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Research Article

A habitat suitability model for capybara (*Hydrochoerus hydrochaeris*) at its core area in Argentina

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Abstract

Habitat loss is one of the main factors reducing wildlife diversity and restricting its conservation. Habitat suitability models are important tools for wildlife management and conservation in order to evaluate the impacts of human activities on wildlife habitats. The capybara (*Hydrochoerus hydrochaeris*) is a semi-aquatic rodent that lives in South American wetlands that are subject to heavy human use. A spatially explicit model of capybara's Potential Habitat Suitability (PHS) was developed for the core area of its distribution in the humid subtropical region of Argentina. Predictive variables in this deductive model were related to capybara habitat requirements, and their values were obtained from existing published papers. The PHS model was performed using two data subsets that evaluated both ecological requirements and anthropogenic threats, resulting in two partial indices: Potential Ecological Suitability (PES), and Risk of Human Impact (RHI). The PES assesses vegetation cover and the presence of lentic and lotic freshwater bodies. The RHI estimates habitat fragmentation and accessibility of poachers. Variables for the habitat requirements were spatially expressed through Geographic Information Systems. The model accuracy assessment was performed through field work and achieved 72% of overall accuracy. Results indicate that 13% of the study area had the highest values of PHS index, characterized by the presence of vast wetlands, habitats with low fragmentation and low accessibility for poachers. These results are a useful tool to improve conservation and management programs for protection of capybara habitat.

Keywords

Capybara, Corrientes, Geographic Information Systems, landscape, wildlife, deductive model

Resumen

La degradación del hábitat es uno de los principales factores que reduce la diversidad de la fauna y restringe su conservación. Los modelos de aptitud de hábitat son herramientas importantes para la gestión y conservación de la fauna con el fin de evaluar los impactos de las actividades humanas sobre los hábitats de la vida silvestre. El capibara (*Hydrochoerus hydrochaeris*) es un roedor anfibio que habita los humedales de Sudamérica y es una de las especies nativas más utilizadas por el hombre. Se desarrolló un modelo espacialmente explícito de Aptitud Potencial de Hábitat para el capibara (PHS) para el área núcleo de su distribución en la región subtropical húmeda de Argentina. Las variables predictivas en este modelo deductivo se relacionaron con los requerimientos de hábitat del capibara, y sus valores se obtuvieron a partir de artículos publicados. El PHS se calculó considerando las necesidades ecológicas y amenazas antropogénicas, lo que resultó en dos índices parciales: Aptitud Ecológica Potencial (PES), y Riesgo de Impacto Humano (RHI). El PES valoró el tipo y la cobertura de la vegetación y la presencia de cuerpos de agua dulce lénticos y lóticos. El RHI estimó la fragmentación y la accesibilidad espacial de los cazadores furtivos. Las variables se expresaron espacialmente utilizando un Sistema de Información Geográfica. La exactitud del modelo, evaluada a través de corroboración a campo, fue de un 72% de precisión global. Los resultados indican que sólo el 13% del área de estudio cuenta con los más altos valores de índice de PHS, que se caracteriza por la presencia de extensos humedales, baja fragmentación y baja accesibilidad para cazadores furtivos. Estos resultados son una herramienta útil para mejorar los programas de conservación y gestión para la protección del hábitat del capibara.

Palabras clave Corrientes, Sistema de Información Geográfica, Paisaje, Vida silvestre, Modelo deductivo

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Introduction

Wildlife Habitat Suitability Models (HSM) are key components of sustainable land use decisions, as they provide links between wildlife knowledge and conservation and management actions [1- 4]. HSM measure the potential abundance and distribution of focal animal species [5], comparing the life requirements of species to the ecological supply of landscape [6- 8]. These models represent functional relationships between the occurrence of species and environmental variables based on intensive field sampling and literature research [9].

Beyond species-habitat relationships, HSM have been applied to wildlife management issues by incorporating threats and effects of human activities [10] and extending the geographical scope of the model to the regional scale [11].

The capybara (*Hydrochoerus hydrochaeris*, Linnaeus 1766) is the world's largest living rodent and is one of the most used wildlife species in South America, for both meat and hides [12]. Although the species is considered globally as least concern [13] and near threatened in Argentina [14], land cover change and high levels of both legal and illegal exploitation (about 20,000 hides exported per year plus an unknown number of animals killed for local hide and food markets) may lead to local extinctions. National wildlife management authorities of Argentina are therefore preparing proposals to regulate harvest activities, together with provincial agencies needing technical tools for decision makers [15].

Capybara distribution is associated with tropical and subtropical wetlands [16, 17], but also extends approximately up to 38° S in Argentina, under temperate climate conditions. The most important populations are between 27° 14' and 30° 45'S in the Corrientes Province (Fig. 1) [12, 18].

Several field studies have described population aspects of capybara [e.g., 19- 22]. Studies on wild populations include habitat use [18], diet, and trophic interactions with domestic livestock [23- 26]; reproductive biology and food habits have been studied in captivity [27- 28]. Adámoli et al. [29] developed the first map of potential habitat suitability for the capybara in Argentina, finding the northeast portion of the country to be the most suitable area, particularly the Corrientes Province (Fig. 1). There, Quintana and Rabinovich [19] studied density and group size of capybara populations in different types of habitat. These authors found that in protected areas capybara density was fifty times greater than that in areas subject to high hunting pressure.

Capybaras live in social groups near water bodies and land-water interfaces [30, 31]. Water is essential for this species, since it is used for mating, as a shelter habitat, as a means of escape, and especially, to regulate body temperature [32]. Capybaras rest under tall herbaceous vegetation, such as riparian forests and closed shrublands [19, 33]. Capybaras also build 'beds' in flooded areas by crushing tall herbaceous plant species such as marsh grasses (*Hymenachne grumosa* and *H. pernambucense*), sedges (*Scirpus giganteus*), giant bulrush (*Schoenoplectus californicus*), pampas grass (*Cortaderia selloana*) and caespitose grass *Melica macra* [18, 33]. Capybaras use the muddy areas close to the water as 'wallows' to remove ticks and other ectoparasites, and grazing areas are restricted to an approximate 1 km-strip next to water bodies [19, 32].

