Human footprint effects on the distribution of the spotted lowland paca (*Cuniculus paca*)

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Human activity has caused the decrease of about 20 % of the planet's vertebrate diversity and 25 % in their abundance. Many large and medium-sized herbivore mammals have gone extinct locally, unleashing a cascade of ecosystem changes. The spotted paca (*Cuniculus paca*) is impacted by hunting and anthropogenic habitat fragmentation and loss. To protect spotted pacas, it is essential to estimate anthropogenic effects on their geographic distribution. Through the use of primary biodiversity data, bioclimatic data, land-cover data, and a human footprint index, we modeled the distribution of *C. paca*. From 105 candidate models, only one model met our selection criteria. The variables with the highest contribution were the human footprint and annual precipitation. According to the model's performance curves, the spotted paca has low to medium tolerance of anthropogenic pressure. *Cuniculus paca* tolerates low to medium anthropogenic disturbance, which we hypothesize is related to reduced predator pressure in habitats modified by humans. Accounting for the costs and benefits of anthropogenic disturbance is essential to paca conservation.

La actividad humana ha disminuido alrededor del 20 % de la diversidad biológica del planeta, así como del 25 % de la abundancia de los vertebrados. Esto ha llevado a mamíferos herbívoros grandes y medianos a extinguirse localmente, desatando una cascada de cambios en los ecosistemas. El tepezcuintle (*Cuniculus paca*) sufre una importante presión antropogénica debido a la cacería y pérdida de hábitat, por lo que es importante estimar sus efectos sobre su distribución para su conservación y manejo. Modelamos la distribución del tepezcuintle mediante el uso de datos primarios de biodiversidad de acceso libre, variables bioclimáticas, cobertura arbórea y un índice de huella humana que refleja la presión antropogénica sobre los ecosistemas. De 105 modelos candidatos, únicamente uno cumplió con los criterios de selección. Las variables con la mayor contribución fueron la huella humana y la precipitación anual. A partir de las curvas de respuesta del modelo, se observó en la especie una tolerancia a la antropización de baja a media. Estos resultados podrían deberse a que en ambientes antropizados los depredadores del tepezcuintle han disminuido sus tamaños poblacionales. Entender los costos y beneficios de la perturbación antropogénica es esencial para la conservación del tepezcuintle.

Keywords: Ecological niche models; species distribution models; spotted paca; human impact.

Introduction

No other species impacts biodiversity, community composition, and function like human beings (Tillman 1999). In the last century, human impact on Earth has increased so considerably that anthropogenic land cover change is the leading cause of biodiversity loss and the current epoch is now recognized as the Anthropocene (Ehlers and Krafft 2006). Indeed, vegetation biomass has decreased by 53 to 58 % in recent years (Erb *et al.* 2018) and 20 % of the planet's biodiversity has been lost (Hill *et al.* 2018; Díaz *et al.* 2019). These disturbances have greatly affected tropical ecosystems; although quantification of deforestation rates is difficult, some studies suggest that around 100 million hectares have been lost in recent years (Shimamoto *et al.* 2018). Approximately 332 terrestrial vertebrates have gone extinct since the 1500s, while around 25 % of vertebrate populations exhibit significant abundance declines, especially tropical birds and mammals (Dirzo *et al.* 2014). Overall, habitat loss is directly associated with the local extinction of large-and-medium-sized herbivorous mammals, unleashing a cascade of changes in ecosystems (Dirzo *et al.* 2014). The latter has a tremendous impact on forests because these species help maintain plant diversity via seed dispersal (Martínez-Ramos *et al.* 2016; Camargo-

Sanabria *et al.* 2015). Moreover, herbivorous mammals also have significant anthropogenic pressure due to hunting for their meat, like the spotted paca *Cuniculus paca*. The spotted paca is an endemic species from America and one of the largest rodents in the world (Emmons 2016). It is distributed from southern Mexico to northern Argentina, from sea level to up to 2800 m elevation (Padilla-Gómez *et al.* 2019). This caviomorph frugivore is an important seed disperser, as well as prey for large carnivores (*e. g.*, jaguar and puma; Figueroa-de León *et al.* 2016). Although the spotted paca is classified as Least-concern on the Red List of the International Union for Conservation of Nature (IUCN 2022), the modification and fragmentation of its habitat most likely threatens its populations; hence, it is crucial to assess its habitat status (Jax *et al.* 2015; Montes 2005). Correlative species distribution models are a helpful tool that allows estimating the relationship between environmental conditions and the presence of a species in the localities where it has been recorded, under the assumption that those environmental combinations where the species occurs are part of its fundamental niche, that is, where the intrinsic growth rate is positive (Franklin 2010; Soberón 2010; Falconi *et al.* 2021). These models have gained relevance for the conservation and monitoring of wildlife, given that they allow the identification of suitable habitats in current and climate change scenarios. Examples using species distribution models include the repopulation and reintroduction of declining or extinct species in the wild (D'Elia *et al.* 2015), as well as the identification of areas susceptible to invasion by exotic species, among many other applications (Jarvie and Svenning 2018; Espindola *et al.* 2019; Núñez-Penichet *et al.* 2021).

