Precipitous decline of white-lipped peccary populations in Mesoamerica

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A R T I C L E   I N F O

A B S T R A C T

Large mammalian herbivores are experiencing population reductions and range declines. However, we lack regional knowledge of population status for many herbivores, particularly in developing countries. Addressing this knowledge gap is key to implementing tailored conservation strategies for species whose population declines are highly variable across their range. White-lipped peccaries (*Tayassu pecari*) are important ecosystem engineers in Neotropical forests and are highly sensitive to human disturbance. Despite maintaining a wide distributional range, white-lipped peccaries are experiencing substantial population declines in some portions of their range. We examined the regional distribution and population status of the species in Mesoamerica. We used a combination of techniques, including expert-based mapping and assessment of population status, and data-driven distribution modelling techniques to determine the status and range limits of white-lipped peccaries. Our analysis revealed declining and highly isolated populations of peccaries across Mesoamerica, with a range reduction of 87% from historic distribution and 63% from current IUCN range estimates for the region. White-lipped peccary distribution is affected by indices of human influence and forest cover, and more restricted than other sympatric large herbivores, with their largest populations confined to transboundary reserves. To conserve white-lipped peccaries in Mesoamerica, transboundary efforts will be needed that focus on both forest conservation and hunting management, increased cross-border coordination, and reconsideration of country and regional conservation priorities. Our methodology to detail regional white-lipped peccary status could be employed on other poorly-known large mammals.

1. Introduction

Globally, many terrestrial mammals are experiencing population declines and range contractions (Ceballos and Ehrlich, 2002; Ceballos et al., 2017). Mid and large-sized mammals may be particularly vulnerable (Laliberte and Ripple, 2004), with population losses leading to range contractions of > 40% for the majority of species and exceeding 80% in some cases (Ceballos et al., 2017). However, not all populations of large mammals are equally vulnerable. Rather, mammal range decline occurs more often in areas of high human influence (highly transformed or populous landscapes), due to the reliance of large-bodied mammals on extensive areas of undisturbed habitat and lack of hunting or persecution (Laliberte and Ripple, 2004; Yackulic et al., 2011; Ripple et al., 2016; Wolf and Ripple, 2017). Range contraction for large mammals is also more likely in certain biome types, areas that are outside of designated protected areas, or areas located at the edge of the range (Yackulic et al., 2011). Despite threats to mammal persistence, many of the species currently thought to be experiencing declines are poorly studied. Consequently, little is known about distribution, ecology, and population trends of these species, particularly in developing regions of the world (Ripple et al., 2015).

Filling this knowledge gap is critical, as regional evaluations of distribution or population status can help target conservation interventions to areas where species experience variable declines and range retractions. That knowledge can provide guidance for local and regional conservation status changes that reflect the situation in particular portions of a species' range (Miller et al., 2007), rather than relying on coarse global status assessments to provide local guidance. In some cases, a species' global status may contrast with its status at national and regional levels, almost inhibiting elevated conservation prescriptions in emergency situations (De la Torre et al., 2017). Large-scale, regional assessments are therefore key to informing conservation strategies for poorly known mammals.

Large mammalian carnivores receive the most attention and conservation investment to help document and mitigate population losses and range contraction. However, more than half of the world's large mammalian herbivores are threatened with extinction or have currently declining populations (Ripple et al., 2015). Large herbivores and frugivores play key roles in ecosystem processes through the activities of plant consumption and seed dispersal and predation (e.g., Fragoso, 1999; O'Farrill et al., 2013; Galetti et al., 2015); thus, extinction and decline of large herbivores has ecosystem-level consequences. For example, loss of herbivorous mammals due to hunting in Neotropical forests alters rates of seed dispersal and predation, plant functional traits, and carbon storage (Wright et al., 2000; Kurten et al., 2015; Peres et al., 2016).

White-lipped peccaries (*Tayassu pecari*) are a wide-ranging social ungulate that inhabits Neotropical lowland forest. This species plays a key role in Neotropical forests as an important seed predator and disperser, food source for large predators and human communities, and ecosystem engineer of water sources (Altrichter 2005; Beck, 2005; Beck et al., 2010; Foster et al., 2010). White-lipped peccaries have an extensive range, with their southern range limit occurring in Argentina, a large core population in Amazonia, and the northern range extent in Central America and southern Mexico (for simplicity we hereafter refer to this northern range extent as 'Mesoamerica'; Supplementary Fig. 1). Due to their social behavior and grouping-based anti-predatory defense, white-lipped peccaries are highly sensitive to hunting pressure (Reyna-Hurtado et al., 2010; Keuroghlian et al., 2013; Nogueira et al., 2015; Briceño-Méndez et al., 2016). Their large area needs, and reliance on widely dispersed fruit and water sources, also makes this species highly vulnerable to forest loss and fragmentation (Altrichter et al., 2012).

A range-wide, expert-based mapping exercise developed in 2005 suggested that white-lipped peccaries had been extirpated from 21% of their historic range, with low probability of long-term survival in another 48% of their current range (Altrichter et al., 2012). Despite this sensitivity, white-lipped peccaries are only classified as Vulnerable by the IUCN due to a wide distribution range and continued persistence in many protected areas, but with recognition that the species is undergoing substantial declines in certain portions of the range (Keuroghlian et al., 2013). In particular, substantial losses of populations may be occurring at the range edges in southern South America and Mesoamerica (Altrichter et al., 2012) and some country-level conservation status listings reflect this increased concern (white-lipped peccaries are listed as critically endangered in Nicaragua, and endangered in Mexico, Costa Rica, and Panama). Thus, status in the peripheral range segments may be much worse than the "global" population, and represent a mismatch in conservation priorities with consequences for the long-term persistence of peccaries in many countries.

Due to the difficulties of studying a wide-ranging and elusive Neotropical forest mammal, only a handful of empirical studies on white-lipped peccary population and habitat ecology have been published. These studies focused primarily on habitat use, diet, movement, and response to hunting, and were conducted at relatively small scales (e.g., Altrichter et al., 2001; Fragoso, 1998; Keuroghlian et al., 2004; Reyna-Hurtado et al., 2009; Reyna-Hurtado et al., 2012). Obtaining a regional perspective on peccary populations is difficult because of a lack of empirical information, and because the range of white-lipped peccary cuts across 18 countries, with distinct conservation and management systems (Thornton and Branch, 2019). Thus, regional knowledge of population limits or status requires bringing together a diverse