Capybaras are selective herbivores [34]. Studies carried out in the Lower Delta of the Paraná River in Argentina, show that their diet mainly consists of short grasses and sedges [24- 26]; in Venezuela, they were also observed feeding on aquatic vegetation, such as water hyacinth (*Eichhornia* spp.) and others [31].

At present the capybara's main predators, such as the puma (*Puma concolor*) and the jaguar (*Panthera onca*), have been removed from its habitat. Conversion of wetlands into rice fields, commercial afforestation, and illegal hunting are among the main threats faced by this species [15, 35, 36]. In hunting areas, capybaras hide during daytime in closed vegetation made by tall herbaceous species in freshwater marshes, bushes, or even woodlands, such as forest patches or riparian forests, going out into open areas only during the evening [37].

Two previous models of capybara habitat suitability were made using ecological niche modeling: Ferraz et al. [38] considered the capybara distribution in agricultural ecosystems in Brazil, and Campos-Krauer and Wisely [39] modeled past and current habitat suitability based on changes in land use over time in Paraguay. These studies use an inductive approach to model capybara distribution, applying a statistical technique to derive the ecological niche of the species from locations where the species occurs. These models assume equilibrium between environmental factors and their spatial arrangement.

In this paper, a spatially explicit model of potential habitat suitability was developed for the Corrientes Province, a large area under the same administrative jurisdiction. This province includes the core area of capybara distribution in Argentina, which has the largest populations of the country. This model considered both the potential ecological suitability and the risk of human impact. It uses a deductive approach based on species-habitat association and ecological requirements to evaluate suitable areas and GIS techniques.

Methods

Study area

The study area corresponds to the Corrientes Province, which is in the northeast region of Argentina (Fig. 1). It covers approximately 88,000 km². The area is located between the Paraná and the Uruguay rivers, and the landscape resembles a complex mosaic of landcover types with a complex geomorphologic history, largely associated with the uplands tholeiitic basalts of Botucatu and Serra Geral Formations (Jurassic-Cretaceous) and with lowlands composed of fluvial sands of the Ituzaingó Formation derived from the drift of the Paraná river during the Pleistocene-Holocene [40, 41]. The area has low relief amplitude between 20 and 220 m.

The climate is humid subtropical, subtype "Cfa" according to the Köppen climate classification [42] without a dry season. Annual average temperature is 21.2 °C, and average annual rainfall ranges between 1,100 and 1,900 mm (Servicio Meteorológico Nacional¹).

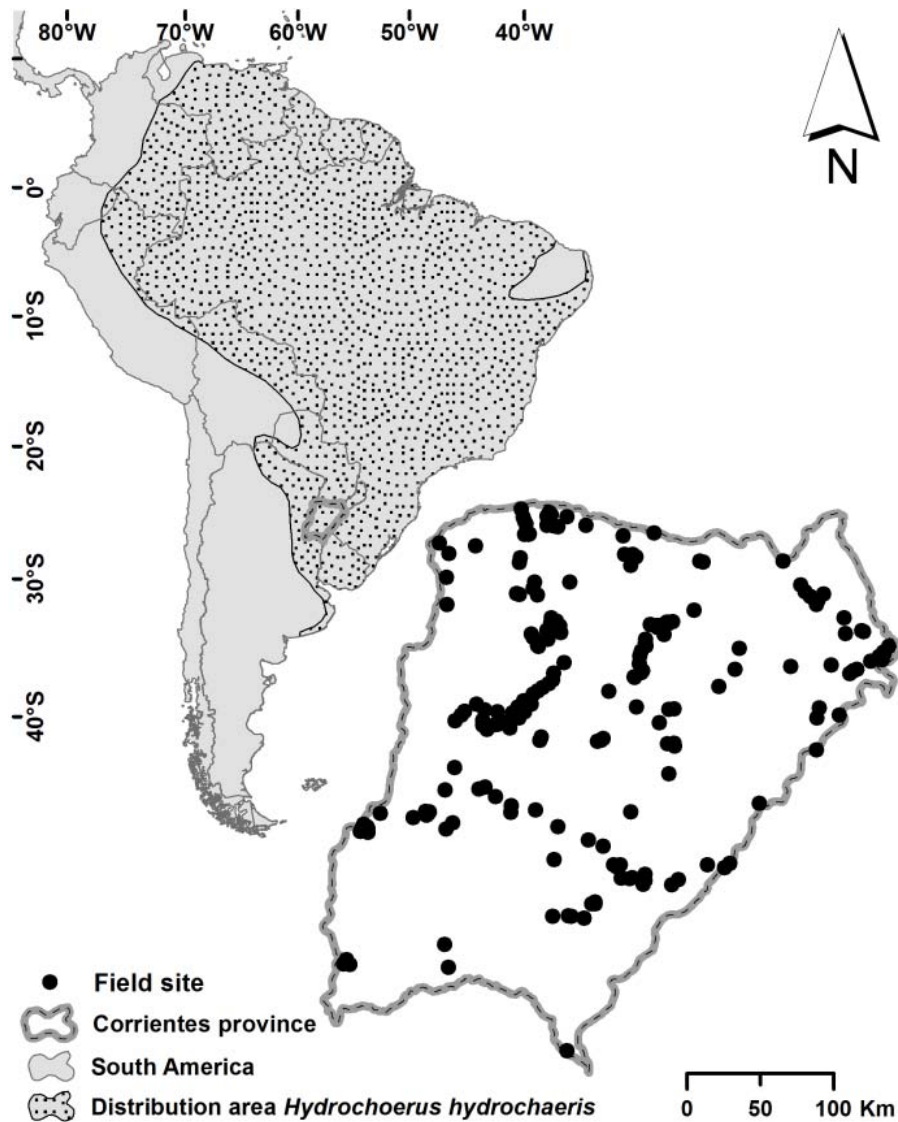


Fig. 1. *Hydrochoerus hydrochaeris* distribution area in South America adapted from Ojasti [12] (dotted area). Location of the Corrientes Province, in northeastern Argentina, between 27° 14' and 30° 45' latitude south and 59° 37' and 55° 37' longitude west with the location of the 204 surveyed field sites for model validation (black dot).

