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Research Article

Potential distributional patterns of three wild ungulate species in a fragmented tropical region of northeastern Mexico

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Abstract

In the northernmost American tropical forests of eastern Mexico, we analyzed the potential distribution of three ungulate species, *Odocoileus virginianus*, *Mazama temama* and *Pecari tajacu*, in response to several physical, climatic, biological, and anthropogenic variables, in order to identify environmental factors affecting distribution and potential key areas for ungulate conservation. Current presence records for these species were gathered, and potential distribution models were built using Maximum Entropy niche modeling (MaxEnt). Model suitability surfaces were used to calculate remaining potential habitat areas in the region, as well as the potential sympatric area and representation of these areas in Natural Protected Areas. Biological and anthropogenic variables were the best species distribution predictors. Landscape composition (the proportion of different land-use and land-cover classes: forest, agriculture, and pasture) within approximately 120 ha, was the most important variable for all models, influencing each species differently with respect to their tolerance of altered habitats. The remaining potential area of all three species is fragmented and has apparently been nearly lost in plains (<14% remaining). Distribution models allowed us to detect an important location in the western portion of our study area which may function as a large biological corridor in the Sierra Madre Oriental mastogeographic province, a region heavily transformed by land use change. In the context of habitat transformation, management promoting quality matrix at the landscape level promises to be a viable alternative for ungulate conservation in tropical regions of Mexico.
Keywords: conservation, land use change, Maxent, Mexico, tropical forest, ungulates.

Resumen

Se analizaron los patrones de distribución potencial de tres especies nativas de ungulados: *Odocoileus virginianus, Mazama temama* y *Pecari tajacu*, en el bosque tropical más septentrional de América en el este de México, en respuesta a diferentes variables físicas, climáticas, biológicas y antropogénicas, para identificar factores ambientales relacionados con su distribución potencial y áreas potenciales clave para la conservación de ungulados. Se obtuvieron registros actuales de presencia para cada especie y se construyeron modelos de distribución potencial utilizando el modelo de nicho ecológico de máxima entropía. Las superficies de adecuabilidad del modelo fueron utilizadas para calcular el hábitat potencial remanente en la región, así como el área potencial de simpatría y la representatividad de éstas en Áreas Naturales Protegidas. Las variables biológicas y antropogénicas predijeron mejor la distribución para las tres especies. La composición del paisaje (proporción de diferentes clases de uso del suelo: bosque, agricultura, agostadero) en un área aproximada de 120 ha, fue la variable más importante para todos los modelos, influyendo diferente a cada especie en relación a la tolerancia de éstas a hábitats alterados. El área potencial remanente para las tres especies parece estar fragmentada y casi eliminada en las áreas de planicie (<14% remanente). Los modelos de distribución nos permitieron detectar una superficie importante en la parte occidental del área de estudio que posiblemente podría funcionar como un gran corredor biológico que promueve la conectividad en la provincia mastgeográfica de la Sierra Madre Oriental en una región altamente transformada por cambios de uso de suelo. Bajo este contexto de transformación de hábitat, el manejo enfocado a fomentar una matriz de calidad a nivel de paisaje, promete ser una alternativa viable para la conservación de ungulados en regiones tropicales de México.

Palabras clave: Conservación, cambio de uso de suelo, Maxent, bosque tropical, ungulados.

Introduction

Land use change is the main cause of habitat loss in tropical ecosystems. The tropical biome contains approximately 44% of the world's forests and is subject to the highest deforestation rates worldwide [1]. For tropical Mexico, the estimated amount of original forest lost to agriculture and cattle grazing is 18.5% - 23.6% [2], resulting in fragmentation of most remaining tropical ecosystems. The Huasteca region of San Luis Potosí, located in northeastern Mexico, harbors the northernmost distribution of tropical forest. The geographical location and the physical and climatic conditions prevailing in this region have promoted the development of agriculture and cattle grazing at the cost of natural ecosystems. Consequently, nearly 37% of the total surface area originally covered by natural vegetation (4288 km²) disappeared between 1970 and 2000 [3]. The remaining forests, however, hold an enormous biological diversity of great ecological and evolutionary value [4]. This region is the sympatric distribution edge of three wild ungulate species: the white-tailed deer (*Odocoileus virginianus*), the Central American red brocket deer (*Mazama temama*), and the collared peccary (*Pecari tajacu*). Through herbivory, seed dispersal, and seed depredation, these species contribute to fundamental plant population, community, and ecosystem dynamics [5,6]. In addition, these species are culturally important since they have historically been hunted for subsistence by local inhabitants of most Mexican rural areas [7]. Therefore, conservation of these species will promote preservation of both well-functioning ecosystems, and the traditional way of living of local inhabitants.

Tropical forest fragmentation dramatically transforms natural dynamics, potentially triggering species extinctions, decreasing survival, and modifying species distributions [8]. Responses to novel habitat conditions depend on species adaptability and tolerance to anthropogenic disturbance. Understanding the factors controlling species distribution patterns is critical for the development of conservation strategies [9]. At the regional scale, ungulate distribution is affected by habitat elements of different types: physical, climatic and ecological aspects including vegetation, ecological interactions such as competition and predation [10,11]; plant associations, food [10,12-16] and water availability; altitude, slope, aspect, salt sources, and temperature [12,15-19]. Anthropogenic aspects influencing ungulate distributions include hunting, roads, accessibility, and forest harvesting [14,20,21].

Understanding these factors is necessary to describe legacy effects of land use on species-specific distribution. The white-tailed deer, a generalist species adaptable to some human disturbance, can occupy transformed areas [22]. The Central American red brocket deer, a more specialized species less tolerant of human disturbance [23], is expected to reduce its distribution under habitat isolation. Finally, the collared peccary is a species of intermediate tolerance, which in spite of using continuous more than fragmented forests [13,24,25], has the ability to use agricultural fields and other areas altered by humans if they are close to natural remaining habitat [12], and it can inhabit fragmented ecosystems without modifying its behavioral patterns [26]. This species will likely not dramatically change its distribution in moderately transformed areas.