Although there have been previous attempts to estimate paca's distribution, they did not evaluate the effect of anthropization throughout the species range (*e. g.*, Cartaya *et al.* 2016; Contreras-Díaz *et al.* 2022). Our main objective in this study was to estimate the effect of the human footprint on the distribution of the spotted paca. We used the spatial human footprint index proposed by Venter *et al.* (2016), which combines different sources of human pressure including human population density, the presence of buildings, crops, induced grasslands, night lights, highways, roads, and navigable waters. By using this as a predictor in distribution models, we determined its effect on distribution and evaluated the paca's tolerance of anthropized environments. We expected *Cuniculus paca* to occur in low anthropized areas across its distribution.

Materials and methods

To estimate the effect of the human footprint on the distribution of *Cuniculus paca*, we evaluated its importance and percentage of contribution to species distribution models. The modeling framework consisted of three stages where we first collected occurrence data and modeling layers from open data repositories. Then we built candidate distribution models using different parameterizations of the Max-

Ent algorithm (Phillips *et al.* 2006), selecting those models that passed statistical significance, good performance tests and low complexity. Finally, using the best model, we estimated tolerance ranges to human footprint via MaxEnt's response curves and evaluated variable contribution and importance according to MaxEnt's Jackknife test.

Data collection and preparation. We obtained species occurrence data across the known distribution of the spotted paca from the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/) and SpeciesLink (https://splink.cria.org.br/). We curated these data following a standard protocol summarized in Cobos *et al.* (2018). We eliminated fossil observations, wrongly georeferenced localities, duplicated records, and doubtful occurrences. We checked the altitude of all the records, and when they were doubtful, we contacted the data providers to verify their validity. We also removed localities with more than 100 m of uncertainty in their coordinates and to ensure better correspondence with the environmental layers used data from before 1990 were eliminated from our dataset. To avoid spatial autocorrelation, we thinned occurrences at 1 km using the 'ntbox' R package (Osorio *et al.* 2020). Finally, we randomly split curated occurrences using 70 % for training and 30% for testing the distribution models.

As modeling layers, we used the bioclimatic variables from WorldClim 2 (Fick and Hijmans 2017), the percentage of forest cover (Tuanmu and Jetz 2014), and the 2009 Global terrestrial Human Footprint map (hereafter Human Footprint; Venter *et al.* 2016), at a spatial resolution of ~ 1 km². The election of bioclimatic and forest layers is based on the spotted paca's biology since this species lives in humid and forested environments (Pérez 1992; Beck-King *et al.* 1999; Gutierrez *et al.* 2017). The Human Footprint measures direct and indirect human pressures on the environment in 2009; this index ranges from 0 to 50, where 0 means natural environment and 50 high-density built environments. To select the layers to be used in the modeling process, we first removed WorldClim 2 variables 8, 9, 18, and 19 because they present abrupt discontinuities in some areas without geographic breaks (Anderson and Raza 2010; Escobar *et al.* 2014; Alkishe *et al.* 2022). Using information from the remaining layers, we estimated Spearman correlations between the environmental values associated with occurrence records and kept only those with correlations ≤ 0.6 to reduce multicollinearity. We clipped the selected layers according to the hypothesis of the accessible area for the species — also known as **M** — (Soberón and Peterson 2005) to avoid negative impacts of inappropriate background choices (Alkishe *et al.* 2022). To do this, we added a buffer of 500 km around the native range polygon of the spotted paca (Emmons 2016), which provided a hypothesis of **M** based on expert knowledge, with an added area likely explored via dispersal.

Calibration and selection of species distribution models. We used MaxEnt 3.4.1 (Phillips *et al.* 2006) as a modeling algorithm using the 'kuenm' R package (Cobos *et al.*

2019). This package allows fitting and evaluating Max-Ent models using different feature classes and regulation multipliers in an automated fashion. Assessment is done using the partial ROC test for statistical significance, omission rates for model performance, and the Akaike Information criteria for model complexity (Burnham and Anderson 2002; Warren and Seifert 2011). We fitted and evaluated 105 candidate models to select the best parameter settings from our modeling layers. The regularization multipliers assessed were: 0.1, 0.25, 0.5, 0.75, 1, 1.5, 2, 2.5, 3, 3.5, 4, 4.5, 5, 5.5, 6. We used all possible combinations of linear (l), quadratic (q), and product (p) feature classes.

For assessing the overall effect of human footprint on the distribution of the spotted paca, we evaluated its importance and contribution to the model, we performed the Jackknife test in MaxEnt for those models that were statistically significant and presented omission rates < 5% of testing data. Tolerances to human footprint were assessed by examining suitability changes in response curves of MaxEnt models.

Results

We obtained 6,420 occurrences from GBIF and 273 from Species Link. From these data, 5,450 and 32 were collected from 1990 onwards, respectively. After the data curation process, due to the elimination of wrong information and both spatial and temporal duplicates, our final data set included 417 records: 406 and 11 occurrences of GBIF and SpeciesLink, respectively.