The study area is characterized by extensive water resources, including rivers, streams, lagoons, ponds and freshwater marshes [43]. The water mainly comes from rainfall and accumulates due to the low slopes, which have a NE-SW course and the frequent presence of impermeable sedimentary layers [44].

¹ Servicio Meteorológico Nacional. Available from: <http://www.smn.gov.ar/>, accessed March 8th, 2012.

This area is covered by different land cover types: deciduous xerophytic forests, with a dominance of willow-leaf red quebracho (*Schinopsis balansae*) and white quebracho (*Aspidosperma quebracho-blanco*), or shorter woody species like espinillo (*Prosopis affinis*) and algarrobo (*P. nigra*), combined with palm groves, savannas, grasslands dominated by *Andropogon lateralis* and *Sorghastrum agrostoides*, and halophytic steppes. In the northeastern portion of the study area, extensive areas of native woody formations have been cleared and replaced by pine and eucalyptus, yerba mate (*Ilex paraguariensis*), and citrus plantations as well as tea orchards. The lowlands are characterized by a complex mosaic of hydrophytic forests, hydromorphic flooded grasslands known as *malezales*, large freshwater wetlands, ponds, and lagoons [43]. Three main conservation areas are included within its territory: the RAMSAR site “Lagunas y Esteros del Iberá” (24,550 ha) [45] and the protected areas “Mburucuyá National Park” (17,660 ha) and “Esteros del Iberá” Provincial Nature Reserve (1,300,000 ha).

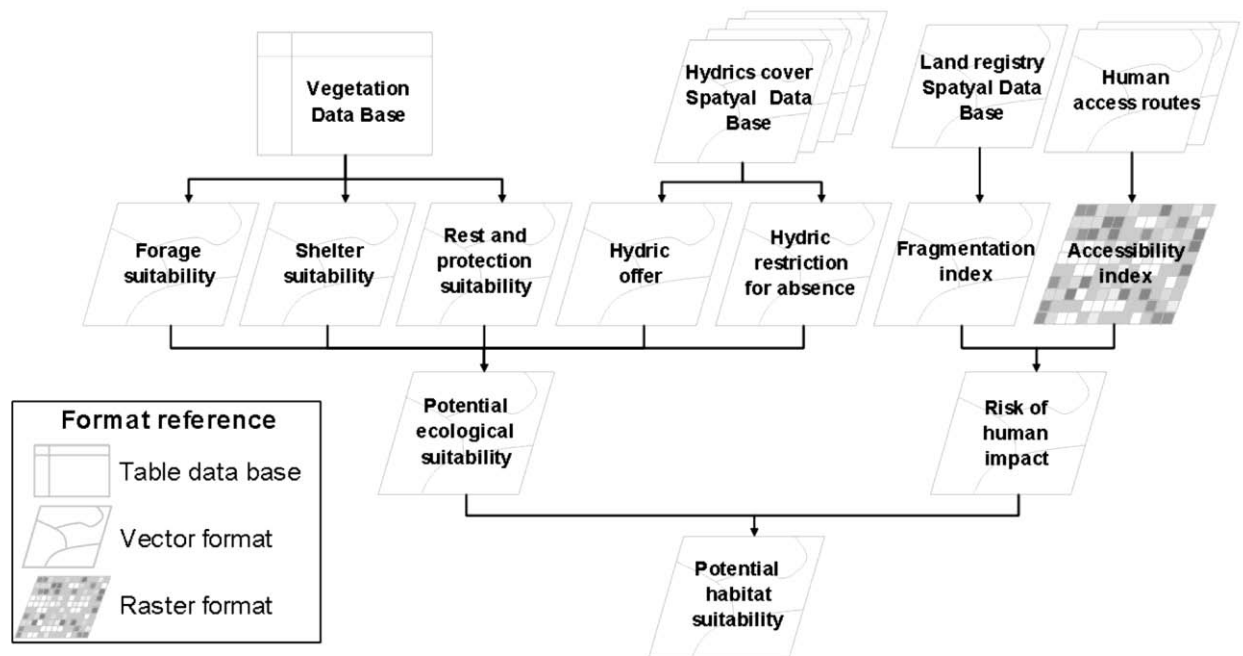


Fig. 2. Conceptual model developed for the Potential Habitat Suitability for Capybara. The variables considered are related to habitat requirements of the species, which included forage, shelter, rest and protection for offspring suitability and, presence of water bodies. Also includes variables related to risk of human impact like estimators of fragmentation index and spatial accessibility for poachers.

Conceptual model

We developed a Potential Habitat Suitability model (*PHS*, Fig. 2) considering a positive association with the ecological requirements of the species (Potential Ecological Suitability, *PES*) and a negative association with the risks caused by human activity (Risk of Human Impact, *RHI*) (**Equation 1**).

$$PHS = f(PES, RHI) \quad (1)$$

PES is assumed positively related with the ecological requirements of forage (*F*), shelter (*S*), rest and protection for offspring (*R*), and the need for water for thermoregulation, mating, and escape (*W*) (**Equation 2**).

$$PES = f(W, F, S, R) \quad (2)$$

The main risks caused by human activity (*RHI*) are related to the access of poachers into capybara habitats through road and river networks (*Acc*), and the degree of land fragmentation (*Fr*) (**Equation 3**).

$$RHI = f(Acc, Fr) \quad (3)$$

Fr, described by the land registry, is an indicator of rural settlement and urban and semi-urban parceling. The smaller the parcels are, the more intensive is the productive use, resulting in fewer suitable habitats for wildlife. This relationship was checked in the field, where it was observed that the highest abundances of capybaras were always associated with larger farms, while in smaller establishments it was not found, even when ecological conditions were adequate for it [19].

Database generation and organisation

The ecological requirements of capybara were translated into the following variables for the *PES* model: availability of water (*W*); forage (*F*), shelter (*S*) and rest and protection for offspring (*R*). The last three variables were derived from vegetation composition and structure.