Previous studies in tropical regions of Mexico have analyzed factors affecting ungulate potential distribution using models based on bioclimatic and topographic variables [e.g. 27]. Others have also incorporated anthropogenic variables in evaluating habitat quality [e.g. 28]. Considering that scale multiplicity is key to understanding spatial patterns and ecological processes [9], our study adds to the findings of previous investigations because we analyzed potential distributional patterns at an intermediate scale consisting of a relatively large (several hundred thousand hectares) region within a single state, San Luis Potosí, simultaneously considering traditional (bioclimatic) variables as well as those derived from local scale studies. Overall, we used physical, climatic, anthropogenic, and biological variables of significant value for the presence of ungulate species to develop ungulate potential distribution models, and used these models to fulfill the following research objectives: (1) to examine and compare physical, climatic, biological, and anthropogenic variables that relate to the potential distribution of each of the focal species, and (2) to identify potential key areas for ungulate conservation in the Huasteca region of northeastern Mexico.

Methods

Study area

The portion of the Huasteca region within the Mexican state of San Luis Potosí is located approximately 300 km NNE from Mexico City (Figure 1). It extends to the east from the Atlantic slope of the "Sierra Madre Oriental" towards the coast plain of the Gulf of Mexico (98°39´-99°31´ W, and 21°10´-22°45´), occupying 11,665 km². The relief is complex, including plains, mountain chains, hills, and micro-valleys, with elevations ranging from 0 to 2,500 m a.s.l. The dominant climate is warm sub-humid and humid, but sub-warm humid is also present. The highest elevations have a temperate climate. Mean annual temperature is greater than 22, 18, and 12°C for each of these climates, respectively. Annual rainfall ranges from 730 mm to 2,200 mm. Rains occur from June to September, and the dry season lasts from October to May [29]. Vegetation communities in the region include tropical evergreen and deciduous forests in the western portion, subtropical oak forests and isolated relicts of cloud forests in the mountains, and pine forests at elevations above 2000 m a.s.l. [4,29].

The Huasteca is a rural agrarian region with a population density of 0.013 people/km². It contains 94% of the statewide indigenous population, and has the highest mean poverty and marginalization within the state [30]. Main economic activities are agriculture and cattle ranching, with sugar cane plantations and pastures surrounding the remaining natural vegetation [29]. Most tropical ecosystems in this region have some degradation and/or succession, especially in areas with favorable climatic and physiographic conditions for either agriculture, farming, or forest harvesting [31]. This region is representative of most of the northeastern Mexican Neotropics.
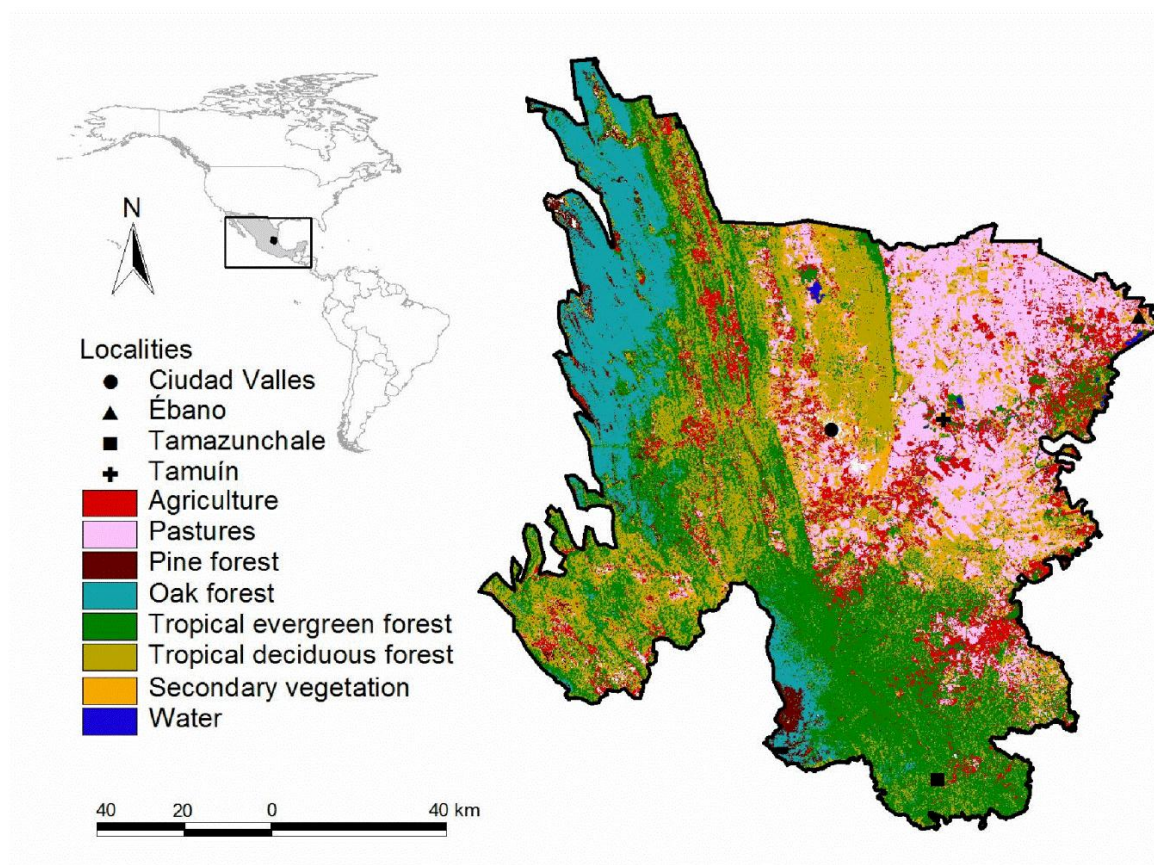
Fig. 1. Location of the Huasteca Potosina, San Luis Potosi, Mexico. Land use and land cover (modified from [33]), and localities of more than 10,000 inhabitants (obtained from [30]).

