Primates
https://doi.org/10.1007/s10329-018-0673-8

ORIGINAL ARTICLE

# Integrating expert knowledge and ecological niche models to estimate Mexican primates' distribution

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Received: 24 February 2017 / Accepted: 26 June 2018

## Abstract

Ecological niche modeling is used to estimate species distributions based on occurrence records and environmental variables, but it seldom includes explicit biotic or historical factors that are important in determining the distribution of species. Expert knowledge can provide additional valuable information regarding ecological or historical attributes of species, but the influence of integrating this information in the modeling process has been poorly explored. Here, we integrated expert knowledge in different stages of the niche modeling process to improve the representation of the actual geographic distributions of Mexican primates (*Ateles geoffroyi, Alouatta pigra*, and *A. palliata mexicana*). We designed an elicitation process to acquire information from experts and such information was integrated by an iterative process that consisted of reviews of input data by experts, production of ecological niche models (ENMs), and evaluation of model outputs to provide feedback. We built ENMs using the maximum entropy algorithm along with a dataset of occurrence records gathered from a public source and records provided by the experts. Models without expert knowledge were also built for comparison, and both models, with and without expert knowledge, were evaluated using four validation metrics that provide a measure of accuracy for presence-absence predictions (specificity, sensitivity, kappa, true skill statistic). Integrating expert knowledge to build ENMs produced better results for potential distributions than models without expert knowledge, but a much greater improvement in the transition from potential to realized geographic distributions by reducing overprediction, resulting in better representations of the actual geographic distributions of species. Furthermore, with the combination of niche models and expert knowledge we were able to identify an area of sympatry between *A. palliata mexicana* and *A. pigra*. We argue that the inclusion of expert knowledge at different stages in the construction of niche models in an explicit and systematic fashion is a recommended practice as it produces overall positive results for representing realized species distributions.

**Keywords** Expert knowledge · Ecological niche modeling · Species distribution models · *Alouatta palliata mexicana* · *Alouatta pigra* · *Ateles geoffroyi* · Maxent · Mexico

## Introduction

The geographic distribution of a species depends on complex and dynamic processes that vary across space and time. It is the result of the responses of species to relatively static (e.g., topography) and dynamic (e.g., resources, biotic interactions) environmental and ecological factors that impact demographic processes, which, in turn, shape their distribution (Lomolino et al. 2010). Delimiting the geographic distribution of taxa is therefore a challenging task, as the process delineated above produces fuzzy and highly dynamic boundaries. Hence, several methods have been developed to delimit the distribution of a species, from purely cartographic in which a collection of records are enclosed by convex polygons (Burgman and Fox 2003), areographic techniques where the size and shape of ranges are estimated with numerical manipulations of regular grids (or circles, hexagons, etc.) drawn around occurrence records (Rapoport 1982), to inferential correlative and mechanistic methods based on the association between species and the

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environment. In the last two decades, correlative methods known as species distribution models or ecological niche models (ENMs) have become the most widely used approach to estimate species distributions (Lobo et al. 2010; Varela et al. 2014).

In general, ENMs are based on associations between occurrence records of the target species and environmental variables to reconstruct the ecological niche and project the niche model onto a geographic area to produce a map representing the potential distribution of that species (Guisan and Thuiller 2005; Martínez-Meyer 2005). The Hutchinsonian niche concept refers to the fundamental niche as all biotic and scenopoetic factors that allow a species to persist indefinitely (Hutchinson 1957). In practice, the vast majority of ecological niche modeling applications only consider scenopoetic factors, such as climate and topography, and do not explicitly include some important ecological or historical factors (e.g., interspecific interactions, dispersal). When only scenopoetic factors are considered, ENMs identify areas of potential distribution that are not necessarily occupied by the species due to further factors, such as the history of the species, biogeographic barriers, dispersal capacity, interspecific competition, predation, among others (Soberón 2007).

Conversely, the realized distribution is the area where both scenopoetic and biotic conditions are favorable and thus where the species is likely to occur (Soberón and Peterson 2005). For studies aimed at finding the geographic area where the species can actually be found, approximating the potential distribution to the realized distribution is a crucial step. For instance, in conservation planning, it is desirable to prioritize areas with high probability of occurrence of a given species over areas that may be an overestimation of its distribution (Rondinini et al. 2006). Overestimated areas may represent environmentally suitable regions to which the species has failed to disperse or where it has gone extinct (Anderson et al. 2003) but can also derive from choices in the modeling procedure (e.g., threshold value for binary classification) or from errors in the input data (species misidentifications or positional errors associated with occurrence records; Rocchini 2011).

Different approaches have been implemented to reduce overprediction, from purely data-driven (Anderson and Martínez-Meyer 2004) to those including the opinion of experts (López-Arévalo et al. 2011). An expert is someone who has knowledge about a topic of interest, obtained by work experience, education, or training (Garthwaite et al. 2005). Expert knowledge has been useful to inform predictive models in conservation (Loiselle and Howell 2003; López-Arévalo et al. 2011; Johnson et al. 2012; Fourcade et al. 2013) and biogeography (Kuhnert 2011). In spite of the promising advantages of including expert knowledge in niche modeling, its inclusion in the modeling process is a poorly explored strategy.

Experts in the biology and ecology of taxa can participate in the niche modeling process in different ways: for example, evaluating information such as occurrence records or providing information regarding interactions with other species that shape the target species' distribution and by reviewing the results. Nevertheless, this approach has been limited because expert information may contain personal biases and preferences that reduce its objectivity and reliability (Kuhnert 2011), or because its implementation has been hindered by the lack of experts in the taxa of interest or by the scarce human and financial resources to carry out an elicitation process through which the information is acquired (Kuhnert et al. 2010; Martin et al. 2012). Therefore, a key element to include expert knowledge in a modeling process is the existence of a group of specialists on a taxonomic group.