set of information and knowledge across multiple countries in a systematic fashion. Although Altrichter et al. (2012) mapped Peccary Conservation Units and provided needed information on range reduction, their analysis was based solely on expert opinion and focused at the scale of the entire range as opposed to regions of highest threat. In contrast, the present work aims to provide finer-grained information on regional white-lipped peccary distribution and population status within the northern range limit of Mesoamerica. The persistence of white-lipped peccaries in Mesoamerica is particularly challenging as the region contains relatively poor protected area coverage (Rodrigues et al., 2004; Jenkins and Joppa, 2009), with protected areas heavily impacted by human activities such as hunting and other forms of resource extraction. Moreover, Mesoamerica is experiencing overall declines in forest cover both within and outside of protected areas (Olsoy et al., 2016). Although the focus of our analysis in on white-lipped peccary, another large-bodied social ungulate, the collared peccary (*Pecari tajacu*), also inhabits the region. Despite being impacted by hunting and habitat loss (Thornton et al., 2011; Briceño-Méndez et al., 2016), collared peccaries appear to be less affected by such disturbances (Peres, 1996; Keuroghlian et al., 2004) though this perception has not been assessed at the regional scale. Given the biological similarities between the species, we include collared peccaries in some of the analyses in this paper to provide a comparison between the patterns seen for white-lipped peccaries with that of another large, social ungulate. Such comparisons help to inform if white-lipped peccaries are especially vulnerable in the region, or if their response is largely reflective of more widespread patterns seen in other large herbivores.

The overall objective of this study is to assess the status of white-lipped peccary populations in Mesoamerica. We do this through use of an expert questionnaire and through modelling peccary distribution via a combination of data sources, including expert-based opinion, presence data, and detection/non-detection data from a camera-trapping meta-dataset derived from numerous researchers across the region. This combination of sources allows us to assess population status, regional distribution, and how boundaries of currently extant populations and suitable habitat relate to country borders. We test several predictions: 1) Given recent increases in human pressure in the region, and our focused regional mapping, we predict that white-lipped peccary populations are decreasing regionally in Mesoamerica, and that the total suitable habitat and area occupied by this species is smaller than previous work suggests. 2) We predict that suitable habitat and area of occupancy for collared peccaries will be more extensive than for white-lipped peccaries at a regional scale, given local evidence of differential vulnerability of the two species. 3) Finally, we predict that regional distribution of white-lipped peccaries will be influenced primarily by forest cover and metrics of human disturbance.

2. Methods

2.1. Study area

The Mesoamerican study area encompassed the historic distribution of white-lipped peccary in Mexico and Central America, and extended from southeastern Mexico through Panama (Fig. 1A). This region includes a diversity of ecosystems, including dry and wet tropical forest, pine-oak forests, wetlands, and cloud forest (Olson and Dinerstein, 2002). Conversion of natural habitats for pasture and agriculture is the key driver of habitat loss (Armenteras et al., 2017). Recent forest cover loss within and outside of protected areas remains a concern, occurring at high rates in comparison to other locations in the Americas (Olsoy et al., 2016). High human population densities in many parts of Mesoamerica lead to other impacts on habitats in the region, including hunting and illegal timber extraction. Protected areas in the study region tend to be small and relatively isolated, with the exception of several major, transboundary protected area complexes that maintain large areas of intact forest cover.

2.2. Expert-based analysis

In June 2016, we sent a questionnaire to experts in each of the seven countries of our study region (Mexico, Belize, Guatemala, Honduras, Nicaragua, Costa Rica, and Panama; white-lipped peccaries are already extirpated from El Salvador; Reyna-Hurtado et al., 2017). We requested that each expert coordinate with other national researchers to compile information regarding populations of white-lipped peccary in their country. Criteria for selecting experts included extensive in-country field research experience, possession of data on white-lipped peccary abundance and distribution, and ability to engage with fellow-researchers in their country.

This questionnaire required the expert coordinators and their in-country contacts to work together to review and compile information related to current population boundaries of white-lipped peccaries within each country. The questionnaire also asked for estimates of population size (within categories of 0–1000, 1000 to 5000, > 5000), estimates of average group size (0–50, 50–100, 100–300, > 300), and whether the population was perceived to be stable, increasing or decreasing (See Supplementary Methods for example of questionnaire).

We brought all expert coordinators together for a symposium held as part of the *XX Congress of the Mesoamerican Society for Biology and Conservation* in Belize City on August 24th, 2016 (Reyna-Hurtado et al., 2017). Information from the questionnaires was compiled across countries, and expert coordinators engaged in a mapping exercise to delineate polygons of current range limits within each country, based on the information they had gathered. These polygons were translated into shapefiles in GIS to calculate total area of current range limits. We compared these range limits with historic limits, as well as limits that were delineated for Mesoamerica by Altrichter et al. (2012) in their previous range-wide, expert-based mapping exercise, and current IUCN range polygons (IUCN, 2019).