Occurrences used in modeling are distributed along an elevation range from 2 to 2,711 m (Figure 1, panel B). However, more than 75 % of the records occur below 1,000 m. Data came from 17 countries along the species distribution (Figure 1, panel C), where Colombia and México had the most georeferenced records (> 80 % of the occurrences in our database; 274 and 64 records, respectively).

Out of 17 predictor variables, seven were the least correlated variables: human footprint, tree cover, annual mean temperature (Bio 1), mean diurnal range (Bio 2), isothermality (Bio 3), annual precipitation (Bio 12), and precipitation seasonality (Bio 15).

With the MaxEnt analyses, we obtained 105 candidate models, but only one model reached the selection criteria: statistically significant, low omission rate, and complexity. The model showed an AUC value of 0.882 ± 0.007, a regularization multiplier of 0.25, and linear, quadratic, and product features. The most contributing variables were human footprint (26.4 %), annual precipitation (21.4 %), and isothermality (19.1 %), while the least contributing variable was annual mean temperature (3.3 %; Table 1).

Regarding the geography, the model showed the most suitable areas in different zones throughout México, Guatemala, Belize, Costa Rica, Colombia, Venezuela, Ecuador, Perú, and some regions in Brazil and Bolivia (Figure 2).
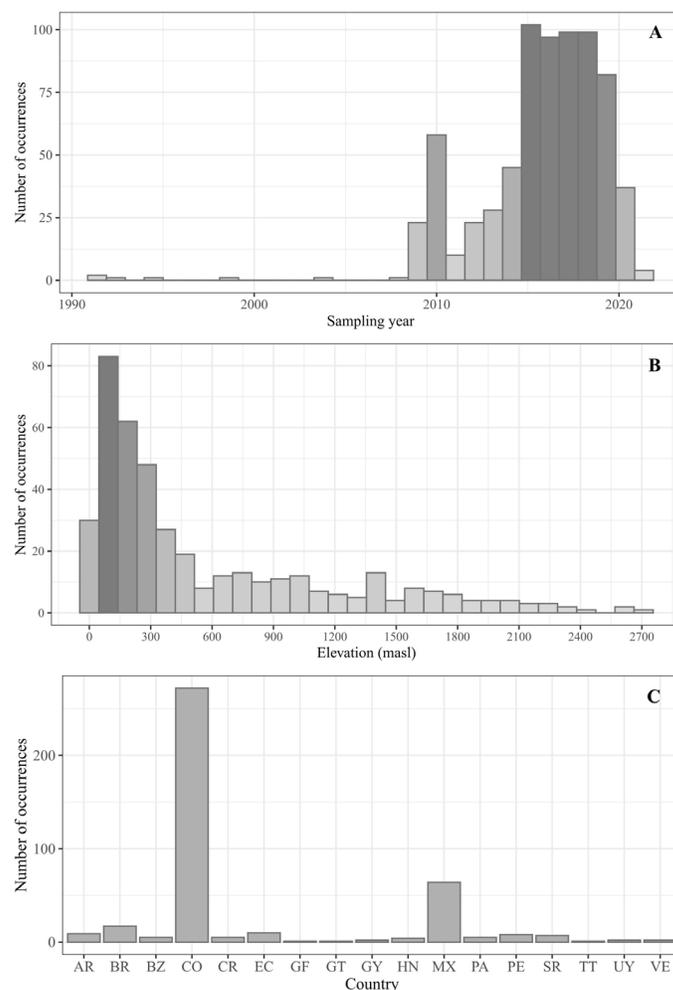
Figure 1. Description of the occurrences used in the modeling selection process: A. Occurrences per sampling year before the temporal and spatial thinning. B. Elevation (masl, meters above sea level) of the occurrences used in the model selection process. C. Occurrences per country used in the model selection process. Country: AR, Argentina; BR, Brazil; BZ, Belize; CO, Colombia; CR, Costa Rica; EC, Ecuador; GF, French Guiana; GT, Guatemala; GY, Guyana; HN, Honduras; MX, México; PA, Panama; PE, Perú; SR, Suriname; TT, Trinidad and Tobago; UY, Uruguay; VE, Venezuela.

The response curves of the model variables showed varying relationships in regard to the environmental suitability for the spotted paca (Figure 3). That is, the relationship between human footprint and environmental suitability showed a normal type form, where suitability decreased at human footprint index values greater

Table 1. Percent contributions for individual environmental variables to the best distribution model.