Species records

Direct and indirect ungulate records from museum collections, photo traps, sightings and tracks were compiled from the following sources: our own field observations from 2006 to 2011, records obtained from personnel of various institutions (T. Escalante; L. Martínez-Hernández, unpublished data), and from Secretaría de Desarrollo Agropecuario y Recursos Hidráulicos (SEDARH), and Secretaría de Ecología y Gestión Ambiental of the State of San Luis Potosí (SEGAM). All records without date and corresponding to areas currently covered by agriculture, grazing fields, or urban developments were eliminated from the database. To avoid autocorrelation, only one record was selected for any given pixel. The pixel resolution was 1 km², which completely includes all three ungulate home ranges [15,17,26].

Environmental variables

Sixteen variables known to influence the distribution of our study species were chosen (Table 1). For interpretation, these variables were grouped into physical, climatic, anthropogenic, and biological. Cartographic information obtained from different sources was used to generate each variable using ArcView [32] as follows:

Climate, temperature and precipitation layers were obtained from the WorldClim database (http://www.worldclim.org). These layers were clipped to the extent of our study area.
For vegetation communities, six bands from the 2006 Landsat ETM image (bands 1, 2, 3, 4, 5, 7) from the study area were used. The panchromatic band (band 6) was not used because it does not depict much information related to vegetation.

To determine key plant species distribution, Maxent 3.3.3e (http://www.cs.princeton.edu/~schapire/maxent/) was employed to generate potential species distribution models for 11 plant species that are consumed by wild ungulates in the study area (Table 2), using 19 bioclimatic variables from the WorldClim database (http://www.worldclim.org), and occurrence records extracted from the herbarium "Isidro Palacios" of the Drylands Research Institute of the Autonomous University of San Luis Potosi; this information was complemented with our own field records collected from August 2010 to February 2011.

For physical variables, we chose: (a) slope, calculated from 0 to 90°, and aspect, classified as north: 316 – 45°, east: 46 – 135°, south: 136 – 225°, and west: 226 – 315°. These layers were generated from the ASTER GDEM (Global Digital Elevation Model [http://www.gdem.aster.ersdac.or.jp/]) using the 3D Analyst tool of ArcGIS 9.0. (b) Soil types were obtained from Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP) and Comisión Nacional para el Uso y Conocimiento de la Biodiversidad (CONABIO [www.conabio.gob.mx/informacion/gis/]).

Layers of water sources, roads, and towns were generated by digitizing polygons through interpretation of the 2006 Landsat ETM image from the study region. Once these polygon layers were completed, the following proximity zones were constructed: (a) For water sources, 300 m, 600 m and >600 m buffers were built because the target ungulates keep their home ranges within 600 m of water sources [11,15]. (b) Towns were grouped in four categories according to total population: I. <150; II. >150-1,500; III. >1,500-10,000; and IV. >10,000 inhabitants. For categories I through III, buffer zones of 0.1, 0.2, and 1.5 km were used respectively. For category IV, the polygons of the urban areas were digitized based on the 2006 Landsat ETM image. These polygons were defined *a priori* as unsuitable habitat for all three ungulate species. (c) Paved roads were classified into primary and secondary, and for each of these categories, proximity buffers of 0.3, 0.9, and 1.2 km representing road effect magnitudes were built.

Habitat fragmentation variables included fragment size, distance from nearest fragment, and landscape composition. The first two of these variables were derived from a land use and land cover map of the study area [33] using the Patch Analyst 3.2 Arc View Extension [32]. For landscape composition, which has been previously defined as the proportion of different land use and land cover types within a given area [9], the study area was subdivided into 1.20 Km² hexagons representing the mean territory size of the study species [11,15,20]. Within each of these hexagons, proportions covered by forest, agriculture, and rangeland were calculated using the Spatial Analyst extension for Arc View [32], and the hexagons were classified in 20 classes according to the surface proportion occupied by each land use class.

Table 1. Environmental variables used to predict suitable habitat conditions for three ungulate species at Huasteca Potosina: *Odocoileus virginianus*, *Mazama temama* and *Pecari tajacu*.

Variable[1]	Description	Study area (values)	Source
P1	Soil types	16 (classes)	www.conabio.gob.mx
P2	Water	2 (classes)	derived from Landsat 2006
P3	Altitude	0-2521 (m.a.s.l.)	www.gdem.aster.ersdac.or.jp
P4	Slope	0-90 (°)	www.gdem.aster.ersdac.or.jp
P5	Aspect	0-360 (°)	www.gdem.aster.ersdac.or.jp
C6	Annual Mean Temperature	135-253 (°C*100)	http://www.worldclim.org
C7	Isothermality	51-64 (°C*100)	http://www.worldclim.org
C8	Annual Precipitation	541-2769 (mm)	http://www.worldclim.org
C9	Precipitation Seasonality	60-99 (mm)	http://www.worldclim.org
A10	Towns	5 (classes)	derived from Landsat 2006 and [30]
A11	Landscape Composition	20 (classes)	derived from [33]
A12	Roads	6 (classes)	derived from Landsat 2006
B13	Fragment Size	0.09-799,782 (ha)	derived from [33]
B14	Distance from nearest patch	0.003-2.141 (km)	derived from [33]
B15	Key plant species [a]	0-1 (probability)	herbarium and field observations records
B16	Vegetation	6 (bands)	Landsat ETM 2006

[1]Variable types: **P.** Physical, **C.** Climatic, **A**. Anthropogenic, and **B.** Biological.
[a] see Table 2.