2.3. Presence-only distribution modelling

Expert-based knowledge of range limits has some limitations, such as subjective biases, lack of knowledge of certain areas, and an inability to account for uncertainty (McBride et al., 2012). Therefore, we created a distribution model based on confirmed detections to better understand distribution and habitat suitability patterns for white-lipped peccaries across our Mesoamerican landscape. This method allows us to make use of a wide variety of data sources on white-lipped peccaries in order to estimate relative habitat suitability across the region. Because similar field methods detected both collared and white-lipped peccaries, we simultaneously conducted a similar exercise for the collared peccary so that we would have a direct comparison with another large social ungulate in the region. We collected presence locations for white-lipped peccaries and collared peccaries from a variety of sources, including camera-trap data, published literature and reports, and Global Biodiversity Information Facility databases (the latter two sources contained presence information obtained from a variety of methods, including line-transect data, and ad hoc direct and indirect observations). Presence data were thinned to only include one presence record within a 5.6 km radius (100 km^2 area) using the spThin package in R (Aiello-Lammens et al., 2015), to adjust for sampling bias that is a common problem with presence-only analysis (Kramer-Schadt et al., 2013). We tried smaller thinning radii (1.8 km and 2.8 km) so that we incorporated more presence records but found resultant models to be unrealistically constrained to areas of greater sampling such as those with a large number of camera-trapping records. We only included presence records collected after 1990 (with > 80% of records from post-2000) as we were interested in modelling suitability of recent time periods. This process resulted in 228 presence points for white-lipped peccary and 317 presence points for collared peccary (Supplementary Fig. 2). We used Maxent modelling to develop habitat suitability maps and examine the influence of environmental drivers on suitability for
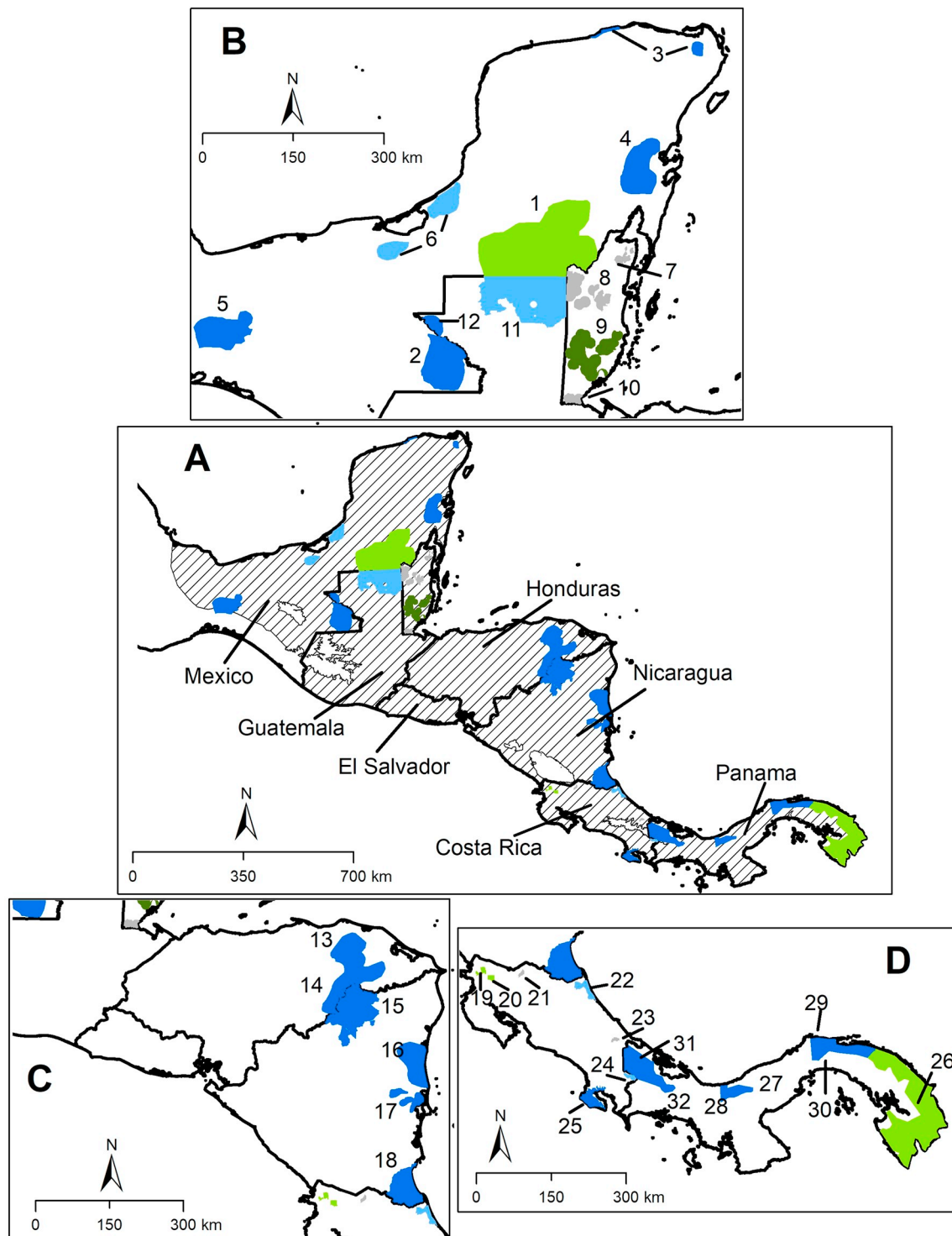
Fig. 1. Maps of extant white-lipped peccary populations in Mesoamerica based on expert opinion. A) Map for the entire Mesoamerican study region. Currently extant populations are colored according to their population status as estimated by experts: Dark green = increasing, light green = stable, dark blue = decreasing, light blue = probably decreasing, gray = unknown. Hatching indicates the historical distribution of the species. B–D provide zoomed in images for northern, central, and southern portions of the study region, respectively. Numbers of each population correspond to the first column in Table 1. These populations are: 1 = Calakmul, 2 = Montes Azules, 3 = Dzilam-Eden, 4 = Sian Kaan, 5 = Chimalapas, 6 = Laguna de Terminos, 7 = NE Belize, 8 = Rio Bravo/Gallon Jug, 9 = Maya Mountains, 10 = Sarstoon-Temash, 11 = Eastern Maya Biosphere, 12 = Sierra del Lacandon, 13 = Rio Plantano/Tawahka/Consejos, 14 = Patuca, 15 = Bosawas, 16 = Awaltara/Prinzu, 17 = Wawashang, 18 = Indio Maiz, 19 = Guanacaste/Santa Rosa, 20 = Rincón de la Vieja, 21 = Caña Negro, 22 = Tortuguero, 23 = Hitoy Cerere, 24 = Las Tablas, 25 = Osa, 26 = Darien, 27 = Santa Fe, 28 = Donoso, 29 = Portobelo, 30 = Chagres, 31 = La Amistad, 32 = Palo Seco. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

each species via response curves. The environmental variables included in this analysis were the human influence index in the year 2000 (which incorporates the effect of population density, human land use and infrastructure and human access; WCS, 2005), forest cover in year 2000 (Hansen et al., 2013), ecoregion categorization (categories included moist tropical forest, dry tropical forest, pine-oak forest, thorn-scrub, and mangroves), elevation, distance from the nearest protected area, and distance to nearest stream. We choose to use data for forest cover and human influence in the year 2000 to better match the midpoint of the timeframe for our presence records. Additional details on these variables, and the Maxent modelling process, are given in Supplementary Methods.

2.4. Occupancy models

Although presence-only modelling techniques can accurately model distributional limits in different contexts (e.g., Searcy and Schaffer, 2016; Proosdij et al., 2016; West et al., 2016), and have advantages in that they allow the use of presence records from a variety of sources (especially important for elusive tropical mammals) and across large spatial extents, these techniques have drawbacks such as vulnerability to sampling bias, modelling of suitability instead of probability of presence, and a failure to account for detection probabilities (Guillera-Arroita et al., 2015). To address some of these limitations, and provide an additional perspective on peccary distribution in Mesoamerica, we also performed region-wide occupancy modelling (MacKenzie et al., 2002). Occupancy modelling is advantageous as it allows for the adjustment of distribution patterns based on detection probability and provides estimates of the absolute probability of presence, but is limited to only datasets for which detection histories can be generated (in our case, only camera-trapping records where we had access to the primary datasets). We collated camera-trapping datasets from across our Mesoamerican study region for the creation of detection histories for both

peccary species. The final dataset was composed of 53 distinct camera surveys (Supplementary Fig. 3) that totaled 1876 camera stations. Studies included in our analysis spanned the time frame of 2005 to 2017 (with 88% of the studies conducted 2010 or later), and we only included studies with at least 10 camera stations. Although these studies varied in their exact designs, the basic features of the studies were similar, with cameras placed along movement pathways and primarily targeted for large bodied mammals. We created detection histories for each camera station by determining detection/non-detection over every 10 days of camera survey. We limited each survey to a maximum of 120-day sampling period.