Primates are a well-known taxonomic group in Mexico, where three taxa can be found: the black howler monkey (*Alouatta pigra* Lawrence, 1933), the Mexican mantled howler monkey (*Alouatta palliata mexicana* Merrian, 1902) and the spider monkey (*Ateles geoffroyi* Kuhl, 1820). Although previous works have estimated the potential distribution of Mexican primates using ENMs (Vidal-García and Serio-Silva 2011), the limits of their distributions are still controversial, particularly for the two howler monkeys *Alouatta palliata mexicana* and *A. pigra* for which a contact zone has been documented in Mexico (Baumgarten and Williamson 2007), and their boundaries have not been accurately delimited yet. Mutual interference is believed to play a role in defining distributional boundaries, as these taxa are closely related (Cortés-Ortiz et al. 2003) and coexist in the same ecosystems and elevation ranges (Baumgarten and Williamson 2007; Cortés-Ortiz et al. 2015).

The study of primates in Mexico gained strength in the early 1980s and currently there are several research groups congregated in the Mexican Association of Primatology (AMP, from its Spanish acronym), many of which have a strong focus on conservation. The main goal of the AMP is to generate scientific knowledge on all aspects of the biology and ecology of Mexican primates, including their current distribution. Therefore, AMP members are a strong group of experts that can provide relevant information in the niche modeling process. In this work, we report the contribution of integrating expert knowledge from AMP members in three stages of the ecological niche modeling of the Mexican primates: (1) building occurrence records datasets by providing and cleaning occurrence records, (2) reviewing model outputs iteratively and providing feedback considering the species ecology, and (3) validating final model outputs. Under this framework (Fig. 1), we produced updated distribution maps of Mexican primates that represent the area where primates have been actually registered by the experts in the last decades. For comparison, we also built models following the common modeling practices when experts are not explicitly

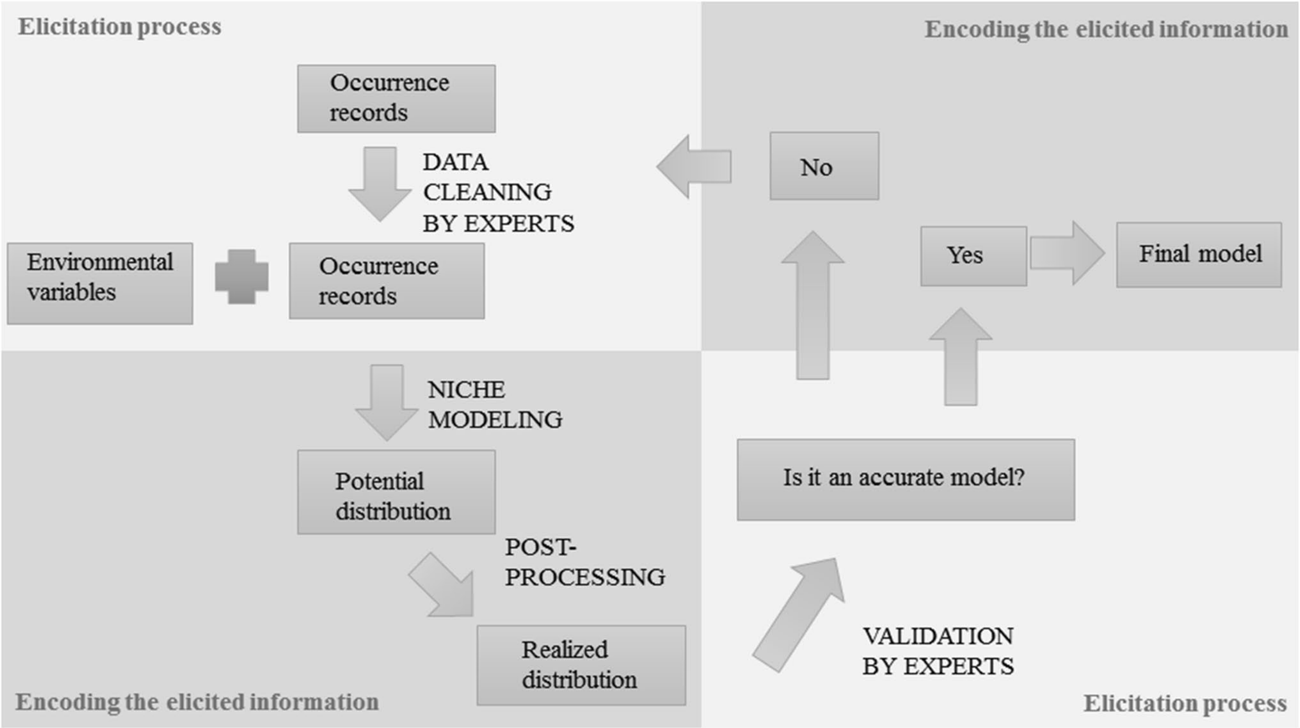

**Fig. 1** Conceptual framework showing the process that we followed to integrate expert information into the modeling process. In the elicitation process, experts participated providing and cleaning occurrence records and validating models. In the encoding information step, information obtained from experts was integrated in the modeling process by modelers

included. Models with and without expert knowledge were evaluated using independent occurrence records with four validation metrics, namely sensitivity, specificity, true skill statistics (TSS), and kappa (Fielding and Bell 1997).