Layers associated with water availability were derived from the national hydrographic GIS databases of Argentinean standard cartography [46], by extracting features representing lotic (line segments of rivers and streams) and lentic freshwater habitats (polygons of shallow lakes, swamps and marshes). Each layer was checked for completeness using Landsat 7 ETM+ imagery [47], and missing water bodies of each type were added by on-screen digitizing. The *W* component included a total of four layers: lotic permanent, lotic temporary, lentic permanent and lentic temporary water bodies.

F, *S* and *R* scores were derived from Carnevali [48]. This work has a comprehensive description of the vegetation at landscape and community scale, in terms of species composition, coverage and structure covering the entire province of Corrientes, which for its detail is unsurpassed. This author recognized 62 landscapes units for the whole study area. These units were differentiated by the composition and coverage of 74 different landcover types in which more than 1,000 plant species were identified in the entire study area. Only those species with reported coverage greater than 1% were considered for the analysis. In order to determine the forage (*F*) suitability, we compiled the list of consumed plant species from diet studies [20, 23- 26] and ranked them based on their frequency as diet items and their size. The ecological requirements *S* and *R* were analyzed based on vegetation features associated with the habitat types used by capybaras described in previous studies [18, 19, 31-33, 49]. The operational definition of both requirements was based on bibliographic data on the potential use of the vegetation for the construction of beds for rest, or conditions for shelter against predators, in accordance with vegetation categories and average sizes [18, 19, 30, 32]. For the different ecological requirements, plant species were grouped into categories based on Quintana and Bolkovic's criteria (unpublished data 2014; Table 1). The obtained groups were then scored. Thus, each habitat requirement of the capybara was valued according to the current plant groups.

Table 1. Decision rules for allocating values of forage, shelter and rest and protection for offspring for different categories in which plant species were grouped according to criteria of Quintana and Bolkovic (unpublished data 2014).

Ecological requirements	Plant category		Mean size	Value	
Forage	Aquatic	<i>Oplimenopsis</i> spp., <i>Luziola peruviana</i> , <i>Leersia hexandra</i>	All	High	3
		All other	All	Low	1
	Broadleaf herbs		All	Low	1
	Sedges		Shorter than 1 m	High	3
			Taller than 1 m	Medium	2
	Terrestrial grasses		All	High	3
	Shrubs		All	Null	0
	Trees		All	Null	0
Shelter	Aquatic		All	Medium	2
	Herbaceous (broadleaf herbs, sedges, and grasses)		Shorter than 0.4 m	Null	0
			Between 0.4 and 0.8 m	Low	1
			Between 0.8 and 1.2 m	Medium	2
			Taller than 1.2 m	High	3
	Shrubs		All	High	3
Rest and protection for offspring	Trees		All	Medium	2
	Aquatic		All	High	3
	Herbaceous (broadleaf herbs, sedges, and grasses)		Shorter than 1 m	Low	1
			Taller than 1 m	High	3
	Shrubs		Shorter than 0.5 m	Low	1
			Between 0.5 and 1 m	Medium	2
			Taller than 1 m	High	3
	Trees		All	High	3

For *RHI* variables, we considered layers of roads and permanent rivers from the National Geographic Institute [46] for *Acc. Fr* was calculated using information of the land registry parcel layer which was obtained from the General Directorate of Cadastre and Cartography of the Corrientes Province (Dirección General de Catastro y Cartografía²).

Model deployment

In order to calculate *PHS* values in Corrientes we subdivided the province into areal units which approximate the species' home range [50, 51]. A grid of regular hexagonal units (HU) was chosen because it is considered the best discontinuous sampling pattern for a spatial function [52]. We used HU of 260 ha to match a circular area of 1 km radius, which is the capybara's maximum standoff distance from water sources [19, 32]. In addition, the spatial resolution of each HU was similar to the home-range of a capybara group defined for the Pantanal wetlands in Brazil [53], which shares certain ecological similarities with the Corrientes wetlands. This procedure resulted in 34,509 HU.

All layers of *PES* variables were intersected by the HU grid using the regional analysis module Patch Analyst ArcGIS [54]. Values for each requirement were calculated as follows:

² Dirección General de Catastro y Cartografía. Available from: <http://www.catastro.corrientes.gov.ar>.

Freshwater supply –W– Given the spatial resolution of the layers associated with water, the three requirements covered by it (thermoregulation, mating, and escape from predators) were evaluated in one single index. In order to create this index, total length of the segments of courses belonging to lotic aquatic habitats (permanent and temporary rivers) and the sum of the area covered by lentic aquatic habitats (ponds and different types of freshwater marshes) were considered in each HU. The values obtained were rescaled from 0 (no water source was present in the analysed area) to 100 (the whole HU was covered by a water body, or for the maximum total river length recorded). In order to calculate the total freshwater supply, ecological differences between permanent and temporary water bodies were taken into account. Because this resource has strong seasonal variation, 50% of the obtained value in the model has been considered by the intersection of the respective layers with the HUs for temporary water bodies, both lotic and lentic.

Vegetation supply –F, S, R– Each ecological requirement related to vegetation supply at landcover type scale was assessed considering the contribution to habitat suitability of each plant species in the different landcover types. The obtained values were weighted by their coverage. Similarly, values of habitat suitability were assessed at landscape unit level. For this, we considered the coverage of each landcover type within the landscape unit. Then, the obtained suitability values for each HU were rescaled from 0 (null suitability) to 100 (optimal suitability).

Hydrological constraint –W₀₁– Because the presence of freshwater is a critical requirement for the capybara, each hexagon was assigned 0 value when no water was present within it, or 1 otherwise.

The **PES (Equation 4)** was calculated as the weighted spatial average of the values obtained for the layers that comply with the ecological requirements related to freshwater (W) and vegetation supplies (F, S, R), multiplying the whole term by the hydrological constraint (W₀₁).

$$PES = \left[\frac{(F + S + R + 3 * W)}{6} \right] * W_{01} \quad (4)$$

where: F = forage suitability, S = shelter suitability, R = rest and protection of the offspring suitability, W = freshwater supply, W₀₁ = hydrological constraint.