Species distribution modeling

Following Phillips et al. [34], potential distribution models for ungulates within our study area were built using the Maxent 3.3.3e algorithm (http://www.cs.princeton.edu/~schapire/maxent/). It has been reported that this algorithm outperforms others when the availability of training data is limited and consists only of presence records and environmental information, which includes both continuous and categorical variables [34]. Following Elith et al. [35], before running the distribution models, masks were used to define urban and human settlement areas, as well as water bodies *a priori* as unsuitable habitat. Then, in order to maintain the greatest amount of information, all cartographic layers were re-sampled to 28.5 m², corresponding to the finest resolution (*i.e.* the Landsat ETM image). Maxent was fed with both the presence records and the layers representing environmental variables, and models were built using 75% of the presence records as training points. The remaining records were used to evaluate model precision. The following parameters were specified: 500 iterations with a convergence threshold of 0.00001, and 10,000 random locations for the covariant space [34]. The algorithm was run independently for each species with 10 replicates for each model [35], and the average model of the replicates was selected.

Table 2. Plant species consumed by target ungulates: *Odocoileus virginianus* (Ov), *Mazama temama* (Mt) and *Pecari tajacu* (Pt) in the Huasteca region, Mexico.

Family	Plant species	Ungulates species			Consumed plant part
		Ov	Pt	Mt	
Asteraceae	*Baccharis trinervis* [c]	1			Leaves
Bombacaceae	*Pseudobombax ellipticum* [c]	1			Leaves
Cactaceae	*Acanthocereus pentagonus* [c]	1			Stems
Euphorbiaceae	*Croton niveaus* [c]	1			Leaves
Fabaceae	*Eysenhardtia polystachya* [c]	1			Leaves
Lauraceae	*Ocotea tampicensis* [a,c]	1			Fruit
Moraceae	*Brosimum alicastrum* [b,c]	1	1		Fruit
Moraceae	*Ficus cotinifolia* [a,c]	1	1		Fruit
Moraceae	*Ficus obtusifolia* [a,c]	1	1		Fruit
Myrsinaceae	*Ardisia escallonioides* [c]	1	1		Leaves, Fruit
Palmae	*Sabal mexicana* [c]	1	1	1	Fruit

1. Plant species consumed by target species.
[a] [6]
[b] [39]
[c] Field observations in study area from August 2010 to February 2011.

Model evaluation

Precision and predictive ability were cross-validated through the Receiver Operating Characteristic (ROC) curves using the Area Under the Curve (AUC) of testing data. Taking into account the limitations associated with the process of evaluating accuracy through ROC curves [36], we evaluated model precision and predictive ability using partial ROC curves as recommended by Peterson et al. [36]. This method entirely avoids absence data and calculates AUC based on "the proportion of the overall area predicted as present rather than using commission error calculated based on data summarizing absences" [36]. For this model evaluation process we used the "Tool for Partial ROC" [37]. We ran partial ROC curves specifying 1,000 repetitions for the resampling with replacement, and 50% of points in the bootstrap, and for each species we ran the partial curves three times using 1-omission threshold greater than 0.99, 0.95, and 0.80 of the curve area for the evaluation. The percent contribution of each environmental variable to the model was evaluated, and a jackknife test was used to evaluate variable contribution. In this test, each variable is consecutively excluded and a model is generated with the remaining variables, and with the isolated variable. The variables that most contribute to the model indicate a loss in gain when excluded, and yield gain when the model is developed only with that variable [38].

Identification of potential suitable habitat areas

Model suitability surfaces were used to identify potential remaining habitat in the region. Suitability values were converted to binary format using the logistic threshold by maximum training sensitivity plus minimum specificity [34]. This allowed us to identify potential distribution areas satisfying the environmental conditions of the fundamental niche of each species. In the model, the fundamental niche was defined based on the input variables associated with the presence locations, and those which failed to satisfy this condition [34]. Thus, potential distribution areas with adequate conditions (i.e., those with associated values greater than the threshold) were classified as potential suitable habitat. Then, sympatric areas were identified as those where suitable habitat for all three ungulate species overlapped. Sympatric areas were overlaid with polygons of the Natural Protected Areas (NPA) of the region to calculate percent overlap. In addition, the number of fragments with greater areas than the minimal home range reported in the literature was calculated for each species; these are >50, >25 and >40 ha, for white-tailed deer, Central American red brocket deer, and collared peccary, respectively [15,20,26]. Because the species could potentially occupy these fragments, these could potentially sustain subpopulations.

Results

A total of 89, 86, and 72 records were used for *O. virginianus, P. tajacu* and *M. temama*, respectively. All distribution models had a reasonable performance based on partial ROC AUC values, such that all three models were significantly better than a random model (P<0.001 for all three species regardless of the proportion of the curve area considered). Five variables: (1) landscape composition, (2) fragment size, (3) annual precipitation, (4) precipitation seasonality, and (5) soil types, had a combined relative contribution of 77.8, 71.4 and 70.3% to the potential distribution models of Central American red brocket deer, white-tailed deer, and collared peccary, respectively (Table 3). Landscape composition was important for all three species (see below).

In addition, the following variables contributed > 10% to define potential distribution for the following species; for *P. tajacu* fragment size, precipitation seasonality, and vegetation; for *O. virginianus* fragment size and soil type; and for *M. temama* annual precipitation and fragment size. The single most important variables contributing to potential distribution models were landscape composition for both the red brocket and the white-tailed deer, and forest fragment size for the collared peccary. The jackknife test identified landscape composition as the most important variable for white-tailed deer and collared peccary, and seasonality and precipitation for the Central American red brocket deer. Response curves showed that occurrence probability of all three ungulate species increased with increasing patch size. In addition, occurrence probability was positively influenced by proportion of forest cover, the landscape composition variable in the model, such that the greatest occurrence probability corresponded to landscapes having >50% covered by forest, and those with 40% forest and the remaining area covered by agriculture and pastures for the Central American red brocket and white-tailed deer, respectively. For the collared peccary, the greatest occurrence probability was predicted for areas covered by either forest and agriculture in similar proportions, or > 80% forest.