## Methods

### Biological data

Primates' occurrence records came from two data sources. The first one was a dataset of occurrence records provided by experts via the AMP, including occurrence records compiled in two primate conservation workshops held in Mexico (CAMP-PACE: Rodríguez-Luna et al. 2009; SEMARNAT and CONANP 2012), and which mainly consisted of field records collected by experts from research projects. The second one was a public dataset with occurrence records gathered from the National Biodiversity Information System (SNIB), which mainly included historical occurrence records from museum collections and observations from projects supported by the National Commission for Knowledge and Use of Biodiversity (CONABIO). These records passed through a quality-control process and are available to the public through CONABIO's geoinformation portal and the Global Biodiversity Information Facility (GBIF) portal. Using these two data sources, we built two datasets: (1) an 'expert' dataset which included the records provided by experts and expert reviewed SNIB records, and (2) a 'non-expert' dataset, which included only the SNIB records. Both expert and non-expert datasets were reviewed to remove duplicates and possible erroneous records due to disparities between locality descriptions and geographic coordinates. The expert dataset was reviewed by members of the working group on conservation of Mexican primates of the AMP and the non-expert dataset was reviewed without the aid of experts. This step was important, as occurrence records came from different survey designs and efforts, resulting in different errors and levels of uncertainty.

To obtain a broad picture of the differences between expert and non-expert datasets, we carried out visual comparisons of the occurrence records of the three taxa displayed in a map and also in a two-dimensional environmental plot of annual mean temperature vs. annual precipitation, as well as in a one-dimensional graph of mean temperature.

### Niche modeling procedure

We implemented the same procedure in all models in order to produce comparable outputs, as follows. We built ENMs using the maximum entropy algorithm (Maxent; Phillips et al. 2006) under default parameters (Appendix 2) and the same environmental data in all cases. We used digital layers of 19 bioclimatic variables describing annual, seasonal, and extreme climatic patterns (Hijmans et al. 2005, Appendix 1) at a spatial resolution of $\approx 1$ km obtained through interpolation of meteorological data from Mexico (Téllez et al. 2010). In addition, we used three digital topographic layers: slope, elevation, and topographic index (USGS 2011). Occurrence records were split in a random 90:10 proportion for training:testing. Maxent probabilistic maps were reclassified into binary maps using the logistic threshold that included all training presences (minimum training presence).

Output maps obtained with this procedure are considered potential distribution maps as they represent the geographic distribution of suitable conditions for species, which frequently extend beyond their historic or current distribution (Peterson et al. 2011). Therefore, to bring a potential distribution map to a realized distribution map, it is necessary to perform a post-process to eliminate historically unoccupied areas. To do so, it is a common practice to use elements of the landscape (e.g., basins) or regionalization maps (e.g., biogeographic provinces, ecoregions) that may represent barriers to dispersal (Martínez-Meyer 2005; Martínez-Meyer et al. 2006; Ballesteros-Barrera et al. 2007; Papeş and Gaubert 2007). Post-processing details for expert and non-expert approaches are described below.

## Expert knowledge approach

We designed a transparent and repeatable elicitation process to acquire the information from the experts (Fig. 1) in order to minimize biased or personal preferences, as the usefulness of expert knowledge depends on the accuracy of data and scientific rigor with which the information is acquired (Kuhnert et al. 2010; Martin et al. 2012). We followed three steps during the elicitation process (Martin et al. 2012): (1) designing the elicitation process to decide which information would be used and how to perform the elicitation; (2) performing the elicitation process; and (3) translating or encoding the elicited information (Fig. 1).

## Elicitation design

The AMP worked together with the National Commission of Natural Protected Areas (CONANP) in the development of the Species Action Plan for primates and invited CONABIO to collaborate in order to improve the knowledge of the distributions of Mexican primates and to guide a process to prioritize areas for their conservation (Tobón et al. 2012). Participating institutions recruited primatologists to participate in the elicitation process. The implemented elicitation was face-to-face in a workshop, and remotely by email surveys.

A total of 46 experts from 17 institutions (non-governmental organizations, government, and academic institutions) responded to the call (Appendix 3). Experts were split into two groups based on their experience and commitment: a core group and a consulting group. The former was composed by members of the working group on conservation of Mexican primates of the AMP and participated during the entire modeling process. The second group was formed by primatologists that agreed to participate in a workshop and a survey sent via email (Appendix 3). The iterative process for incorporating expert knowledge in the ecological niche modeling consisted of reviews of occurrence records, suggestions for the construction of niche models, and evaluation of model outputs to provide feedback.

## Ecological niche models incorporating expert knowledge

We produced two generations of ENMs using the standard modeling procedure. The first generation was a prospective model using the expert dataset and the second generation was built after the experts reviewed the first generation models (FGM) and made suggestions.

FGM for each species consisted of niche models produced with the expert occurrence dataset and resulting maps were clipped with the level IV ecoregions map for Mexico (INEGI-CONABIO-INE 2008a, b) to remove environmentally suitable areas in ecoregions where taxa have not been recorded.

FGM were presented and discussed with the experts at a workshop in 2011. During the workshop, models were presented in a plenary session previous to a discussion about the accuracy of occurrence data and generalities of ENMs. Then, experts were divided into three working groups based on their regional experience: Yucatan Peninsula, Veracruz-Tabasco, and Oaxaca–Chiapas. Each working group reviewed the FGM for each region and the elicitation was carried out in two steps: (1) an elicitation with a categorical scale where each group described a region as: "Generally suitable", "Yes, most of the areas", "Yes, some areas", "No, most of the areas", or "Unsuitable", and (2) the identification, made by experts, of areas that they considered to be over- or under-predictions using a grid of 2.5-km spatial resolution over each distribution map. The aim was to produce an uncertainty grid for each species' distribution model.

All the information was encoded after the workshop. Good and poor models were identified based on the categorical answers, where only those models rated as "Generally suitable" and "Yes, most of the areas" where classified as good. Models rated as "Generally suitable" by the majority of experts were considered as the final models. For models identified as not accurate, i.e., rated as "Yes, some areas", "No, most of the areas", or "Unsuitable," the core group reviewed the occurrence again and produced refined datasets.