Risk of human impact –RHI– Was estimated using **Equation 5**. For *Acc*, the straight-line distance from the centroid of the HU to the closest access road was measured. Distances were rescaled from 100 to 0 using a decreasing monotonic linear function, with the maximum values occurring when the road crosses the centre of the HU and 0 when the same distance is equal to or greater than 10 km, where human accessibility influence is considered negligible [55]. *Fr* was generated by counting the number of parcels in each HU using the *ArcGis* extension *V-Late* [56]. Values were rescaled from 0 (a single polygon accounted for the whole HU) to 100 (the maximum number of polygons observed).

$$RHI = \frac{Fr + Acc}{2} \quad (5)$$

where: *Fr* = fragmentation index and *Acc* = accessibility value in the considered area.

The **PHS (Equation 6)** was obtained by deducting the *RHI* from the *PES* and rescaling the index from 0, for the minimum to 1, for its maximum *PHS* value. Finally, it was multiplied by W₀₁.

We included the component W₀₁ in the model because its inclusion assures a null suitability for the HU where water is absent.

The following equation shows the expression of the final model:

$$PHS = \left[\left(\frac{PES - RHI}{200} \right) + 0.5 \right] * W_{01} \quad (6)$$

where: *PES* = potential ecological suitability, *RHI* = risk of human impact, *W₀₁* = hydrological constraint.

Model Validation

Assuming that the abundance of capybaras is directly related to habitat quality, the accuracy of the model was evaluated through a contingency matrix between the *PHS* values and the categories surveyed with field data. Overall accuracy (**Equation 7**) and a Kappa index (**Equation 8**) were calculated [57, 58]. For this purpose, fieldwork was carried out between 2007 and 2013, and capybaras were found in 154 sites (Fig. 1) through observations of animals or their signs. In addition, 50 sites were derived from unstructured interviews with local people [59] in order to get additional information about capybara presence.

Field data were classified into 5 categories:

0- No presence of capybaras was detected.

1- Presence of a very low number of animals was inferred through finding old faeces (such as dried faeces). In addition, interviews indicated occasional presence in the area.

2- Presence of recent faeces (dried on the outside, but humid in the inside); interviews revealed presence of isolated animals or small groups (2-3 individuals).

3- Presence of fresh faeces indicating recent animals activity in the area at that time; interviews indicated a relatively high abundance of capybaras in the area.

4- Presence of capybaras was confirmed by direct observation of several animals in the field; the interviewed people stated that the animals were abundant at the site.

$$\text{Overall Accuracy} = \frac{\sum_{i=1}^r x_{ii}}{N} \quad (7)$$

$$\text{Kappa index} = \frac{\left[N \sum_{i=1}^r x_{ii} - \left(\sum_{i=1}^r x_{i+} * x_{+i} \right) x_{ii} \right]}{\left(N^2 - \sum_{i=1}^r x_{i+} * x_{+i} \right)} \quad (8)$$

where *N* = total number of observations, *r* = number of categories, *x_{ii}* = number in row *i* and column *i*, *x_{i+}* = total for row *i*, and *x_{+i}* = total for column *i*.

In order to establish the relationship between the values surveyed on the field and those from the model, the latter were classified into five classes according to the Jenks natural breaks classification method. Classes are based on natural groupings inherent in the data, minimizing internal differences between elements of the same group and maximizing the differences between groups [60].

Results

The obtained water supply (*W*) layer is showed in **figure 3a**. The areas with higher *W* values correspond to extensive subtropical swamps including Iberá, Batel, Batelito, Santa Lucía, del Riachuelo and Miriñay wetlands. Other areas with high *W* value were those associated with permanent water courses, such as Corriente and Miriñay rivers and their floodplains, Sarandí and Barracas streams, and Cuay Grande and Cuay Chico marshes, as well as the Paraná River floodplain, on the west side of the Province.