Variable	Percent contribution	Permutation importance
Human footprint map for 2009 (HFP2009)	26.4	30.9
Annual precipitation (Bio 12)	21.4	29.1
Isothermality (Bio 3)	19.1	6.5
Tree cover	12.3	10.1
Mean diurnal range (Bio 2)	11.6	12.0
Precipitation seasonality (Bio 15)	5.9	5.5
Annual mean temperature (Bio 1)	3.3	6.0
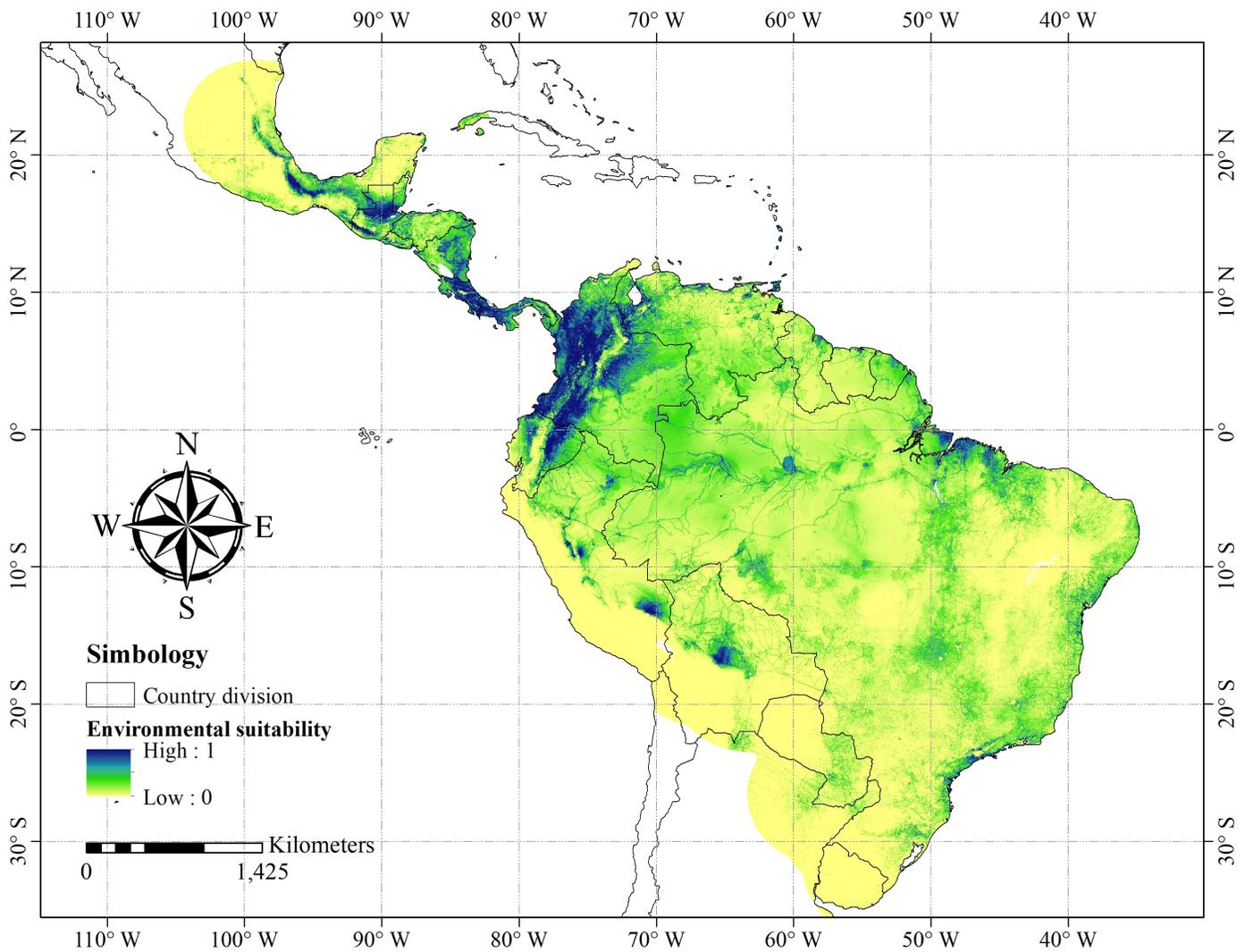
Figure 2. Species distribution model with the best performance. The MaxEnt regularization multiplier and feature type used were 0.25-linear-product-quadratic.

than 20. The same bell curve was found for tree cover and annual mean diurnal range (Bio 2). Regarding tree cover, suitability increased with the percentage of trees and slowly decreased at values of ~70 %. According to Bio 2, the spotted paca can be found along temperature variations of ±7; higher variations negatively affected suitability. The curve for annual precipitation accumulation (Bio 12) showed a positive relationship with suitability, while as precipitation seasonality (Bio 15, which measures variations in precipitation) increased, suitability decreased. Finally, we found a negative relationship between isothermality (Bio 3) and suitability for values < 60 and a positive relation for higher values (Figure 3). Isothermality quantifies the day-to-night temperature oscillations relative to the summer-to-winter oscillations (measured in percent). An isothermal value of 100 indicates that the daily temperature range is equivalent to the annual temperature range (O'Donnell and Ignizio 2012). Maximum suitability values for Bio 3 were found at 100, which indicates that this species prefers non-fluctuating temperatures.