Table 3. Results of the Jackknife test of regularized training gain for three ungulate species: *Mazama temama*, *Odocoileus virginianus* and *Pecari tajacu*. We present variable contribution to the model and gain when one variable is omitted and used in isolation. Values in bold represent highest contribution values.

Variable	*Mazama temama*			*Odocoileus virginianus*			*Pecari tajacu*		
	Contribution (%)	Without variable	With only variable	Contribution (%)	Without variable	With only variable	Contribution (%)	Without variable	With only variable
P1	2.7471	1.0816	0.2364	**26.4439**	0.9371	0.3592	7.2386	0.8518	0.1702
P2	1.6133	1.097	0	0.5756	1.0179	0	1.5097	0.9216	0.0352
P3	0.3587	1.1057	0.3749	1.2125	1.0313	0.223	1.3563	0.9256	0.2545
C6	3.4603	1.1058	0.306	1.2103	1.0126	0.2744	9.5101	0.9268	0.2694
C7	0.8707	1.1042	0.1134	8.2962	0.9615	0.0433	5.5032	0.9002	0.0163
C8	**17.2608**	1.0508	0.3837	2.0228	1.0016	0.025	5.3785	0.8444	0.0444
C9	9.1823	1.0188	0.0882	10.5313	1.0264	0.2222	**14.3619**	0.9245	0.2332
A10	6.8318	1.042	0.0851	4.1888	0.9947	0.0299	3.0955	0.9046	0.0212
A11	**24.4888**	1.0979	0.5082	**29.2208**	0.912	0.372	**13.7273**	0.8375	0.3131
B13	**24.129**	1.1032	0.4408	3.2781	1.0317	0.2026	**19.9265**	0.9309	0.2187
B14	0.6387	1.104	0.435	1.6863	1.0107	0.2549	1.0604	0.9276	0.2522
B15	3.7896	1.0861	0.3752	2.8818	0.989	0.0119	3.1219	0.9316	0.093
B16	4.6286	1.1092	0.35715	8.4515	1.0239	0.2414	14.2101	0.9185	0.1449
TOTAL	100	1.085		100	0.996		100	0.903	

P1. Soil types, **P2**. Water, **P3**. Altitude, **C6**. Annual Mean Temperature, **C7**. Isothermality, **C8**. Annual Precipitation, **C9**. Precipitation Seasonality, **A10**. Towns, **A11**. Landscape Composition, **B13**. Fragment Size, **B14**. Distance from nearest patch, **B15**. Key plant species, **B16**. Vegetation.

White-tailed deer had the widest potential distribution with 4,426 km² representing 38% of the study area, and including sub-tropical oak forests, tropical evergreen and deciduous forests, pine forests, and secondary vegetation. The potential distribution for the Central American red brocket deer covered 3,156 km², 27% of the study area, which included sub-tropical oak forests, deciduous, and to a greater extent, tropical evergreen forests. Finally, the collared peccary had the smallest potential distribution area with only 1,756 km², representing 15% of the study area and mainly occupying sub-tropical oak and tropical forests restricted to mountain chains, and some pine and cloud forests at the southwestern portion of the study area (Figure 2).
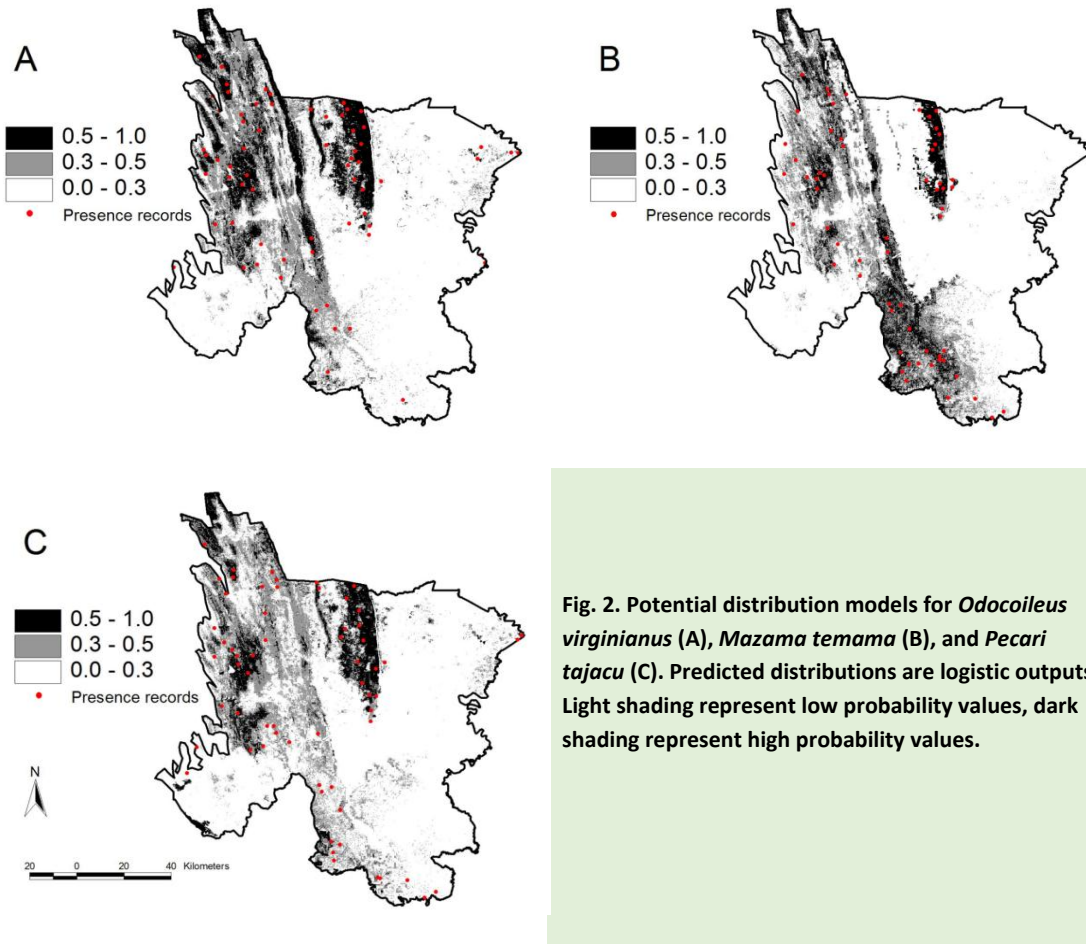
Fig. 2. Potential distribution models for *Odocoileus virginianus* (A), *Mazama temama* (B), and *Pecari tajacu* (C). Predicted distributions are logistic outputs. Light shading represent low probability values, dark shading represent high probability values.