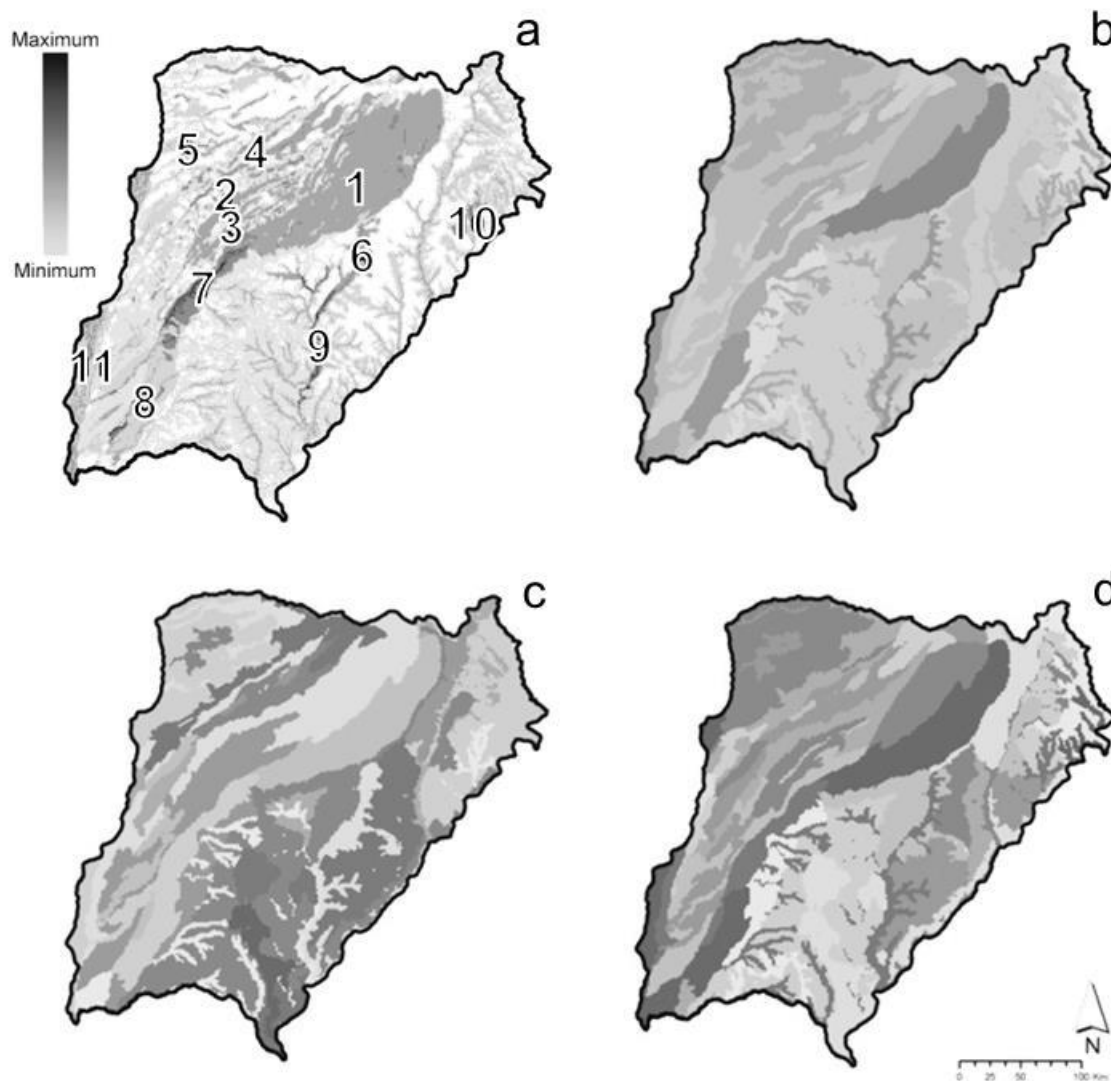


Fig. 3. a- Freshwater supply (W) for the Corrientes Province Iberá (1), Batel (2), Batelito (3), Santa Lucía (4), Riachuelo (5) and Miriñay (6), which form large areas covered by water. Other areas with high value of the index were associated with the Corriente River and its floodplain (7), Barrancas and Sarandí streams (8), Miriñay River and floodplain (9), Cuay Grande and Cuay Chico esteros (10) and the insular area of the Paraná River (11). Habitat requirements covered by vegetation: b- Forage availability (F), c- Shelter availability (S), d- Rest and protection of young availability (R) for the Corrientes Province from the vegetation composition of each landscape unit.

Regarding life requirements closely related to vegetation features F (Fig. 3), the areas with highest forage values were those related to landscapes with a predominance of landcover types largely covered by grasses or sedges shorter than 1 m, such as *malezales*³, grasslands and prairies. The lowest values of F appeared in areas with high forest coverage such as landscapes dominated by riparian and xerohalophytic forests (Fig. 3b). This type of habitat limits the development of lower herbaceous strata, which is the main source of forage for capybara. The areas with the highest shelter (S) are

³ *Malezales* are typical grassland areas dominated by a few grass species growing on waterlogged soils. They are characterized by superficial water erosion which generates an irregular surface composed of pedestals that are stabilized by herbaceous vegetation. Pedestals are surrounded by small channels up to 1 m wide and 1 m deep.

characterized by the presence of tall herbaceous plants which are typical of different types of freshwater marshes. They successfully protect the capybara from predators and poaching. At the other end, the areas with the lowest S values were those with significant coverage of low herbaceous strata, crawling species, and areas of bare soil (Fig. 3c).

The highest values of R were recorded in areas with a high coverage of tall plants, like woody species, both from forests and gallery forests, or by tall sedges and grasses that dominate different types of freshwater marshes. The areas with the lowest value were those dominated by low herbaceous vegetation and a large presence of bare soil (Fig. 3d).

The highest suitability values of the PES index (Fig. 4a) were found in the corridor formed by the Iberá wetland, its natural drainage through the Corriente River and the Sarandí and Barracas streams, and the Batel-Batelito and Santa Lucía wetlands (located at the west of Iberá), besides the Miriñay wetland and its basin in the south. Those environments combine an important water supply with vegetation made up of short grasses and sedges in the interfaces, providing high forage value and high herbaceous cover for shelter and rest. A good combination of the different variables was also recorded in the islands of the Paraná River floodplain and the Aguapey River basin. The areas with the lowest values are those regions with non-waterlogged or non-flooding areas, which is an essential requirement for capybara. Low values were also recorded in elevated areas, on terrace planes, covered by xerophytic forests or open savannas dominated by *Schinopsis balansae*, close to the towns of Herlitzka and Lomas de Vallejos. Elevated areas around the town of Berón de Astrada, dominated by *Schinopsis* and without water supply classified this area as null for PES for capybara at this scale of analysis.