Using this new expert occurrence dataset and the standard modeling procedure, we built a SGM. These models were post-processed to reduce overprediction using the uncertainty grid produced with the aid of the experts instead of the ecoregions maps used for clipping the FGMs. Finally, maps representing the realized distributions were sent by electronic survey to both the core and consulting groups with the question: "How accurate do you think these species' distribution maps are?" Based on the answers, the percentage of expert agreement with each ENMs was calculated.

## Ecological niche modeling without expert knowledge

Models without expert knowledge were also built for each species for comparison. For these, data cleaning and post-processing were made without the advice of experts, which is a common practice when experts are not explicitly included. ENMs were built using only the non-expert dataset under the standard modeling procedure. To reduce overprediction, environmentally suitable areas in ecoregions where taxa have not been recorded were removed using the level IV ecoregions map for Mexico (INEGI-CONABIO-INE 2008), under the assumption that occurrence sampling is reliable at the ecoregions level.

## Model validation

Binary models (i.e., thresholded with the minimum training presence criterion) with and without expert knowledge and before and after post-processing were validated using four threshold-dependent metrics: sensitivity, specificity, true skill statistics (TSS) and kappa (Fielding and Bell 1997). These metrics provide measures of accuracy for presence-absence predictions. Sensitivity represents the proportion of correctly predicted presences, whereas specificity represents the proportion of correctly predicted absences (Fielding and Bell 1997). Kappa and TSS are calculated taking into account the interaction between sensitivity and specificity with the difference that TSS is not affected by prevalence (i.e., the size of the occupied area by the species; Allouche et al. 2006). For this reason, TSS has been proposed as a good alternative when presence-absence maps are evaluated (Marcot 2012).

Validations were performed in all cases using presences and pseudo-absences independent from model calibration (Table 1). Presences used for validation were occurrence data obtained after the elicitation and modeling process (between 2011 and 2017), and they came from three sources: the Regional System for Primates' Monitoring in Mexico (SRMP, Spanish acronym), *Naturalista* (Mexican version of iNaturalist, www.naturalista.mx) and SNIB. SRMP was implemented by two institutions, *Conservación de la Biodiversidad del Usumacinta A.C.* and CONANP, between 2013 and 2016 in nine protected areas and five priority regions for primate conservation (Tobón et al., 2012) in southeastern Mexico (Pozo-Montuy et al. 2013; 2015). SRMP was carried out by 34 monitoring groups and 215 people under standardized methods (line transect, complete census, and explorations) recording the geographical location of each observation (www.cobius.org). *Naturalista* is a citizen science project that collects occurrence records in an online database. Because observation skills and knowledge of participants could be lower than those of professional scientists (Kremen et al. 2011), we only used records that had been validated by a curator or where the *Naturalista* community agreed with the identification of the record. *Naturalista* occurrences were recorded between 2011 and 2017. Finally, records obtained from the SNIB were all presences recorded after 2011.

In addition to presence data, validation metrics also require absence data. When true absence data are lacking, pseudo-absences have been used instead, which are locations at which the species has not been recorded, such that neither presence nor absence is confirmed (Zaniewski et al. 2002; Soberón and Peterson 2005). We used ArcMap 10.2 to generate a set of random pseudo-absences in a 5:1 proportion (absence:presence) from non-presence pixels across the study region for use in model validation. Random selection of pseudo-absences has shown better results over other sampling schemes (Barbet-Massin et al. 2012).

In addition to our presence and pseudo-absence datasets, we had available 362 true absences directly recorded in the field by SRMP teams (181 for *Ateles geoffroyi*, 71 for *Alouatta pigra,* 110 for *A. palliata*). However, we

**Table 1** Number of presences, absences, and pseudoabsences used for calibrating and validating models

| Taxa | Calibration | | Validation | | |
|---|---|---|---|---|---|
| | Presences without expert knowledge | Presences with expert knowledge | Presences | Pseudo-absences | Absences |
| *Ateles geoffroyi* | 73 | 119 | 287 | 1254 | 181 |
| *Alouatta palliata mexicana* | 56 | 41 | 86 | 320 | 110 |
| *Alouatta pigra* | 110 | 58 | 625 | 3054 | 71 |

decided not to use them to calculate model validation metrics because monitoring was carried out in focal areas and not systematically across regions, and also because the number of absences was relatively small compared to presences; consequently, they contain bias that would not reflect model performance adequately. Nevertheless, these data are important, so we reported the proportion of correctly predicted absences as an additional measure of model accuracy. Absences were considered places where the presence of taxa had not been recorded over a period of 2–4 years (between 2013 and 2016).

## Results

### Comparison between expert and non-expert occurrence datasets

Both expert and non-expert occurrence datasets covered the distribution area of the taxa in full. Nevertheless, non-expert datasets showed several records isolated from areas with higher density of occurrences that correspond to somewhat different environments, as observed in the temperature-precipitation biplot (Fig. 2). The temperature boxplot revealed that although the mean value is very similar for all three