The combined potential distribution of all three species represents 52.7% of the study area, 31.5% of which is shared by all three species. This potential sympatry area includes 94 fragments >50ha with a mean area of 21.17 km² (CV=4.13). These convergence areas, located at the western portion of the study area, are partly connected and include tropical deciduous and sub-tropical oak forests, both associated with mountain chains; only 11.4% of this potential suitable distribution area lies within the two largest NPAs of the region: the "Abra-Tanchipa" Biosphere Reserve, and the "Xilitla" National Forest Reserve (Figure 3). The region contains nine NPAs encompassing 547 km², corresponding to 4.6% of the study area, and 97.2% of these NPAs are located in mountain chains. Finally, the study region had 169 fragments with an average area of 9.82 km² (CV=4.6), 162 fragments with a mean area of 20.72 km² (CV=7.3), and 138 patches averaging 34.43 km² (CV=10.6) of potential distribution for the peccary, Central American red brocket deer, and white-tailed deer, respectively. The largest proportion (>99%) of most fragments which fall within NPAs is actually located outside these reserves. However, with the exception of the Tancojol and Bosque Adolfo Roque Bautista, all other Natural Protected Areas had potential suitable habitat in most of their areas (Table 4).

Table 4. Fragmentation patterns of potential distribution areas of three ungulate species within Natural Protected Areas of the Huasteca region of San Luis Potosí, Mexico. Target species included: *Odocoileus virginianus* (Ov), *Mazama temama* (Mt) and *Pecari tajacu* (Pt).

Name and Category[1]	Surface of NPA [ha]	Main vegetation types[2]	Number of fragments[3]	Recorded presence inside NPAs	Area of fragments inside NPAs [%]	Potential distribution area inside of NPAs [%]
			Ov-Pt-Mt	Ov-Pt-Mt	Ov-Pt-Mt	Ov-Pt-Mt
Bosque Adolfo Roque Bautista [b,SP]	30	Tr	0-0-0	0-0-0	0-0-0	0-0-0
Cuevas de Mantetzulel [b,NM]	698	ND	1-0-1	1-0-0	<1-0-<1	96-0-99
Cuevas del Viento y de la Fertilidad [b,SS]	8	Tr	1-0-1	0-0-0	<1-0-<1	94-0-100
La Hoya de las Huahuas [b,NM]	409	Tr	1-2-1	1-1-1	<1-<1-<1	94-<1-100
Porción Boscosa de San Luís Potosí (Xilitla) [a,NFR]	29,885	Pf,Of,Tr,Cf	3-7-2	1-4-3	3-56-11	74-34-82
Sierra del Abra Tanchipa [a,BR]	21,464	Td,Tr	1-2-1	6-2-7	5-41-61	99-75-90
Sierra del Este y de En medio [b,SR]	1,795	Tr,Td	1-3-3	2-2-1	<1-16-1	97-68-73
Sótano de las Golondrinas [b,NM]	285	Tr,Pf,Of	1-0-1	0-0-0	<1-0-<1	84-0-95
Tancojol [b,ER]	95	Tr,Td,Sv	0-0-0	1-0-0	0-0-0	0-00

[1] Category: [a.] Federal Protected Areas, [b.] State Protected Areas, **SP**. State Park, **NM.** Natural Monument, **SS**. Sanctuary, **NFR**. National Forest Reserve, **BR**. Biosphere Reserve, **SR**. State Reserve, **ER**. Ecological Reserve.

[2] Main vegetation types: **Pf**. Pine forest, **Of**. Oak forest, **Cf**. Could forest, **Tr**. Tropical evergreen forest, **Td**. Tropical deciduous forest, **ND**. No data, **Sv**. Secondary vegetation.

[3] Number of fragments: fragments were estimated for *Odocoileus virginianus* (Ov) > 50 ha, *Pecari tajacu* (Pt) > 40 ha and for *Mazama temama* (Mt) > 25 ha.

Discussion

In spite of extensive land use changes, our study region still contains potential suitable ungulate habitat. In general, ecological and anthropogenic variables were the best predictors of ungulate potential distributions, whereas physical variables such as water sources, aspect and slope that are important at the local scale were irrelevant at the regional extent (see below). Responses to predictor variables differed among species.

White-tailed deer

Our models yielded a potential distribution area 30% greater for the white-tailed than for the Central American red brocket deer, and a clear separation in plant community associations and landscape composition, in which the white-tailed deer was associated with open habitats. Segregation of habitat types is critical for resource partitioning among co-existing species [13], and in tropical ecosystems where these species co-exist, the white-tailed deer preferentially uses deciduous forests and open habitats [39,40]. The use of open habitats by this species may be associated with its large body size and the structure of male antlers, which influence movement and feeding [40]. The greater presence probability of this species near towns of 150 – 1,500 inhabitants may be related to wood extraction, which maintains the surrounding forests in highly productive early successional stages [41], thus increasing food availability [14]. On the other hand, white-tailed deer in southeastern Mexico can damage corn (*Zea mays*) and bean (*Phaseolus vulgaris*) crops through browsing [42]. Thus, food availability in crops near towns may contribute to its distributional pattern.