Discussion

To estimate the effect of the human footprint on the distribution of the spotted paca, we used species distribution modeling and a rigorous process of model selection based on statistical significance, predictive power, and model complexity (Cobos et al. 2019). Using these criteria, we found a single model that best characterized the distribution of the species. Most occurrence records are below 1,000 m elevation (see Figure 1, panel B), as reported in previous studies (Beck-King et al. 1999; Cartaya et al. 2016); however, about 3.3 % of presences occur above 2,000 m, which agrees with recent studies in México where the species has been up to 2,800 m (Padilla-Gómez et al. 2019). Based on the theory of species distributions, we hypothesized that some of the higher altitude occurrence patterns are related to exploration activities and might not be part of its fundamental niche (Pulliam 2000; Osorio-Olvera et al. 2016). It is known that when primary productivity decreases, C. paca explores areas outside of its range in search of food and for predator avoidance (Martínez-Ceceñas et al. 2018). Also, this strat-
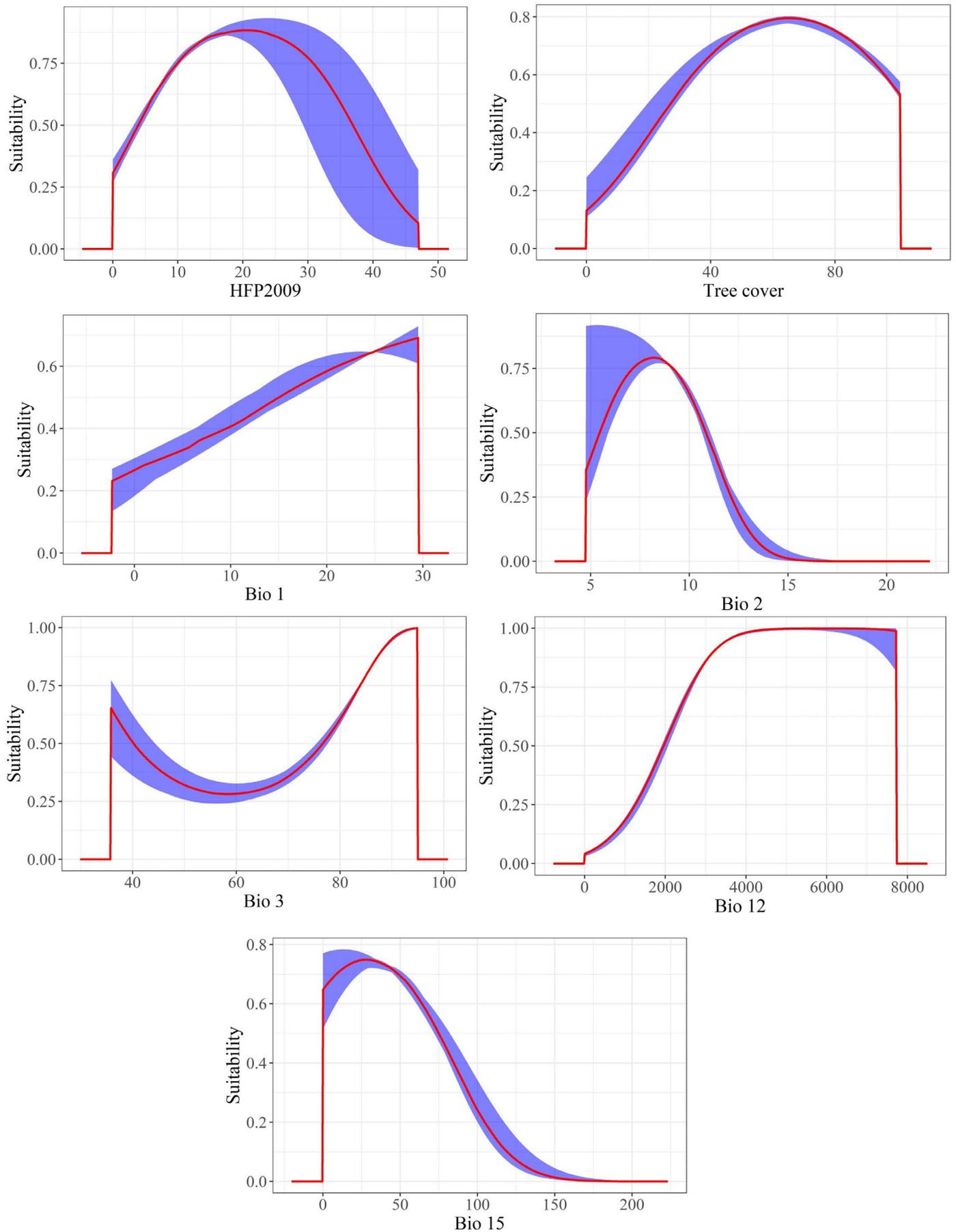
Figure 3. Variable response curves for the best distribution model. HFP2009, human footprint; tree cover; Bio 1, annual mean temperature; Bio 2, mean diurnal range; Bio 3, isothermality; Bio 12, annual precipitation; Bio 15, precipitation seasonality.

egy could be a response to climate change, as it has been documented with changes in latitudinal and altitudinal distribution patterns of many species in the world (Rowe *et al.* 2015; Feldmeier *et al.* 2020; Abbas *et al.* 2021).