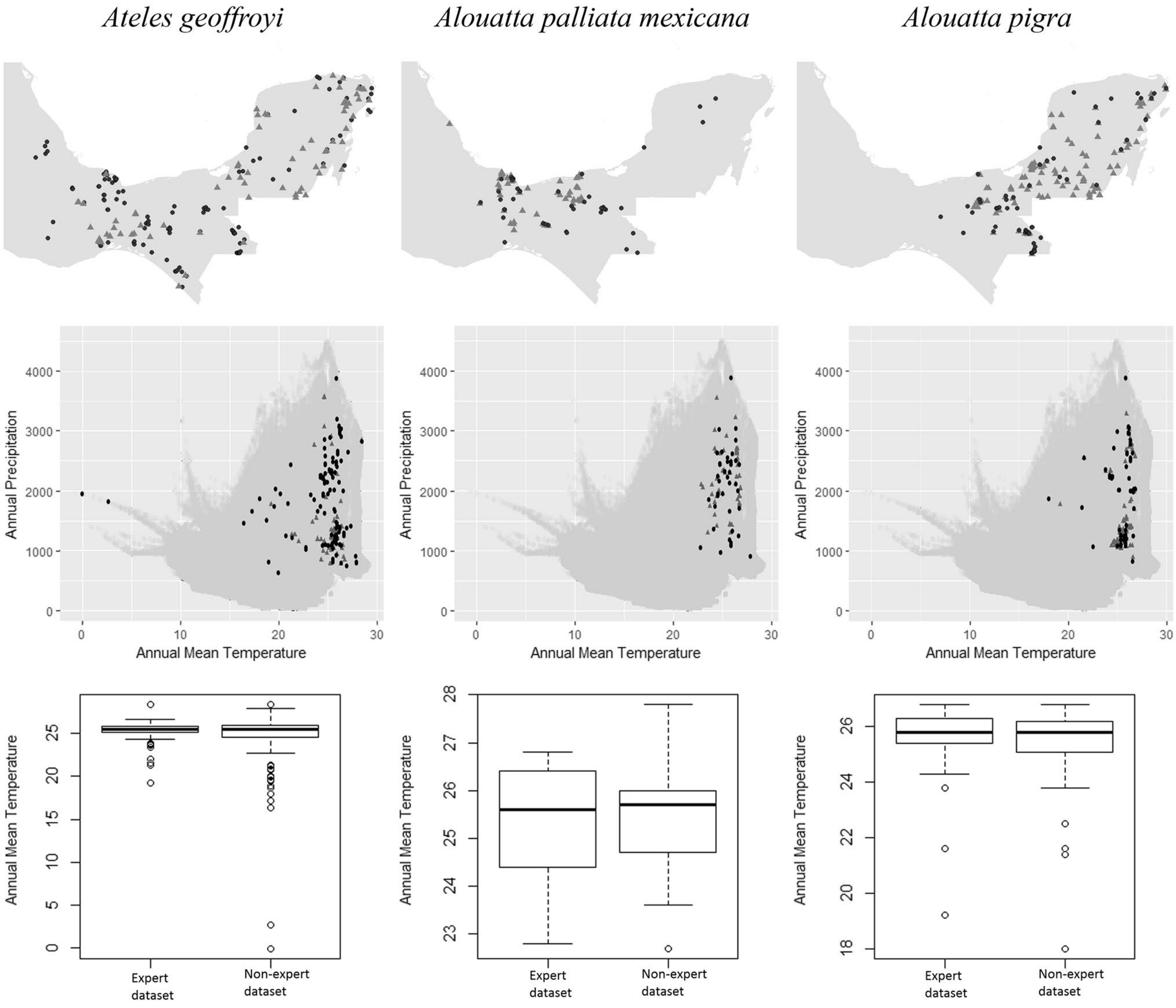

Fig. 2 Environmental, geographic, and statistical dispersion of training occurrence records. The upper panel shows the geographic dispersion of occurrence records. In the center, the distribution of training occurrence records in two environmental dimensions: annual mean temperature and annual precipitation. Boxplots at the bottom show the statistical dispersion of occurrence records over annual mean temperature. Gray dots are the environmental conditions in Mexico (background), black triangles are occurrence records reviewed by experts and black dots are occurrence records not reviewed by experts

taxa, occurrences belonging to non-expert datasets contained a slightly higher proportion of outliers (all data point that is located outside whiskers) (Fig. 2). For *Ateles geoffroyi*, 13% of non-expert occurrence records were outliers, whereas it was 12% for the expert dataset. For *Alouatta palliata mexicana*, the proportion of outliers in the non-expert vs. the expert dataset was 2.4 and 0%, respectively; and for *Alouatta pigra* it was 6.9 vs. 2.7%, respectively (Fig. 2).

## Ecological niche modeling with expert knowledge

The first generation model (FGM) produced for *Ateles geoffroyi* (Fig. 3a) was evaluated as "Generally suitable" for two of the three regions (Oaxaca–Chiapas and Yucatan Peninsula) and "Yes, most of the areas" for Tabasco–Veracruz (Table 2) because experts identified some areas as under-predicted (Fig. 3a). Nevertheless, experts agreed that the map was generally suitable. Therefore, it was considered the final model and did not require a second generation (SGM).

For *Alouatta palliata mexicana*, there was no consensus between the three regions evaluated. For Tabasco–Veracruz and Oaxaca–Chiapas, experts rated it as "Yes, most of the areas" and "Inadequate" for the Yucatan Peninsula (Table 2). In the latter, experts identified some areas as over-predictions. Finally, experts rated as "Yes, most of the areas" for all three regions of the *A. pigra* model (Table 2), although they indicated some areas of overprediction mainly in the Tabasco–Veracruz region. Hence, a second generation of models for *Alouatta palliata mexicana* and *A. pigra* was produced.

After the first experts' assessment, we found a geographical pattern: most disagreements were in areas where the distributions of *A. palliata mexicana* and *A. pigra* overlapped. These results were confirmed in the plenary session of the workshop, where experts commented that models of *A. palliata mexicana* and *A. pigra* overlapped beyond their field observations. Therefore, the core group reviewed the CAMP-PACE and SNIB database again after the workshop for *A. palliata mexicana* and *A. pigra* and all records for the two species dated before 1970 were removed from the databases because before this year there was a taxonomic confusion between the two howler monkey species that may have introduced some errors in the database. The uncertainty grid built with the opinion of experts was used to guide the selection of an element of the landscape that could delimit the contact zone between the two howler monkey species. Hydrological basins represent natural features of the landscape (Cotler-Ávalos et al. 2010) and the limits of hydrological sub-basins matched with the distributional limits of taxa identified by the experts. Therefore, a digital layer of the hydrological sub-basins map (CONAGUA 2007) was used along with the uncertainty grid to remove areas of over-prediction in a post-processing step. In this case, we defined over-prediction as environmentally suitable areas within hydrological sub-basins with both uncertainty and with no occurrence records. The resulting maps (Fig. 3a–c) were evaluated by experts and the majority (80%) considered the results "Generally suitable". Estimated potential and realized distribution areas for each taxa are shown in Table 3.