Roads may positively or negatively influence deer distribution through either avoidance [43], or possible attraction because some plants eaten by white-tailed deer might be abundant near roads [44]. Similarly, water sources have been regarded as a key habitat element for the species [18]. The lack of contribution of these two variables to our potential distribution model is likely related to the relatively large scale of our model. Our sources of geographical information do not represent some water reservoirs such as concave rocks, natural or artificial depressions and small natural dams, which contain rain water throughout most of the year. These elements are locally more important than the large water bodies that we identified in the Landsat images. Our model also failed to identify slope and aspect as critical determinants of white-tailed deer potential distribution at the regional scale in spite of their reported importance at local scales [17,27,28]. While slope and aspect could influence this species at the local scale [17], at the regional scale these variables may be irrelevant. Soil type, however, was the second most important variable for this species at the scale of our analysis, followed by isothermality and precipitation seasonality (Table 3). Along with topography, these factors determine the structure and function of ecosystems, and thus influence fundamental habitat features.

Central American red brocket deer

The Central American red brocket deer, a highly specialized species intolerant of human presence [39], is a frugivorous ungulate whose distribution is determined by fruit availability, but most importantly by its diet specialization. Consequently, presence probabilities were affected by key plant species distribution. This species mainly consumes fruits in tropical ecosystems of Central America and southeastern Mexico [39], and herbaceous vegetation in cloud forests of the SMO south of our study area [45], but the proportion of plant parts consumed in this area has not been reported. Lack of information about its diet makes comparisons of our results with those from previous studies difficult. On the other hand, our findings are consistent with previous studies

indicating that in areas where it co-exists with white-tailed deer, the Central American red brocket deer prefers dense and perennial ecosystems [39,40]. Presence probabilities for this species increased in areas covered by forest with small amounts of agroecosystems and with increasing fragment size, but were independent of patch isolation. Consistent with our results, it has been documented that the Central American red brocket deer inhabits areas distant from human settlements [23], prefers sites with greater vegetation cover and avoids deforested areas [46], and that in remote sites and those with intricate topographies, it feeds on corn and beans from subsistence crops in small agroecosystems [42].

As far as we are aware, no previous studies analyzed road effects on Central American red brocket deer, but it has been suggested that site accessibility may promote ungulate hunting [21]. On the other hand, abrupt topography, salt, and water sources are identified as important habitat features for this species [16,19]. We failed to document important effects of these variables. As with our findings for white-tailed deer, particular small-scale water and salt sources could not be detected with the small resolution of our study.

Collared peccary

Our original expectation of intermediate susceptibility to habitat change by the peccary could not be confirmed. Some studies have described this as a species of wide ecological flexibility [10], whose herd size and group behavior remain unchanged between fragmented and large, unaltered forests [26]. However, there are some discrepancies about peccary tolerance to altered habitats [6,12,24]. Our model is supported by preliminary findings of small abundances of this species relative to the white-tailed deer and similar to the red-brocket deer, estimated through different methods for the Huasteca region (A. Hernández-Saint-Martin, A. Martínez-Hernández, & G. García-Marmolejo, unpublished data) indicating some degree of sensibility. Regional studies have reported restricted and stable activity patterns among seasons for the peccary, and the finding that home ranges differ among herds has been attributed to spatial variation in resource availability [26]. The localized dispersion pattern, spatially and temporally stable home range, and apparent small relative abundance of the species partially explain its restricted potential distribution in the Huasteca region. In addition, habitat loss at the Atlantic coastal plain, where more than half a century ago the collared peccary was abundant [47], presumably contributed to our model results, too. Most of this area, where slopes are <5°, is now covered by agroecosystems and pastures, and our model estimated that only 5.4% of this area contains suitable peccary habitat. Therefore, most potential distribution areas identified by our model correspond to sub-tropical oak forest, consistent with the finding that this species uses oaks more than deciduous tropical forests in the neighboring state of Tamaulipas [48].

In comparison with the white-tailed and the Central American red brocket deer, peccary potential distribution was independent of key plant species potential distributions. Peccary habitat partitioning occurs at fine scales, while at the landscape scale this species only uses one type of vegetation [13]. In tropical ecosystems, the peccary is mainly frugivorous [5], although it has also been reported as an opportunistic forager [10]. For our study region, its feeding habits still remain undocumented, but local inhabitants affirm that it eats young leaves of *Bromelia pinguin* (García-Marmolejo personal observation), an abundant understory species. Because this plant species has not been sampled, it was not included in our modeling, perhaps causing the lack of contribution of key plant species distribution to the modeled peccary distribution. On the other hand, fragment size and landscape composition were the most important factors for peccary potential

distribution, yielding potentially suitable distribution areas in landscapes primarily composed of forest or agroecosystems. These results are consistent with reports of peccaries preferentially inhabiting sites with abundant understory vegetation located far from human settlements [24], and with their preference of conserved in comparison with disturbed habitats [6]. This species causes damage to subsistence crops associated with water sources at large distances (>1km) from small towns [40]. The potential distribution and presence of this species in abandoned crops with abundant resources can be explained by occupation of suboptimal fragmented habitat with limited resource availability by a species which is territorial at the herd level [11].