The variable that contributed the most to the models was human footprint, followed by precipitation, temperature isothermality, and tree cover. These findings are in agreement with the natural history of the spotted paca given that the last three variables are crucial for its survival (Contreras-Díaz *et al.* 2022). El Bizri *et al.* (2018) found that precipitation fluctuations match reproductive cycles where mating and conception occur in the dry season, while pregnancies and births happen in the rainy season. Our results also show that *C. paca* is found in environments with less seasonal variation. High annual fluctuations in temperature and precipitation can affect food availability because fruit production depends on the rainy season, which also affects tree cover (Dubost and Henry 2017). For the spotted paca, tree cover and precipitation importance cannot be underrated, as it is an herbivore that depends on water bodies for survival and reproduction (Figueroa de León *et al.* 2016; Contreras-Díaz *et al.* 2022).

The contribution of the footprint variable highlighted the crucial role of anthropogenic pressures on spotted paca distribution and movement (Tucker *et al.* 2018). Environmental suitability increases when the human footprint index ranges from 0 to 20. A value of zero corresponds to natural areas with no human impact and values greater than 20 to highly impacted areas (Di Marco *et al.* 2018; Venter *et al.* 2016). Although the paca seems to tolerate low to medium human impacts, an exploration of the components of the human footprint index shows that this species is found in places where the human population density is on average $\leq 15/km^2$, as well as places with low pressures due to roads and pasture lands (see Supplementary Material). Our results agree with Di Marco *et al.* (2018), who observed that the human footprint is a fundamental predictor of the risk status for different mammal species and found that richness decreases drastically from a value of 20, which supports our conclusion that pacas tolerate a certain level of human disturbances if adequate conditions exist for its reproduction and feeding activities. Although anthropogenic disturbance has negative effects such as habitat fragmentation and roadkill risk, some benefits need to be analyzed (Parsons *et al.* 2018). For example, certain studies report that the spotted paca can be favored by induced vegetation and crops, because it consumes fruits of cultivated species such as mango, avocado, and citrus, among others (Gallina 1981; Zucaratto *et al.* 2010). Using such modified habitat may be related to seasonality and the productivity decrease in the species' environment, forcing it to disperse to areas with higher human impact (Martínez-Ceceñas *et al.* 2018). In addition, movement to these areas could be related to predator evasion behavior (Parsons *et al.* 2018). It has been hypothesized that the spotted paca is flexible in terms of its habitat pref-

erences, where areas with a certain degree of disturbance would present lower predator densities (*e. g.*, felines) and predation risk (Michalski and Norris 2011). It is important to highlight that the apparent tolerance of the spotted paca to medium levels of disturbance could also be linked to biases in presence data due to more intensive sampling along roads, highways, areas near towns, and protected areas. However, this does not seem to be a limiting factor in the predictive power of the distribution models (McCarthy *et al.* 2011). Even if the spotted paca tolerates medium ranges of anthropogenic pressure, the highest values of environmental suitability we found indicated a tree cover of ≥ 60 % (see Figure 3), an adequate coverage to carry out their exploration and feeding activities (Pérez 1992; Beck-King *et al.* 1999; Gutierrez *et al.* 2017).

To conclude, we must recognize that humans are the main driver of habitat loss. However, as some species are more or less adapted to these changes, it is crucial to study the mechanisms that enable wildlife species to coexist with us, describe their environmental requirements and how they respond to changes in their habitat. For example, by studying North American mammals, Hantak *et al.* (2021) documented that large species tend to be smaller in anthropized environments. Indeed, more studies assessing species' tolerances to human activities are needed to understand the factors determining species distributions in the Anthropocene. Furthermore, the relationship between species and their environment is not static, it is scale-dependent, and thus we need studies at local and coarse spatial resolutions at different temporal scales to better design and implement conservation strategies.

Literature cited

Abbas, S., J. E. Nichol, and M. S. Wong. 2021. Trends in vegetation productivity related to climate change in China's Pearl River Delta. Plos One 16:e0245467.

Alkishe, A., *et al.* 2022. Ecological niche and potential geographic distributions of *Dermacentor marginatus* and *Dermacentor reticulatus* (Acari: Ixodidae) under current and future climate conditions. Web Ecology 22:33–45.

ANDERSON, R. P., AND A. RAZA. 2010. The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary tests with montane rodents (genus *Nephelomys*) in Venezuela. Journal of Biogeography 37:1378–1393.

BECK-KING, H., O. V. HELVERSEN, AND R. BECK-KING. 1999. Home Range, Population Density, and Food Resources of *Agouti paca* (Rodentia: Agoutidae) in Costa Rica: A Study Using Alternative Methods 1. Biotropica 31:675–685.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Springer. New York, U.S.A.