## Ecological niche modeling without expert knowledge

Potential and realized distribution models built without expert knowledge produced areas substantially larger for the three taxa compared to models built considering expert knowledge (Table 3). Without expert knowledge, the realized distribution of *Ateles geoffroyi* extended from the Yucatan Peninsula to central areas of Mexico (Fig. 4a). The realized distribution of *Alouatta pigra* included the Yucatan Peninsula and reached the central area of Veracruz (Fig. 4b), and the realized distribution of *Alouatta palliata mexicana* spanned from central Veracruz to the northern Yucatan Peninsula (Fig. 4c). It is remarkable that the contact zone projected between *A. palliata mexicana* (Fig. 4c) and *A. pigra* (Fig. 4b) without expert knowledge encompassed the whole distribution area of *A. palliata mexicana* (Fig. 4c).

## Model validation

Final potential and realized distribution models (i.e., maps before and after post-processing, respectively) of all taxa were generally reliable ($>0.75$) according to most accuracy measures, except for kappa that presented lower values ($<0.7$) for *Ateles geoffroyi* and *Alouatta pigra* (Tables 4 and 5). In all cases, kappa and TSS values were higher for models that were post-processed than those that were not, because specificity (i.e., pseudo-absences correctly predicted) was higher in the former but sensitivity (i.e., presences correctly predicted) was higher in the latter (Tables 4 and 5). In other words, post-processing left some presences out (slightly increased omission error) but reduced over-prediction notably.

Finally, in all cases, the proportion of true absences correctly predicted was higher when expert knowledge was integrated into the modeling process (Table 6), except for *Alouatta palliata mexicana*, for which models with and without expert advice correctly predicted the totality of absences. However, for *Alouatta pigra* none of the approaches predicted more than 61% of the true absences, and for *Ateles geoffroyi* the proportion of absences correctly predicted was very low (0.5–6.63%; Table 6).

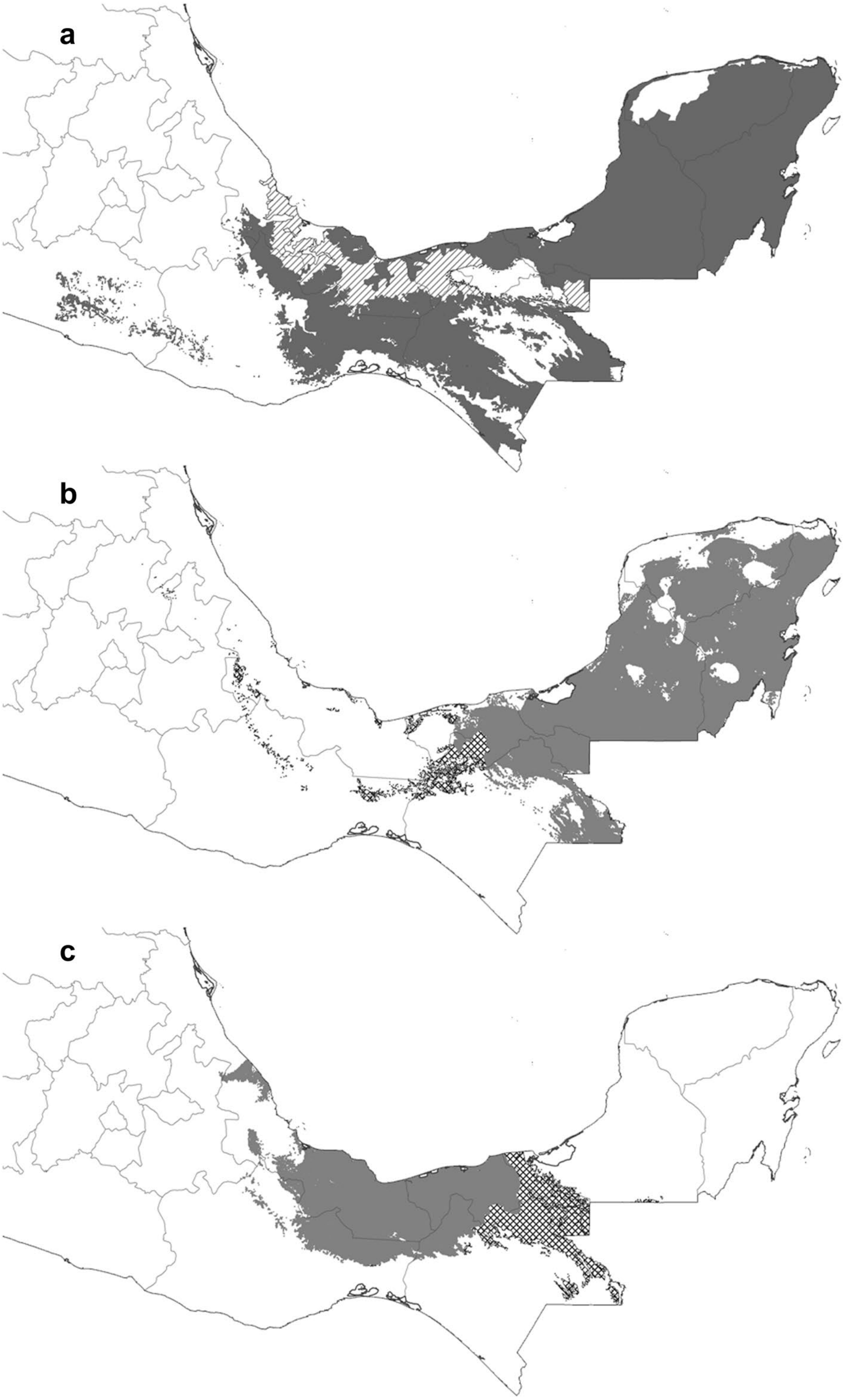

**Fig. 3** Realized distribution maps based on expert knowledge (gray area) and uncertainty area (dashed area) of: **a** *Ateles geoffroyi,* **b** *Alouatta palliata mexicana*, **c** *Alouatta pigra*