We analyzed occupancy patterns at the scale of a 36 km^2 hexagonal cell. Analysis at the level of the 36 km^2 cell provides a coarser-grain measurement of drivers of species distribution (MacKenzie et al., 2017), and for the wide-ranging species here, may better reflect true patterns of occupancy. The 36 km^2 size was chosen because it falls toward the low end of estimates for white-lipped peccary home range size from Mesoamerica (Carrillo et al., 2002; Reyna-Hurtado et al., 2009; Moreira-Ramírez et al., 2018). For analyses at the cell level, we combined detections for all cameras that fell within a grid cell for each 10-day period to record detection histories. We tested the influence of several covariates that we suspected would drive detection or occupancy patterns of our species. We considered the number of cameras within a 36 km^2 cell, season of survey (wet vs. dry), year of survey, effort (# of days all cameras were active within a cell), and country of the survey (to account for unmodelled differences in survey techniques or regional abundance) as our detection covariates. Occupancy variables considered were forest cover in the year 2010 (Hansen et al., 2013), a human footprint layer for the year 2015 (similar to the human influence layer used in Maxent modelling, and incorporating human access, forest cover, permanent lights, human population density, and forest fires; Hugo Ramos, unpublished data), elevation, distance to edge of protected area, and distance to streams. We used covariates for

Table 1
Estimated population size, group size, and population trend of white-lipped peccary populations from seven countries of Mesoamerica, based on expert opinion.

Map #[a]	Country	Populations	Population size (range)	Group size (range)	Trend
1	Mexico	Calakmul Biosphere Reserve	1000–5000	< 50	Stable
2	Mexico	Montes Azules Biosphere Reserve	1000–5000	50–100	Decreasing
3	Mexico	Dzilam-Eden	1–1000	< 50	Decreasing
4	Mexico	Sian Kaan Biosphere Reserve	1–1000	?	Decreasing
5	Mexico	Chimalapas region	1000–5000	< 50	Decreasing
6	Mexico	Area de Protección de Flora y Fauna Laguna de Terminos	1–1000	< 50	Probably decreasing
7	Belize	Northeastern Belize	1–1000	Unknown	Unknown
8	Belize	Rio Bravo and Gallon Jug Private Conservation Areas	Unknown	Unknown	Unknown
9	Belize	Maya Mountains Massif	Unknown	50–100	Increasing
10	Belize	Sarstoon-Temash National Park	1–1000	Unknown	Unknown
11	Guatemala	Eastern Maya Biosphere Reserve	1000–5000	50–100	Probably decreasing
12	Guatemala	Sierra del Lacandon National Park	1–1000	< 50	Decreasing
13	Honduras	Rio Platano Biosphere Reserve, Tawahka, Consejos Territoriales	1000–5000	< 50	Decreasing
14	Honduras	Patuca National Park	1–1000	< 50	Decreasing
15	Nicaragua	Bosawas Biosphere Reserve	1–1000	< 50	Decreasing
16	Nicaragua	Awaltara, Prinzu Auhya Un, and Prinzu Awala territories	1–1000	50–100	Decreasing
17	Nicaragua	Wawashang	1–1000	< 30	Decreasing
18	Nicaragua	Indio Maiz	1–1000	50–100	Decreasing
19	Costa Rica	Guanacaste and Santa Rosa National Park	1–1000	< 50	Stable
20	Costa Rica	Rincón de la Vieja National Park	1–1000	< 50	Stable
21	Costa Rica	Caño Negro Wildlife Refuge	1–1000	< 50	Unknown
22	Costa Rica	Tortuguero National Park and Barra del Colorado Wildlife Refuge	1–1000	< 50	Probably decreasing
23	Costa Rica	Hitoy Cerere Biological Reserve	1–1000	< 50	Unknown
24	Costa Rica	Las Tablas Protective Zone	1–1000	50–100	Probably decreasing
25	Costa Rica	Osa Peninsula	1–1000	50–100	Decreasing
26	Panama	Darien National Park	1000–5000	50–300	Stable
27	Panama	Santa Fe National Park	1–1000	< 50	Decreasing
28	Panama	Donoso Multiple Use Area	1–1000	< 50	Decreasing
29	Panama	Portobelo National Park	1–1000	< 50	Decreasing
30	Panama	Chagres National Park	1–1000	< 30	Decreasing
31	Panama	Parque Internacional de la Amistad	1–1000	50–100	Decreasing
32	Panama	Palo Seco Bosque Protector	1–1000	50–100	Decreasing

human influence and forest cover that were more recent to better match the time period of the occupancy surveys. We used single season occupancy models to project occupancy probabilities across the Mesoamerican landscape, determine the number of occupied cells and total area occupied, and examine response curves to environmental variables. Additional details of the modelling process are given in Supplementary Methods.

3. Results

3.1. Expert-based analysis

Our experts identified 32 populations of white-lipped peccaries scattered across seven countries of Mesoamerica (Table 1). Experts classified 22 of the 32 populations (68.8%) as decreasing or probably
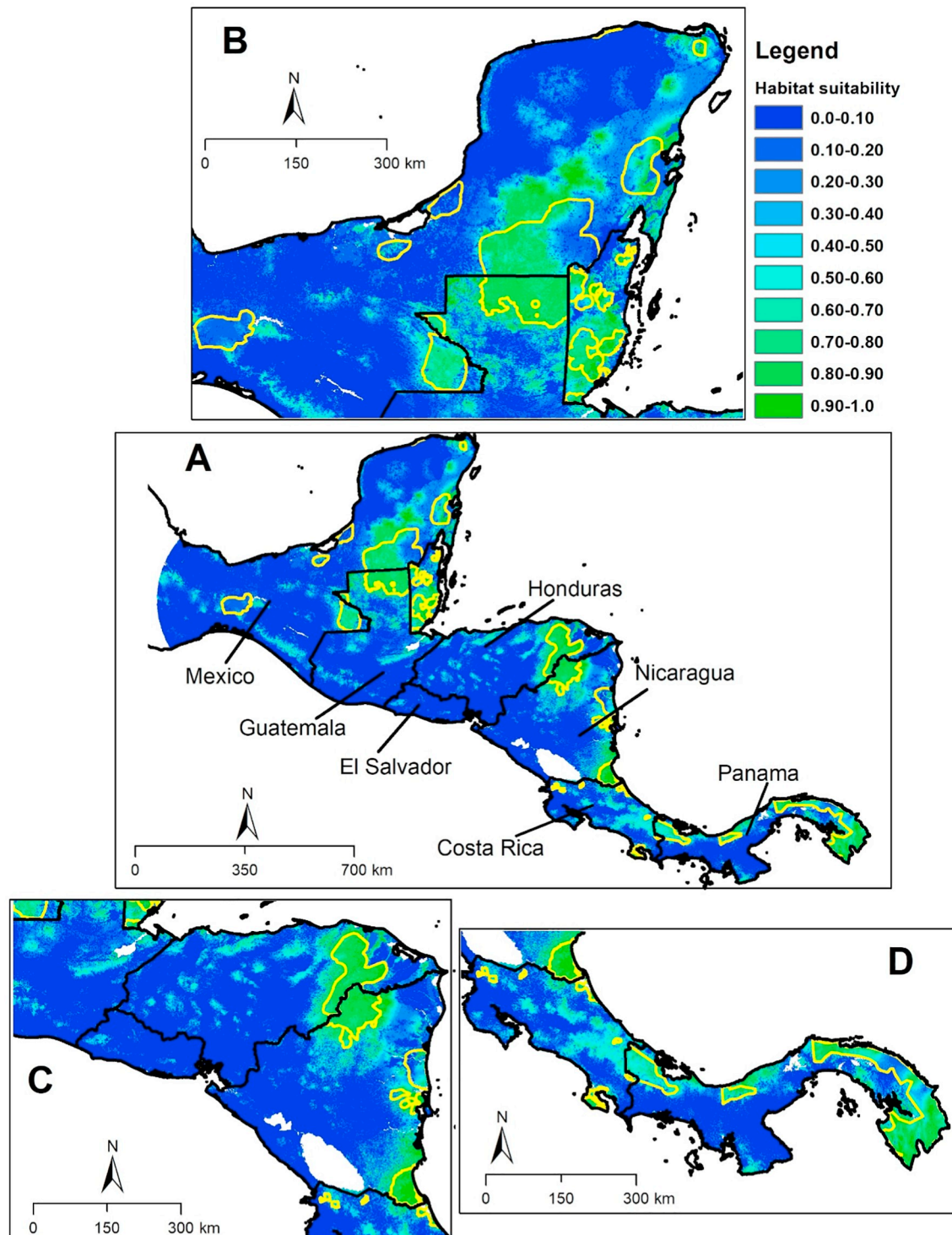
Fig. 2. Habitat suitability maps based on Maxent models for white-lipped peccaries in Mesoamerica. A) Map for the entire Mesoamerican study region. Yellow polygons show location of expert-based opinion on boundaries of currently extant populations of white-lipped peccaries. B–D provide zoomed in images for northern, central, and southern portions of the study region, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