CAMARGO-SANABRIA, A. A., ET AL. 2015. Experimental defaunation of terrestrial mammalian herbivores alters tropical rainforest understory diversity. Proceedings of the Royal Society B: Biological Sciences 282:20142580.

CARTAYA, S., C. ANCHUNDIA, AND R. MANTUANO. 2016. Distribución geográfica potencial de la especie *Cuniculus paca* en el occidente de Ecuador. La Granja: Revista de Ciencias de la Vida 24:134–149.

COBOS, M. E., ET AL. 2018. Sample data and training modules for cleaning biodiversity information. Biodiversity Informatics 13:49–50.

COBOS, M. E., ET AL. 2019. kuenm: an R package for detailed development of ecological niche models using Maxent. PeerJ 7:e6281.

CONTRERAS-DÍAZ, R. G., ET AL. 2022. On the relationship between environmental suitability and habitat use for three neotropical mammals. Journal of Mammalogy 103:425–439.

D'ELIA, J., ET AL. 2015. Activity-specific ecological niche models for planning reintroductions of California condors (*Gymnogyps californianus*). Biological Conservation 184:90–99.

DÍAZ, S., ET AL. 2019. Pervasive human-driven decline of life on Earth points to the need for transformative change. Science 366:eaax3100.

DI MARCO, M., ET AL. 2018. Changes in human footprint drive changes in species extinction risk. Nature Communications 9:4621.

DIRZO, R., ET AL. 2014. Defaunation in the anthropocene. Science 345:401–406.

DUBOST G., AND O. HENRY. 2017. Seasonal reproduction in neotropical rainforest mammals. Zoological Studies 56:2.

EHLERS, E., AND T. KRAFFT. 2006. Managing global change Pp. 5-12, *in* Earth System Science in the Anthropocene (Ehlers, E., and T. Krafft, eds.). Springer. Berlin, Heidelberg.

EL BIZRI, H. R., ET AL. 2018. Breeding seasonality in the lowland paca (*Cuniculus paca*) in Amazonia: interactions with rainfall, fruiting, and sustainable hunting. Journal of Mammalogy 99:1101–1111.

EMMONS, L. 2016. *Cuniculus paca*. The IUCN Red List of Threatened Species 2016:e.T699A22197347.

ERB, K. H., ET AL. 2018. Unexpectedly large impact of forest management and grazing on global vegetation biomass. Nature 553:73–76.

ESCOBAR, L. E., ET AL. 2014. Potential for spread of the white-nose fungus (*Pseudogymnoascus destructans*) in the Americas: Use of Maxent and NicheA to assure strict model transference. Geospatial Health 9:221–229.

ESPINDOLA, S., J. L. PARRA, AND E. VÁZQUEZ-DOMÍNGUEZ. 2019. Fundamental niche unfilling and potential invasion risk of the slider turtle *Trachemys scripta*. PeerJ 7:e7923.

FALCONI, M., L. OSORIO-OLVERA, AND R. G. CONTRERAS-DÍAZ. 2021. Distribución de especies. Un punto de vista teórico. Revista de Modelamiento Matemático de Sistemas Biológicos 1:16–24.

FELDMEIER, S., ET AL. 2020. Shifting aspect or elevation? The climate change response of ectotherms in a complex mountain topography. Diversity and Distributions 26:1483–1495.

FICK, S. E., AND R. J. HIJMANS. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37:4302–4315.

FIGUEROA-DE LEÓN, A. 2016. Dinámica de ocupación de cavidades y uso de hábitat del tepezcuintle (*Cuniculus paca*) en la Selva Lacandona, Chiapas, México. Ph.D. Dissertation. El Colegio de la Frontera Sur. San Cristóbal de Las Casas, Chiapas, México.

FRANKLIN, J. 2010. Mapping species distributions: spatial inference and prediction (Ecology, biodiversity and conservation). Cambridge University Press. New York, U.S.A.

GALLINA, S. 1981. Contribución al conocimiento de los hábitos alimenticios del tepezcuintle (*Agouti paca* Lin.) en Lacanjá–Chansayab, Chiapas. Publicación del Instituto de Ecología de México 6:55–67.

GBIF.ORG. 2021. GBIF Occurrence Download. https://doi.org/10.15468/dl.5u4dvg. Accessed on 4 February 2021.

GUTIERREZ, S. M., ET AL. 2017. Ranging behavior and habitat selection of pacas (*Cuniculus paca*) in central Belize. Journal of Mammalogy 98:542–550.

HANTAK, M. M., ET AL. 2021. Mammalian body size is determined by interactions between climate, urbanization, and ecological traits. Communications Biology 4:972.

HILL, S. L. L., ET AL. 2018. Worldwide impacts of past and projected future land-use change on local species richness and the Biodiversity Intactness Index. BioRxiv 311787.

IUCN. 2022. The IUCN Red List of Threatened Species. Version 2022-1. https://www.iucnredlist.org. Accessed on 8 July 2022.

JARVIE, S., AND J. C. SVENNING. 2018. Using species distribution modelling to determine opportunities for trophic rewilding under future scenarios of climate change. Philosophical Transactions of the Royal Society B 373:20170446.

