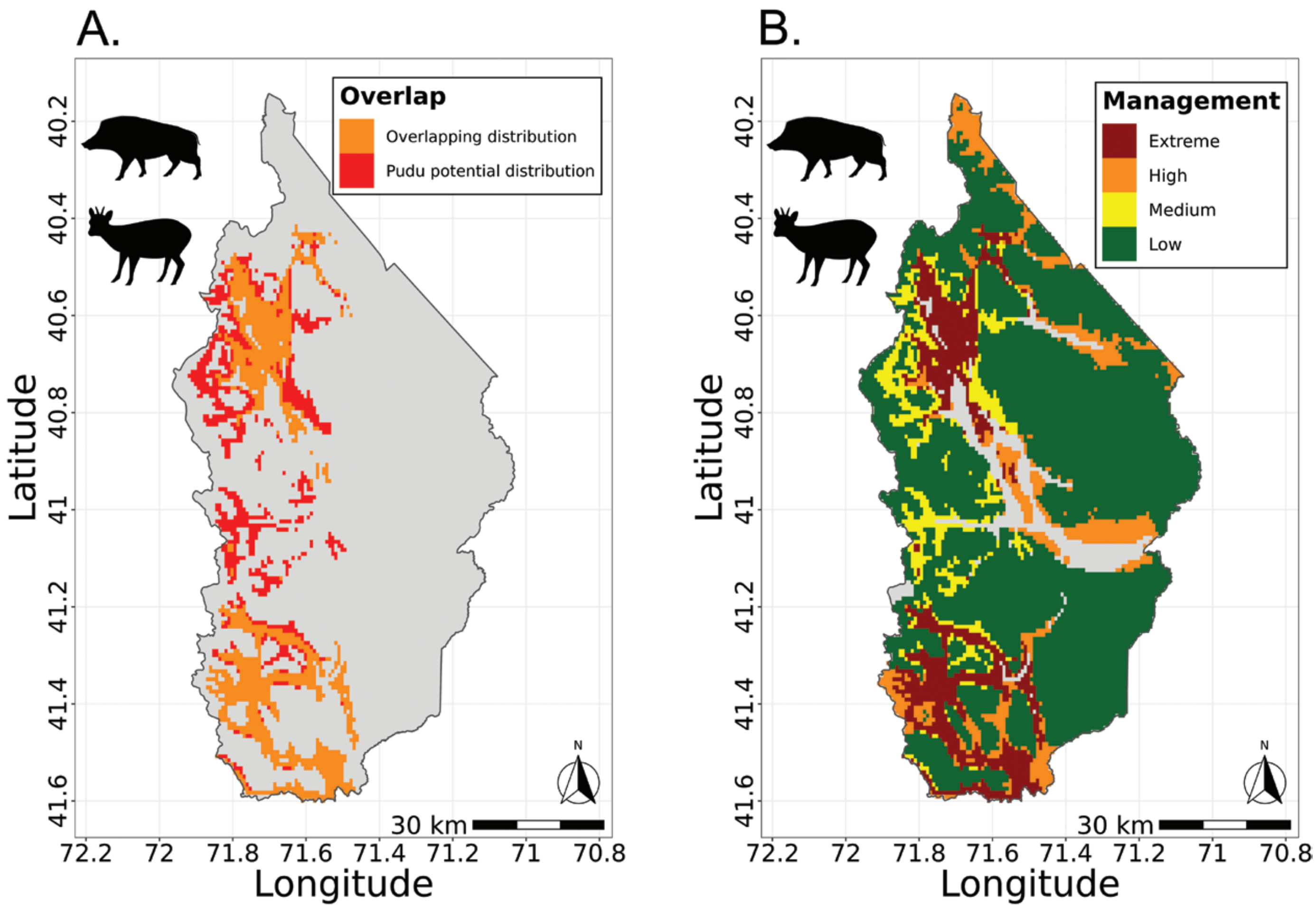

Fig. 4.—A) Pudu potential distribution, with the areas without wild boar overlap in red and the areas with potential overlap in orange. B) Priority areas for wild boar management in Nahuel Huapi National Park (NHNP), Argentina.

of the *Nothofagus* forests, an important vegetation feature in the NHNP, and an important host of biodiversity, being the main area of occurrence of southern pudu (Relva and Veblen 1998; Simberloff 2003; Cuevas et al. 2016).

Protected areas are highly cost-effective in protecting biodiversity (Balmford et al. 2002); nevertheless, conservation efforts and investments are scarce and need to be wisely directed and focused. We also suggest the use of an "adaptive management system," in which models should be validated and updated over the years to track the results of applied management practices and add new information collected in the field during the management and monitoring campaigns. Another recommended improvement to these SDMs would be the addition of data on the population abundance of the subject species; however, this would require an extensive investment in population density estimation. Considering the potential of SDMs as management tools for conservation areas, as demonstrated by this study and by an extensive literature (Araújo and Guisan 2006; Ferraz et al. 2012), we recommend that every conservation area implements SDM at local scales, tuning it to meet local specifications and updating it over the years to track temporal changes in target species within the protected site.

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Records of *Pudu puda* in the Nahuel Huapi National Park (NHNP), Patagonia, Argentina.

Supplementary Data SD2.—Records of *Sus scrofa* in the Nahuel Huapi National Park (NHNP), Patagonia, Argentina.

Supplementary Data SD3.—Maps of the records of *Pudu puda* and *Sus scrofa* in the Nahuel Huapi National Park (NHNP), Patagonia, Argentina.

Supplementary Data SD4.—Description of the environmental variables used to perform SDMs.

Supplementary Data SD5.—Scree plot of the contribution of each axis from the PCA-env.

Supplementary Data SD6.—Absolute frequency and percentages of the records of pudu and wild boars, organized by source, zone and vegetation type within the NHNP, Patagonia, Argentina.

Supplementary Data SD7.—Box plot resuming the AUC values from the six evaluated model, for *Pudu puda* and *Sus scrofa*.

Supplementary Data SD8.—Areas and threshold used to transform the continuous suitability map into a potential presence and absence map, in Nahuel Huapi National Park (NHNP), Argentina. The extensions of the areas in the different levels of priority for wild boar management are also displayed.

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