decreasing, 5 as unknown (15.5%), 4 populations as stable (12.5%), and only one as increasing (3.2%). The majority (78%) of populations were estimated to be fewer than 1000 animals, and in most cases where data were available, current group sizes were estimated to be fewer than 50 animals (66%) (Table 1). Stable populations or populations > 1000 individuals were reported only in the Maya Forest (Calakmul Biosphere Reserve in Mexico, Maya Biosphere Reserve in Guatemala), Darien National Park in Panama, and Osa Peninsula of Costa Rica, with increasing populations in the Maya Mountains complex of Belize. According to experts, many other populations are experiencing rapid decreases. Experts indicated that the declines are due to habitat loss, hunting pressure, and loss of connectivity.

According to the expert-based mapping exercise, the 32 populations of white-lipped peccaries in Mesoamerica cover an area of 97,596 km^2. This current distribution represents a reduction of 87% when compared to the historic range (Fig. 1). Further, this current estimate of occupied area is a reduction of 51% from the previous mapping exercise in 2005 (Altrichter et al., 2012) and a 63% reduction from the current IUCN range map (which is based largely on the Altrichter mapping exercise, except for two additional population polygons in southeastern Mexico). If we eliminate from consideration any areas designated by the IUCN range map as "Probably Extant", then this reduction is 45% (Supplementary Fig. 4). The largest discrepancies between our expert-based range map and the previous range maps (Supplementary Fig. 4) are that we estimated a much reduced distribution in Nicaragua and Honduras, particularly northern Honduras and central Nicaragua – both areas of rapid recent deforestation and degradation. In contrast, our expert-based maps predict extra isolated populations in certain areas that were not included in previous maps, particularly in Coastal ecosystems of southeastern Mexico.

3.2. Presence-only distribution modelling

Average suitability maps for white-lipped peccaries reveal restricted and isolated pockets of suitable habitat for this species (Fig. 2). Many of the expert-based polygons fall within areas identified as highly suitable based on Maxent models, suggesting general agreement between the two modelling exercises. Exceptions to this agreement include several highly isolated and peripheral populations identified by experts in southeastern Mexico and Costa Rica that appear to contain little suitable habitat. We also note several areas of highly suitable habitat that occur outside expert-based polygons, but these usually fall at the edges of current polygons and thus may represent relatively minor underestimates by experts or overestimates by the Maxent models.

In comparison, collared peccary models have many of the same highly suitable clumps of habitat, but generally have more suitable habitat across the landscape, including many more isolated and diffuse pockets of suitability that occur in more disturbed and fragmented areas of Mesoamerica (Supplementary Fig. 5). Based on evaluation metrics

for spatially held out test data, both models were able to accurately discriminate actual presence locations from background locations (see Supplementary Methods). Area-Under-the-Curve values, which range from 0 to 1 (perfect discrimination of presence and background data) were 0.85 for white-lipped peccary models and 0.77 for collared peccary models.

White-lipped and collared peccary habitat suitability were best explained using Maxent settings for response curves that included linear and quadratic features, with a regularization of 1 for white-lipped peccaries and 1.5 for collared peccaries (see Supplementary Methods). Based on jackknife estimates of parameter importance, human influence, forest cover, distance from protected areas, and ecoregion were the most important variables in determining relative suitability for both peccary species. Consistent with the mapping results, both peccary species were influenced in a similar manner by increasing human influence and distance from protected areas, and declining forest cover, but white-lipped peccary suitability was affected more strongly and negatively by these factors (Supplementary Fig. 6).

3.3. Occupancy models

Best-fitting cell-level occupancy models for both species included only human footprint index and elevation (Table 2; see Supplementary Results for full list of models tested), with detection models containing country of survey and number of cameras in a cell. Parameter estimates (± SE) for the best fitting model for white-lipped peccaries were –1.60 (0.26), 0.06 (0.50), −1.17 (1.70) for human influence, elevation, and elevation^2, respectively; estimates for collared peccaries were –0.76 (0.16), −0.80 (0.40), 0.78 (0.39), for human influence, elevation, and elevation^2, respectively. Increasing human footprint exerted a negative impact on both species, but was much more pronounced for white-lipped peccaries (Fig. 3). Conditional occupancy estimates indicated that white-lipped peccaries were predicted to occupy 93.8 (95% CI = 76.7–118.6) of the 470 hexagonal cells that were sampled. This amounts to an occupancy rate of 0.19 (95% CI = 0.16–0.25). Collared peccaries were predicted to occupy 225 (95% CI = 201.6–250.8) of the 445 hexagonal cells that were sampled, which is a significantly higher occupancy rate of 0.51 (95% CI = 0.45–0.56). There was some evidence of minor overdispersion for white-lipped peccaries (c-hat = 2.01).