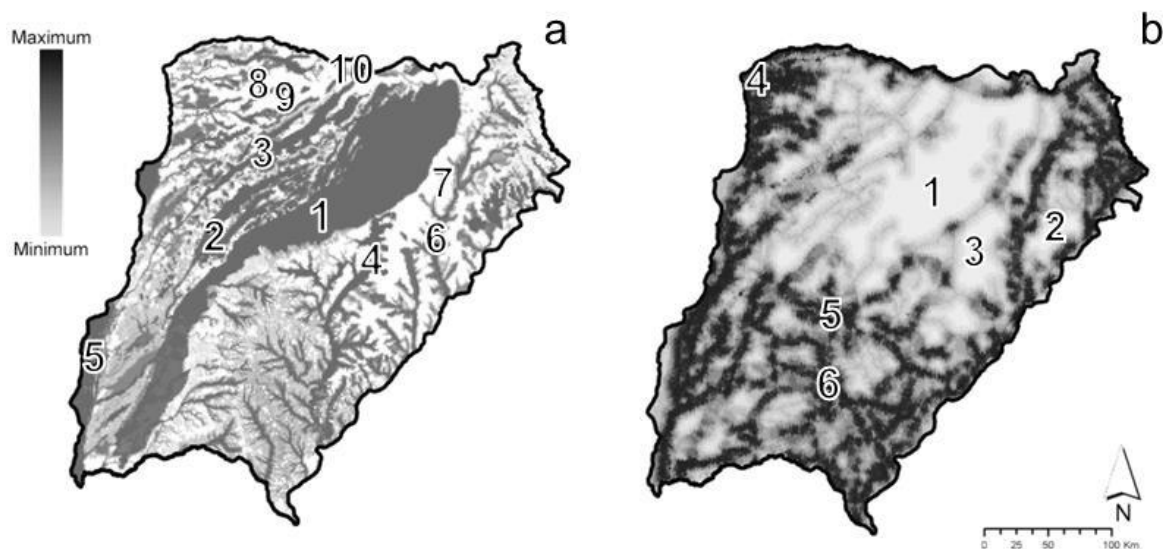


Fig. 4. a- Potential Ecological Suitability (PES) for the capybara in Corrientes Province are distinguished by their high value: the corridor formed by the esteros of Iberá, Corriente River natural drainage, and Sarandí and Barrancas streams (1), and the esteros of Batel-Batelito (2), the Santa Lucía (3), Miriñay esteros and basin (4), the floodplain of the Paraná river (5), Aguapey river's basin (6). In areas of lower PES highlight the area between the Aguapey River and Iberá esteros (7), towns of Herlitzka (8), Lomas de Vallejos (9) and Berón de Astrada (10). b- Risk of Human Impact (RHI) for the capybara in the Corrientes. It is noteworthy the wetland system associated to the Iberá esteros (1), Cuay Grande and Cuay Chico esteros (2), and the *malezales* area between the Aguapey and Miriñay rivers (3) because of its low value of RHI . The higher values of the index are the national routes 12 and 14 at western boundary and eastern boundary respectively, and urban areas with maximum expression in the Capital Department (4) and the cities of Mercedes (5) and Curuzú Cuatiá (6).

Three regions stand out in the spatial expression of the *RHI* index due to their low fragmentation and the scarcity of access routes: the Iberá wetland, the Cuay Grande - Cuay Chico wetlands, and the area of *malezales* between the Miriñay and the Aguapey rivers (Fig. 4b). At the other end of the *RHI* index were urban areas and national routes, with a maximum expression in the Capital Department and the cities of Mercedes and Curuzú Cuatiá.

The areas that showed the highest values of *PHS* index were mainly characterized by the presence of vast wetlands, comprising 13% of the Corrientes Province territory including the Iberá (7,600 km²), Santa Lucía (320 km²), Batel, Batelito (830 km²), Miriñay (195 km²), Cuay Grande and Cuay Chico (260 km²) marshes. High values were also recorded in the Corriente River (750 km²), the Sarandí and Barrancas streams (190 km²), the basin of the Aguapey River (310 km²) and the floodplain of the Paraná River (230 km²) (Fig. 5). These areas accounted for 12% of the Corrientes Province territory. The remnant area with high *PHS* values (1%) corresponded to a highly fragmented mosaic of small patches less than 100 km². Good suitability areas comprise 17%, whereas regular suitability areas cover 22% and low suitability areas 27%. On the other hand, the lowest values of *PHS* index were for areas far away from water sources, accounting for 21% of the province surface. They were located in the northwest region of the province and were included in the departments of Capital, Empedrado, San Cosme, and Itatí, well as the western portion of San Luis del Palmar (500 km²).

Areas with high *PES* showed low *PHS* values when they were located near roads and navigable rivers. This results in fragmentation of large continuous areas with high *PES*, such as the corridor formed by the Iberá marshes, the Corriente River, and the Sarandí and the Barrancas streams (Figs. 4a and 5).

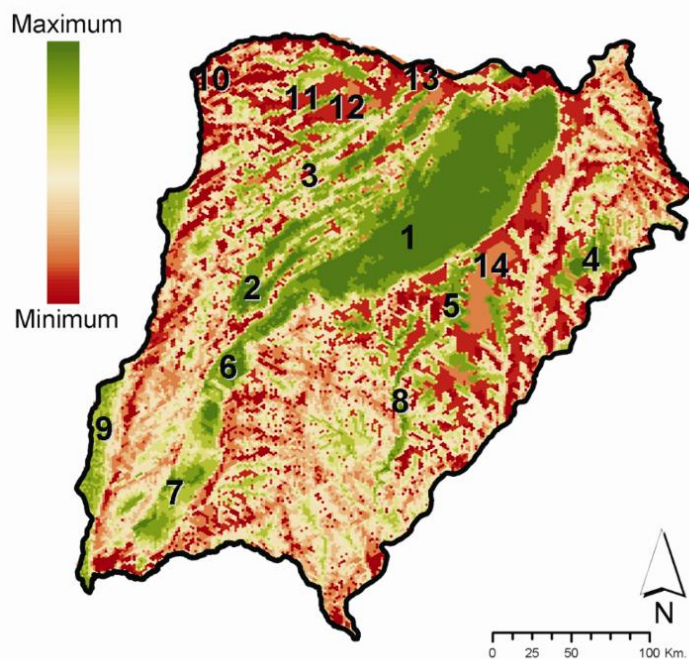


Fig. 5. Potential Habitat Suitability (*PHS*) for capybaras in the Corrientes Province. The map highlights the areas with the highest values of *PHS*: the esteros of Iberá (7600 km²) (1), Batel-Batelito (830 km²) (2), Santa Lucía (320 km²) (3), Cuay Chico and Cuay Grande (260 km²) (4), esteros of Miriñay and its watershed (195 km²) (5), Corriente's river (750 km²) (6), Barrancas and Sarandí streams (190 km²) (7), the basin of the Aguapey River (310 km²) (8) and the floodplain of the Paraná's river (230 km²) (9). On the other hand the departments of Capital (192 km²) (10), San Luis del Palmar (720 km²) (11), General Paz (565 km²) (12), Berón de Astrada (755 km²) (13) in northwest of the province, and *malezales* between the Miriñay and Aguapey (1735 km²) (14) showed areas with lower values of *PHS*.

The contingency matrix for the model validation showed an overall accuracy of 72% and a Kappa coefficient of 0.64 (Table 2). The model was more accurate in the prediction of the categories with the lowest presence and with direct observation of individuals. Moreover, this model presented its lowest accuracy and the largest dispersion when evaluating mid abundances (41%).

Table 2. Contingency matrix used to evaluate the model's accuracy in predicting potential habitat for the capybara. 0, 1, 2, 3 and 4 are the categories of abundance of the sites surveyed in the field and the intervals at which the index was divided *PHS*.