**Table 2** Expert assessment of the first generation of ecological niche models (FGM)

| Region | Species evaluated | | |
|---|---|---|---|
| | *Ateles geoffroyi* | *Alouatta palliata mexicana* | *Alouatta pigra* |
| Yucatan Peninsula | Generally suitable | Inadequate | Yes, most of the areas |
| Tabasco–Veracruz | Yes, most of the areas | Yes, most of the areas | Yes, some areas |
| Oaxaca–Chiapas | Generally suitable | Yes, some areas | Yes, most of the areas |

**Table 3** Distribution area predicted (in km$^2$) for the three Mexican primates

| | *Ateles geoffroyi* | | *Alouatta palliata mexicana* | | *Alouatta pigra* | |
|---|---|---|---|---|---|---|
| | Potential distribution | Realized distribution | Potential distribution | Realized distribution | Potential distribution | Realized distribution |
| Without expert knowledge | 440,513 | 329,982 | 211,046 | 127,096 | 306,499 | 226,044 |
| With expert knowledge | 328,568 | 221,753 | 85,191 | 63,257 | 139,119 | 131,219 |

## Discussion

In this study, we evaluated the effect of the explicit inclusion of expert knowledge in three stages of the ecological niche modeling process for the three Mexican primates (*Ateles geoffroyi*, *Alouatta palliata mexicana*, and *A. pigra*): data cleaning, the approximation of realized distributions from potential distributions (post-processing), and model validation. Our analyses indicate that the inclusion of experts had an overall positive impact on the final models because although sensitivity slightly decreased due to increased omission error, overprediction (commission error) was largely reduced thus improving overall model performance. Particularly, intervention of experts in data cleaning reduced the number of outliers (Fig. 2), which leads to improved potential distribution maps. Intervention of experts in post-processing also improved realized distribution maps of the three primate taxa by reducing potentially suitable areas that resulted in overprediction. In all cases, models built without expert knowledge produced much larger distribution areas (in some cases more than twice larger) than those generated with expert knowledge; thus the proportion of true absences correctly predicted was higher in the maps produces with expert knowledge.

In the case of the three Mexican primates, distribution maps were necessary to prioritize conservation areas as part of the Species Action Plan for primates (Tobón et al. 2012), so it was crucial to identify areas where species were most likely to be present. The realized distribution maps built with expert advice were more restricted and accurate than those without expert advice, for that reason the former were used in the prioritization process. In this case, involvement of experts not only helped in improving the accuracy of models but also enhanced the trust and reliability in the process as models were approved by 80% of the experts, and this was a key step to developing policy recommendations. We are aware that the areas trimmed from the potential distribution maps may represent genuine environmentally suitable areas for the taxa, but where they are not present due to other factors, such as habitat loss, hunting, or biotic interactions. Hence, they are shown as uncertainty areas that could be used in the future to lead new surveys or recovery actions.

Besides the improvements on potential and realized distribution maps, the interaction between modelers and primatologists was useful to propose a contact zone between *Alouatta palliata mexicana* and *A. pigra*. It is well known that *A. palliata mexicana* and *A pigra* overlap at the limits of their distributions in Chiapas and Tabasco (Cortés-Ortiz et al. 2003; Baumgarten and Williamson 2007; Cortés-Ortiz et al. 2015), and hybridization between the two species has been documented (Cortés-Ortiz et al. 2015); nevertheless, the limits of this area remain controversial due to the lack of an apparent physical barrier constraining the distribution of the two primates (Baumgarten and Williamson 2007; Cortés-Ortiz et al. 2015). This suggests that the interaction and possible interference between the two taxa may have played a role in shaping their ranges in Mexico. According to a biogeographic model of the expansion of primates in Mesoamerica (Ford 2006), *A. pigra* reached this region about 3.5–3.0 mya, and may have spread farther north before the arrival of *A. palliata* in a second wave of expansion, around 2.0 mya. This biogeographic model suggests that *A. palliata* migrated northwards and displaced *A. pigra*, confining it to its current distribution in the Yucatan Peninsula (Ford 2006). Molecular studies indicate that *A. palliata mexicana* and *A. pigra* are closely related taxa (Cortés-Ortiz et al. 2003), thus, phylogenetic niche conservatism—i.e., the magnitude of retention of traits of the fundamental ecological niche of species in a lineage (Peterson et al. 1999)—must be strong, and competition is expected to be also strong (Peterson 2011). Ecological niches of the two taxa are expected to be similar, therefore when modeling the ecological niche of *A. palliata mexicana* a fraction of the geographic distribution of *A. pigra* is captured and vice versa, making it difficult to delimit the range of the two species and their sympatric area. The involvement of primate experts in the modeling process enabled to propose an area of contact (Fig. 5). This area coincides with previous records of mixed groups composed of individuals of both species (Smith 1970; Horwich and Johnson 1986; Cortés-Ortiz et al. 2015) and areas of hybridization, in Tabasco, Mexico (Cortés-Ortiz et al. 2015).