When projecting the best-fit model across the entire Mesoamerican study area, white-lipped peccaries have isolated patches of medium occupancy probabilities that match well with expert-based polygons (Fig. 4). Again, several contiguous areas of predicted occupancy lie across country borders (e.g., Mexico-Guatemala-Belize and Honduras-Nicaragua). Some mismatch between expert-based polygons and areas of predicted occupancy are apparent in the isolated Mexican populations, similar to the Maxent modelling. Predicted occupancy probabilities for white-lipped peccary do not often exceed 0.50, even in

Table 2
Top four best-fitting single season occupancy models for our study species. Detection models (not shown) were the same for both species and included both country of survey and number of cameras in the cell as covariates. K = number of parameters, AIC = Akaike's Information Criterion, w_i = model weight, LL = Log-Likelihood.

White-lipped peccary occupancy models	K	AIC	w_i	LL
Human influence index + elevation + elevation^2	12	1025.51	0.29	−500.75
Human influence index	10	1025.91	0.24	−502.93
Human influence index + elevation + elevation^2 + distance to protected area	13	1027.24	0.12	−500.61
Human influence index + elevation + elevation^2 + distance to streams	13	1027.51	0.11	−500.76

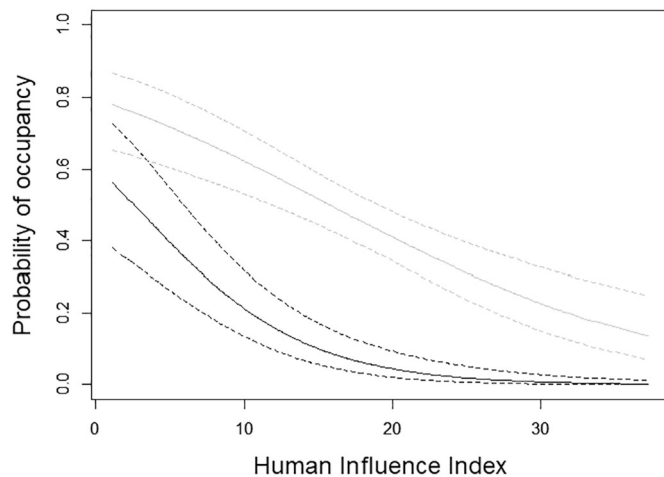| Collared peccary occupancy models	K	AIC	w_i	LL
Human influence index + elevation + elevation^2	12	2429.88	0.28	−1202.94
Human influence index	10	2430.68	0.19	−1205.338
Human influence index + elevation + elevation^2 + distance to protected area	13	2431.01	0.16	−1202.503
Human influence index + distance to protected area	12	2431.35	0.13	−1204.677

Fig. 3. Occupancy response curves from our best-fitting occupancy model that depict how probability of occupancy changes as a function of the human footprint index. Curves show mean and 95% confidence intervals for white-lipped peccary (black) and collared peccary (gray). Note that white-lipped peccary probability of occupancy declines rapidly to zero, even at relatively low levels of human disturbance (the index ranges from 0 to 74 for our study region).

areas of extremely low human influence. Based on unconditional occupancy estimates, 2133 (95% CI = 1610–2766) of the 21,490 cells in the entire Mesoamerican region were predicted to be occupied, for an occupancy rate of 0.10 (95% CI = 0.08–0.12). This amounts to a predicted 76,788 km^2 of occupied area (95% CI = 57,960 km^2–99,576 km^2), which is ~15,000 km^2 smaller than the estimate based on expert polygons (after accounting for the expert polygon in southern Mexico that lies outside the area for which we could predict occupancy; see Fig. 4), and a 90% reduction from historic distribution in the region.

Collared peccaries have a much more diffuse area of predicted occupancy than white-lipped peccaries (Supplementary Fig. 7), which is pattern also reflected in the Maxent models. Collared peccary predicted occupancy extends outside of protected areas and into more heavily disturbed landscapes. Overall, occupancy probabilities were much higher than for white-lipped peccaries, something that is not as apparent from examining habitat suitability patterns from Maxent. Collared peccaries are predicted to occupy 8042 (95% CI = 6751–9517) cells in the entire study region, for an occupancy rate of 0.37 (95% CI = 0.31–0.44) and a total predicted area of occupancy of 289,512 km^2 (243,036 km^2–342,612 km^2).

4. Discussion

The global and rapid decline of large herbivore populations necessitates data at appropriately large scales to inform effective conservation planning and management. Our regional analyses reveal that white-lipped peccary populations exist in small and highly isolated patches of habitat in Mesoamerica, and that their populations are in more of a critical condition than previously thought. These results are supported by multiple range mapping exercises involving different analyses, and indicate the advantage of bringing together diverse expertise and datasets from multiple countries for generating regional knowledge of species status. The methods we used here could be employed on other poorly-known large herbivores from developing regions to better assess current population status and limits for species thought to be rapidly declining. Our estimate of area occupied by white-lipped peccaries is a substantial reduction from the previous 2005 estimate (Altrichter et al., 2012) and current IUCN range maps, and a concerning 87–90% reduction from likely historical distribution

in the study region (depending on the analysis considered). This reduction from previous range estimates may be, in part, an artifact of a better definition of area inhabited by the species in our assessment, which focused exclusively on Mesoamerica and included both expert-based and empirical estimates, than previous assessments that focused on the entire range of the species and only included expert opinion. But, at the same time it may also indicate continued rapid population decline in recent decades. Moreover, expert opinion suggests that the majority of the populations remaining in Mesoamerica are declining, with much smaller group sizes than in other areas of the range with less disturbance (Altrichter et al., 2012; Reyna-Hurtado et al., 2016).

The three range-mapping exercises demonstrated that the largest contiguous blocks of habitat for white-lipped peccaries occur in several major transboundary reserves. This includes the Maya Forest of Guatemala, Mexico and Belize, the Rio Platano/Patuca/Bosawas complex of Honduras and Nicaragua, the Indio Maiz and Tortuguero National Park complex of Nicaragua and Costa Rica, and the Darien/Los Katios National Park complex between Panama and Colombia (although we did not model peccary habitat in Colombia, Los Katios National Park is immediately adjacent to Darien). In addition, the La Amistad Biosphere Reserve between Costa Rica and Panama may be another large transboundary patch of habitat, based on occupancy and Maxent modelling, though the area on the Costa Rica side is poorly known and hence was not identified as an extant population in our expert-based assessment. Although population estimates for white-lipped peccaries are highly uncertain, experts estimated that these same transboundary areas likely harbor the highest populations of remaining peccaries. For example, fewer than 2000 white-lipped peccaries may survive in the Calakmul Biosphere Reserve of Mexico, within the northern section of the tri-national Maya Forest (Reyna-Hurtado et al., 2010); however, together with the contiguous forests of the Maya Biosphere Reserve in Guatemala and Rio Bravo in Belize, the entire Maya Forest hosts the largest white-lipped peccary population stronghold in Mesoamerica, with an estimated population of around 5000 individuals. The remote forests of the bi-national complex of the Rio Platano/Patuca and Bosawas Biosphere Reserves in Nicaragua may harbor around 3000 white-lipped peccaries. These large transboundary populations may exist as somewhat separate subpopulations in a larger metapopulations, or could function more as one single population (sensu Biondo et al., 2011).