JAX, E., ET AL. 2015. Habitat use and relative abundance of the spotted paca *Cuniculus paca* (Linnaeus, 1766) (Rodentia: Cuniculidae) and the red-rumped agouti *Dasyprocta leporina* (Linnaeus, 1758) (Rodentia: Dasyproctidae) in Guatopo National Park, Venezuela. Journal of Threatened Taxa 7:6739–6749.

MARTÍNEZ-CECEÑAS, Y., ET AL. 2018. Ecología alimentaria del tepezcuintle (*Cuniculus paca*) en áreas conservadas y transformadas de la Selva Lacandona, Chiapas, México.. Revista Mexicana de Biodiversidad 89:507–515.

MARTÍNEZ-RAMOS, M., ET AL. 2016. Anthropogenic disturbances jeopardize biodiversity conservation within tropical rainforest reserves. Proceedings of the National Academy of Sciences 113:5323–5328.

MCCARTHY, K. P., ET AL. 2012. Predicting species distributions from samples collected along roadsides. Conservation Biology 26:68–77.

MCNAUGHTON, S. 1975. r-and K-selection in Typha. The American Naturalist, 109:251–261.

MICHALSKI, F., AND D. NORRIS. 2011. Activity pattern of *Cuniculus paca* (Rodentia: Cuniculidae) in relation to lunar illumination and other abiotic variables in the southern Brazilian Amazon. Zoologia 28:701–708.

Montes, R. 2005. El tepezcuintle, un recurso biológico importante. Biodiversitas 63:6–10.

Nuñez-Penichet, C., *et al*. 2021. Geographic potential of the world's largest hornet, *Vespa mandarinia* Smith (Hymenoptera: Vespidae), worldwide and particularly in North America. PeerJ 9:e10690.

O'Donnell, M. S., and D. A. Ignizio. 2012. Bioclimatic predictors for supporting ecological applications in the conterminous United States. U.S. Geological Survey Data Series 691:1–10.

Osorio-Olvera, L. A., M. Falconi, and J. Soberón. 2016. Sobre la relación entre idoneidad del hábitat y la abundancia poblacional bajo diferentes escenarios de dispersión. Revista Mexicana de Biodiversidad 87:1080–1088.

Osorio-Olvera, L., *et al*. 2020. ntbox: an R package with graphical user interface for modelling and evaluating multidimensional ecological niches. Methods in Ecology and Evolution 11:1199–1206.

Padilla-Gómez, E., *et al*. 2019. Noteworthy records of jaguar (*Panthera onca*), tayra (*Eira barbara*), and paca (*Cuniculus paca*) from southern Mexico. Notas sobre Mamíferos Sudamericanos 1.

Parsons, A. W., *et al*. 2018. Mammal communities are larger and more diverse in moderately developed areas. eLife 7:e38012.

Pérez, E. M. 1992. *Agouti paca*. Mammalian Species 404:1–7.

Phillips, S. J., *et al*. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190:231–259.

Pulliam, H. R. 2000. On the relationship between niche and distribution. Ecology Letters 3:349–361.

R Core Development Team. 2019. R: A language and environment for statistical computing. Vienna, Austria. https://www.R-project.org/.

Rowe, K. C., *et al*. 2015. Spatially heterogeneous impact of climate change on small mammals of montane California. Proceedings of the Royal Society B: Biological Sciences 282:20141857.

Soberón, J. 2010. Niche and area of distribution modeling: a population ecology perspective. Ecography 33:159–167.

Soberón J., and A. T. Peterson. 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. Biodiversity Informatics 2:1–10.

SpeciesLink. 2021. Red Species Link. Reference Center for Environmental Information (CRIA), Research Support Foundation of the State of São Paulo (FAPESP). http://www.splink.org.br. Accessed on 10 February 2021.

Shimamoto C. Y., *et al*. 2018. Restoration of ecosystem services in tropical forests: A global meta-analysis. Plos One 13:e0208523.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80:1455–1474.

Tuanmu, M. N., and W. Jetz. 2014. A global 1-km consensus landcover product for biodiversity and ecosystem modelling. Global Ecology and Biogeography 23:1031–1045.

Tucker, M. A., *et al*. 2018. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. Science 359:466–469.

Venter, O., *et al*. 2016. Global terrestrial Human Footprint maps for 1993 and 2009. Scientific Data 3:1–10.

Warren, D. L., and S. N Seifert. 2011. Ecological niche modeling in Maxent: The importance of model complexity and the performance of model selection criteria. Ecological Applications 21:335–342.

Zucaratto, R., R. Carrara, and B. K. Siquiera Franco. 2010. Dieta da paca (*Cuniculus paca*) usando métodos indiretos numa área de cultura agrícola na Floresta Atlântica brasileira. Biotemas 23:235–239.

Supplementary material

www.revistas-conacyt.unam.mx/therya/index.php/THERYA/article/view/2237/2237_Supplementary%20material