In terms of physical variables, collared peccary presence probability was greatest between 1,500 and 2,400 m a.s.l., whereas elimination of slope and aspect increased model predictability. For this species, ravines and caves used as refuges, rocky hills [47], slopes, and higher elevation habitats have been reported as suitable in sympatric areas with the white-lipped peccary (*Tayassu pecari*) [26]. Finally, though water has been regarded as an important habitat feature for this species [11], soil type and water sources did not contribute substantially to its potential distribution model, and the elimination of roads increased model predictability, suggesting that these variables may be more important at finer scales.
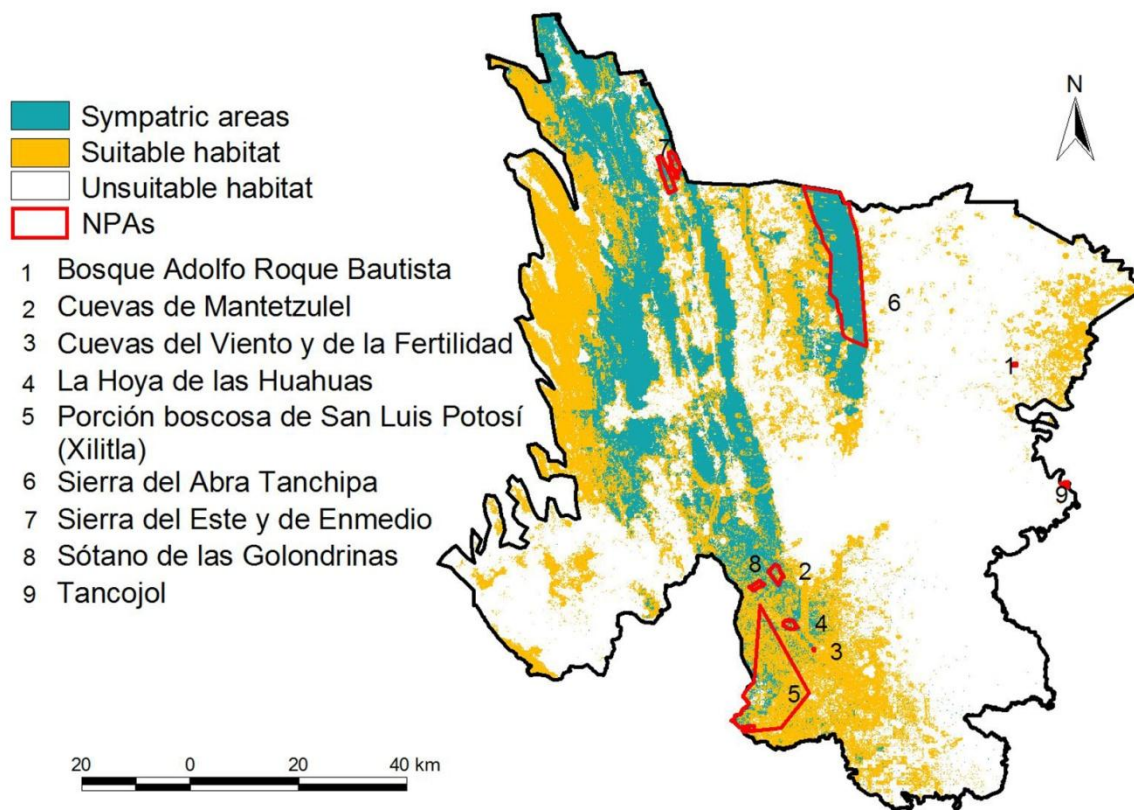

Fig. 3. Sympatric potential distribution areas of the three ungulates and Natural Protected Areas in the Huasteca Potosina, Mexico.

Implications for conservation

As explained below in detail, potential distribution models based on key variables for our three target species have potential applications for studies in other areas of northeastern Mexico and the entire continent, which have barely been studied and suffer rapid transformation through land use change.

In spite of the fragmentation patterns prevailing in our study area, our models showed relatively large and continuous potential distribution areas mainly at the western region of the study area. Previous research by Mandujano and González-Zamora [49] proposed a minimum critical area of 1,667 and 16,670 ha for maintaining long-term viability of a population of 500 and 5,000 white-tailed deer, respectively. If we assume that these areas are appropriate for the Huasteca region, then we calculate that our study area would only contain between one and nine fragments depending on these theoretical values of minimum population size. Most of these fragments would be located outside of NPAs and across a relatively continuous area at the western portion of the study area, which corresponds to the mountains. With our results we cannot conclude whether fragmentation in the Huasteca may influence population viability of our target species. However, we emphasize that our results suggest that the Sierra Madre Oriental contains the main remaining ungulate potential habitat in the study area. Our potential distribution models suggest that this mountain chain may constitute a corridor promoting connectivity within the region. The potential of our study area as a corridor at this regional scale, however, still deserves further investigation, and a corridor analysis using this data set would be published elsewhere.

Based on the importance of landscape composition for our target species, the large proportion of potential distribution areas located outside of NPAs, and the characteristics of the Social Ecological System of the Huasteca region, we conclude that conservation strategies should also consider areas outside NPAs. A management approach focusing on Nature´s Matrix proposed by Perfecto and Vandermeer [50] is the most realistic alternative to preserve ungulates. Such an approach proposes a quality matrix through ecological landscape and agroecological management of ecosystems that would simultaneously conserve wildlife habitat and encourage human food production. The traditional model for biodiversity conservation, conceived as a territorial divergent arrangement, isolated Natural Protected Areas for wildlife conservation into a highly transformed matrix dominated by human activities. This is clearly not a viable alternative for the Study Region and other tropical regions, at least in Mexico. From an ecological point of view, wildlife populations in isolated areas suffer insulation, inbreeding, and finally local extinctions. The Huasteca region is not an uninhabited territory, and its human population continues to increase. Thus, wildlife conservation must view ecosystems as social-ecological systems. Specific recommendations for ungulate conservation at the Huasteca region include habitat management to enhance foraging habitat quality at the local scale, and promoting habitat diversity within the agricultural matrix at the landscape scale [11, 50]. Habitat diversity maintains alternative feeding resources, thus providing long-term population viability even in fragmented ecosystems [6].

At the fine scale, additional research is needed to determine the local influence of key habitat elements that were unimportant at the regional extent, but are fundamental for ungulate management. Future studies should integrate some variables likely to influence species distributions, including ecological interactions such as competition and predation [10, 11], habitat

disturbance by anthropogenic processes [26], and subsistence hunting, which is considered the main cause of wild tropical ungulate population declines [7].

Acknowledgements

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