Outside of the transboundary landscapes, remaining populations of white-lipped peccaries were generally scattered and isolated. Occupancy and suitability mapping show limited occupied or suitable habitat in most of these populations, with experts estimating generally small and declining populations. However, three isolated white-lipped peccary populations in Costa Rica and Belize were either stable or increasing, likely due to the efficacy of conservation interventions in these areas (i.e., little habitat loss, limited hunting). These stable populations may be areas to focus on in terms of enhancing connectivity with surrounding populations, to benefit long-term meta-population persistence. However, we emphasize that preservation of the largest blocks of habitat, those in transboundary landscapes, will be the most important for maintaining larger white-lipped peccary populations that can persist in the coming decades.

The fact that all three modelling exercises, which used different datasets and analysis methods, were in general agreement about white-lipped peccary distribution, provides additional support to our findings. In some rare cases, the occupancy and/or Maxent modelling revealed areas of potential distribution that are currently outside existing expert-based polygons. These areas may represent landscapes where there are suitable conditions but no current peccaries due to historic or other factors, or areas where there are good conditions but limited knowledge. Such areas should be targeted for future surveys (e.g., the large swaths of mid-suitability in southeastern Costa Rica that are outside any expert based polygons). In other cases, several peripheral and isolated expert-based polygons appeared to contain little suitable habitat or had
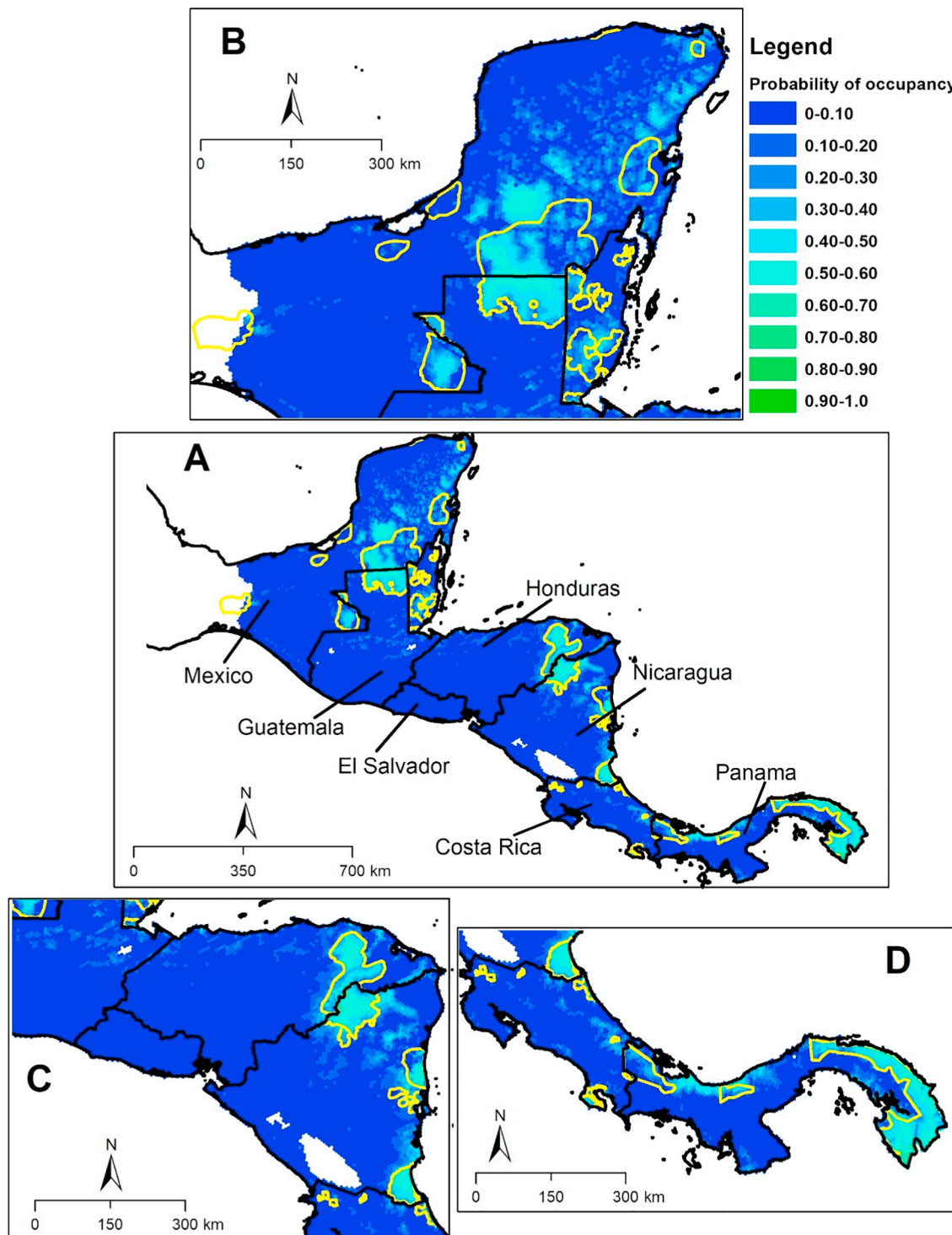
Fig. 4. Probability of occupancy projected across our entire study region for white-lipped peccaries, based on the best-fitting single season occupancy model. A) shows the entire Mesoamerican study region with B–D depicting zoomed in images for northern, central, and southern portions of the study region, respectively. In general, white-lipped peccaries have low-medium probabilities of occupancy across the region. Large contiguous patches of medium occupancy probabilities are found concentrated in several transboundary regions. Note that our human footprint layer did not extend far enough west in Mexico to encompass the most western polygon delineated by experts, and thus we could not predict occupancy in that area.

relatively low estimated probability of presence (e.g., Laguna de Terminos and Chimalapas populations). These could be populations likely to decline further, or could be areas with unique environments or where we were missing appropriate covariate data to model response. Maxent and occupancy models generally agreed, with the caveat that occupancy models revealed generally mid-low probability of presence

across the region that could not be discerned with Maxent models. Maxent models also predicted isolated pockets of high suitability in certain areas where occupancy models suggested low probability of presence, such as central and southeastern Guatemala and northern Honduras. Given that peccaries are likely absent from these regions based on expert knowledge and limited surveys, occupancy models

might be better reflective of distribution outside of larger pockets of habitat. The methodological approach we outline here will not be applicable to all poorly known large mammals. However, the large number of camera-trapping datasets that are available (e.g., Steenweg et al., 2017), and the degree of local knowledge or records that tends to exist for large mammals, suggests that our approach could be useful for generating better regional knowledge of a wide variety of mammalian species.