	Field data						User precision	Omission error
	0	1	2	3	4	Total		
0	20	3	1	0	0	24	0.83	0.17
1	1	24	14	1	0	40	0.60	0.40
2	1	3	20	5	0	29	0.69	0.31
3	0	1	11	32	10	54	0.59	0.41
4	0	0	3	3	51	57	0.89	0.11
Total	22	31	49	41	61	204		
Producer precision	0.91	0.77	0.41	0.78	0.84		Overall accuracy	72%
Commission error	0.09	0.23	0.59	0.22	0.16		Kappa index	64%

Discussion

Our results improve the spatial resolution and discriminating suitability values with a high level of detail for Argentina's core distribution area the capybara's potential presence and population abundance, compared to the previous model proposed by Adamoli et al. [29], which considered four suitability categories for the whole provincial territory. In that study, 40% of Corrientes was included as "optimal suitability", 11% as "high suitability", 14% as "good suitability" and 35% as "regular suitability," and no surface was found to have null suitability. In contrast, our model shows a more discriminating rank of suitability values, which could be grouped in different categories according to the settled objective.

The inductive approach modeled by Ferraz et al. [38], on the other hand, differs from our model not only for its methodological approach but also because it was developed specifically for agroecosystems. Their results showed a strong association between the potential distribution of capybara and the proximity both to water bodies and to modified landcovers, particularly areas with high levels of agricultural use. The authors pointed out that crop fields offer high food availability to capybara (comprised by 43% of pastures), remove natural predators, and are protected by enforcement of laws banning poaching. Campos-Krauer and Wisely's [39] inductive model suggests that the conversion of dry tropical forest to pastures favoured expansion of capybara populations in the Paraguayan Gran Chaco eco-region. In Corrientes, despite the observed trend in changing natural vegetation for other land uses (mainly rice crops and forest plantations), these changes are recent if compared to the large and deep changes in land use that took place in the Chaco region in the last decades. The area under rice production represents only 1.1% of the Corrientes Province [61, 62] while pine and eucalyptus afforestations cover barely 4.7% of this region [63]. Therefore, in our model these two landcover types were not considered. Furthermore, in this province capybaras rarely live near crop fields due to conflicts with farmers [19]. For example, rice crops offer high-quality forage and good freshwater supply, but capybaras foraging and trampling result in increased persecution by

farmers [38]. In addition, forest plantations also have negative effects on capybara populations through loss of forage and water supply (pers. observ.). Our results show that the distance from capybara habitat to roads and navigable rivers plays an important role in defining large areas of high habitat suitability. Negative effects of road access on ecosystems and habitat quality for other mammal species, such as an increase of poaching and traffic deaths, habitat loss, and changes in both structure and function of ecosystems, have been widely highlighted in other studies [e.g., 55, 64- 67].

The 92% of high *PHS* areas comprised vast and well-conserved wetland areas that support large capybaras populations. The remnant 8% was small fragments inserted in a heterogeneous mosaic. These small fragments could play an important role in landscape connectivity. In this regard, it was noted the importance of small patches as stepping stones for connecting non-adjacent elements [68], and they should be considered in regional land use planning.

This habitat suitability model achieved a 72% overall accuracy, which represents strong agreement with the validation fieldwork. The Kappa index shows a good agreement, and the proposed model has been 64% more accurate than that randomly obtained [69]. The misclassified cases may be due to multiple causes, such as a low detectability of faeces in complex habitat structures [70], incomplete surveys that increase commission errors [71], or underestimated capybara abundance by the proposed model in some cases. In this case, we consider that the differences between the predicted values and the recorded field data appear to be related to habitat characteristics detected at a local scale but not at a regional one. For instance, small natural or artificial water bodies and minor courses are underestimated for the hydric layer, which is developed at landscape-regional scale (1:250,000). According to several authors [19, 30, 32], these small water resources have an important role for the sustainability of capybara groups at a local scale. Similarly, the scale of analysis used for the vegetation does not enable the study at local levels, since the minimum unit considered in the current map is at landscape level.

It is noteworthy that the shelter value becomes less relevant in areas with no or low hunting pressure, such as protected areas. Therefore, this requirement could be not considered when habitat suitability was assessed. In this regard, a new term could be added to the model as a spatial variable to assess fauna management and protection measures. Other layers of information could also be incorporated in this model, such as seasonal variation in water supply or plant species coverage, in order to improve it. The intra-annual variation of water supply could be evaluated, for instance, from the measurement of the frequency in which a pixel remains covered by water from medium-resolution images such as Landsat TM / ETM+ with a multitemporal approach and using Normalized Difference Vegetation Index (NDVI) [72].

Implications for conservation

The development of habitat suitability models are a key tool for conservation planning because habitat quality is a critical link between land use decisions, viability of wild animal populations [1], and conservation management plans [37]. In addition, the predictive character of these models was used to indicate priority areas for management in order to reduce conflicts with wildlife [55, 64]. Deductive models have been extensively applied to many species [73], demonstrating the importance of fine-resolution distribution data for the development of conservation strategies [74, 75].

We consider this model a valuable tool for the implementation of a capybara management plan in a large area under the administrative jurisdiction [15] of the Argentinean national wildlife authority within the national capybara management strategy. This model constitutes a useful instrument for detecting priority areas to be considered for conservation and management of capybaras in Corrientes Province. In addition, this work provides a conceptual and methodological basis for developing similar models for the rest of the capybara distribution area in Argentina [37] based on ecological requirements and habitat characteristics (Fig. 6).



Fig. 6. Capybaras (*Hydrochoerus hydrochaeris*) feeding on the edge of a water body and with their offspring. Capybara in a muddy area removing ticks and other ectoparasites. Signs such as a footprint or faeces are also shown. Photo credit: all photos by Facundo Schivo.

Although this model was built for a regional scale, it is sufficiently flexible to be adjusted to landcover level, as could be obtained from satellite images, allowing a new approach with a higher spatial resolution [e.g., 10, 38, 64].

Contrary to the inductive approach niche models popular in today's literature [76], models with a deductive approach as presented here are an important predictive tool for conservation and management of species such as capybara with limited availability of data [77] in Argentina.

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