Although direct comparisons of white-lipped peccary status with other species are problematic, we found that collared peccaries, another large, hunted herbivore in the Neotropics, had much higher levels of occupancy (occupancy rates were almost 3 times higher for collared peccaries) and a more widespread distribution in Mesoamerica than white-lipped peccaries. Additionally, Baird's tapir (*Tapirus bairdii*), the largest herbivore in Mesoamerica, has occupancy rates and distribution patterns more similar to collared peccaries (Thornton, unpublished data; Schank et al., 2017). Taken together, these findings suggest that white-lipped peccaries are the most vulnerable large herbivorous mammal in Mesoamerica, and perhaps the most vulnerable large mammal of any kind in the region.

Human influence is a key predictor of range retraction and population decline for large mammals globally (Ripple et al., 2015; Ripple et al., 2016), and was of overriding influence for white-lipped peccaries. Although suitability and occupancy of both collared and white-lipped peccaries declined as human influence/human footprint increased, white-lipped peccaries responded particularly strongly, with occupancy probabilities declining quickly to near zero at fairly low levels of human disturbance (Fig. 3). This likely relates to both the need for large tracts of intact habitat for this wide-ranging species and sensitivity to human hunting (Altrichter et al., 2012; Keuroghlian et al., 2013). Similar results were obtained when modelling group size in this species across all its distribution range with larger groups found in areas far from human communities (Reyna-Hurtado et al., 2016). Targeted and sustained hunting pressure may extirpate entire populations of white-lipped peccaries even from areas of relatively well-preserved forest (for example, in large "ejidos" or communal forests of southern Mexico; Reyna-Hurtado et al., 2010), and likely the combination of targeted hunting and habitat loss is the worst scenario for the conservation of white-lipped peccaries in Mesoamerica. In contrast, collared peccaries were able to maintain higher occupancy and suitability at greater levels of human disturbance, demonstrating that regional distribution was reflective of patterns seen at more local scales, where this species appears somewhat tolerant to fragmentation and human disturbance (e.g., Altrichter and Boaglio, 2004; Michalski and Peres, 2007; Thornton et al., 2011). The greater resilience of collared peccaries could be driven by a more generalist diet than the more specialist white-lipped peccary (Sowls, 1997; Fragoso, 1999) which may lead to smaller home ranges across a great range of habitats, and a slightly higher intrinsic rate of increase (Robinson and Redford, 1986). Collared peccaries may also have a greater tendency for groups to flee when threatened (Peres, 1996; Keuroghlian et al., 2004), which should decrease their vulnerability to human hunting. Their smaller group sizes may also make them less conspicuous to human hunters, and decrease the number that can be killed at any one time. In contrast, large groups of white-lipped peccaries sometimes aggressively face threats (Nogueira et al., 2015) which increases their vulnerability to hunters.

Our data demonstrate the dire status of white-lipped peccaries in Mesoamerica. Of particular concern to the plight of white-lipped peccaries in Mesoamerica is the status of the most important remaining strongholds of peccaries - the Maya Forest of Guatemala, Mexico, and Belize, the Rio Platano/Patuca/Bosawas complex of Honduras and Nicaragua, and the Darien complex in Panama and Columbia. All these forests are under particularly grave threat from human activities. For example, in the past 15 years, wildlands (those areas with limited human influence) have been reduced by 30% in the Rio Platano/Bosawas complex and by 25% in the Maya Forest (Hugo Ramos, unpublished

data). These two forests are at also at imminent risk of losing their contiguity due to expansion of both sugar cane and cattle ranching.

The critical nature of white-lipped peccary populations in much of Mesoamerica is not always well reflected in their listing status at the country level. Currently, there remains a mix of designations and attention given to the species in those countries, with only 4 of the 7 countries listing white-lipped peccaries as endangered or critically endangered. In some cases, listing status should be reassessed in order to provide proper levels of attention to this species. Accurate listing of a species in national lists (Red Lists, or Endangered Species lists) has ramifications for Environmental Impact Assessments and for the management of subsistence and sport hunting. Although the range reduction we documented is substantial at the regional level, the reduction could be driven by both better methods to document range limits as well as ongoing declines. Thus, additional data collection on regional population trends and range retraction would be beneficial in determining if white-lipped peccaries would be a candidate for uplisting at the regional level based on IUCN criteria.

Our analysis suggests that both local and regional conservation actions will be needed to maintain white-lipped peccary populations. Although maintenance of intact forest cover is obviously of high importance to the species, our analysis reveals the potential impact of hunting and other forms of disturbance independent of forest loss. Conservation actions will have to include working with local indigenous and non-indigenous communities in and around protected areas to better manage legal and illegal harvesting of peccaries, and provide suitable alternatives where historical rates of hunting may no longer be sustainable due to landscape level deforestation dynamics. Given the transboundary nature of many of the largest peccary populations, coordinated, large-scale, transboundary conservation efforts in Mesoamerica also will be needed to help ensure the long-term persistence of white-lipped peccaries. Research and conservation efforts that span international borders in these areas could aid in habitat, population and connectivity management of this species, and may bring a diverse set of other benefits such as sharing of expertise, pooling of resources, and more accurate population/distribution data (Kark et al., 2015; Vasilijević et al., 2015; Bischof et al., 2016; Gervasi et al., 2016). The fact that protected areas tend to be clustered near borders in the Americas (Thornton et al., in press), including several transboundary complexes in this analysis, should aid coordinated efforts within the framework of protected areas management. Moreover, similarities in country-level conservation listing status of white-lipped peccaries would likely enhance mechanisms for coordinated management, which may be particularly important for species with wide-ranging movements (Thornton and Branch, 2019). Although these transboundary regions are perhaps most important for white-lipped peccaries, they are also areas of high occupancy/suitability for other large mammals, including collared peccaries (Supplementary Figs. 5 and 7), tapirs (Schank et al., 2017), and jaguars (Rabinowitz and Zeller, 2010), and thus conservation efforts would benefit multiple landscape species. Finally, increased public awareness of the plight of white-lipped peccaries, and its ecological significance, should be elevated to bring additional attention to this highly threatened symbol of national and regional patrimony.

CRediT authorship contribution statement

Daniel Thornton: Conceptualization, Methodology, Formal analysis, Writing - original draft, Funding acquisition.**Rafael Reyna:**Conceptualization, Methodology, Formal analysis, Writing - original draft, Funding acquisition.**Lucy Perera-Romero**: Methodology, Formal analysis, Investigation.**Jeremy Radachowsky**: Conceptualization, Writing - review & editing, Funding acquisition.**Mircea G. Hidalgo-Mihart:**Investigation, Writing - review & editing.**Rony Garcia:**Investigation, Writing - review & editing. **Roan McNab:**Investigation, Writing - review & editing.**Lee**

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Declaration of competing interest

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https:// doi.org/10.1016/j.biocon.2020.108410.

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