Although expert knowledge has been recognized as an important source of information to delimit the geographic distribution of species, its use in ecological niche modeling has been limited because the judgment of experts is

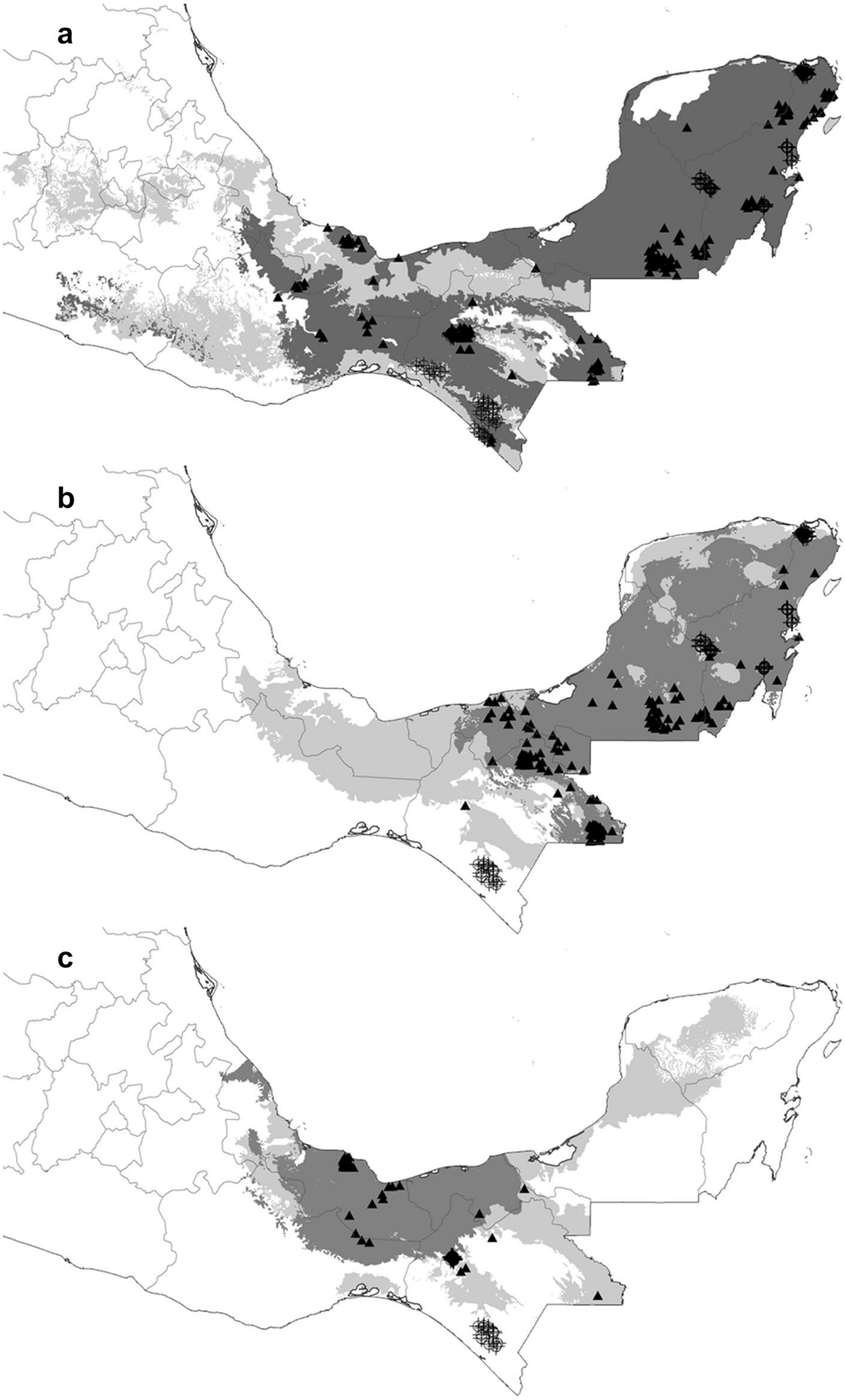

**Fig. 4** Realized distribution maps with and without incorporating expert knowledge of: **a** *Ateles geoffroyi*, **b** *Alouatta palliata mexicana*, **c** *Alouatta pigra.* Light gray realized distribution without expert knowledge. Dark gray realized distribution with expert knowledge. *Triangles* presences for validation. *Crosses circles* absences

susceptible to personal biases, preferences, beliefs, and experiences that reduce its reliability (Kuhnert 2011; McBride and Burgman 2012). To avoid these shortcomings, we designed a transparent and repeatable process. The inclusion of experts coming from different types of institutions offers more diversity of knowledge backgrounds and frameworks. The formation of two expert groups (core and consultant) provided a double independent verification of information. This double verification reduced the possibility of bias due to motivational reasons or the particular context of experts (McBride and Burgman 2012). In addition, experts focused their participation in reviewing the results

**Table 4** Results of validation metrics for potential distribution models with and without expert knowledge

| | *Ateles geoffroyi* | | *Alouatta palliata mexicana* | | *Alouatta pigra* | |
|---|---|---|---|---|---|---|
| | Without expert knowledge | With expert knowledge | Without expert knowledge | With expert knowledge | Without expert knowledge | With expert knowledge |
| Sensitivity | 0.983 | 0.9444 | 0.965 | 0.871 | 0.995 | 0.942 |
| Specificity | 0.789 | 0.844 | 0.886 | 0.97 | 0.857 | 0.931 |
| True skills statistics | 0.772 | 0.788 | 0.852 | 0.840 | 0.852 | 0.873 |
| Kappa | 0.547 | 0.612 | 0.703 | 0.832 | 0.663 | 0.784 |

**Table 5** Results of validation metrics for realized distribution models with and without expert knowledge

| | *Ateles geoffroyi* | | *Alouatta palliata mexicana* | | *Alouatta pigra* | |
|---|---|---|---|---|---|---|
| | Without expert knowledge | With expert knowledge | Without expert knowledge | With expert knowledge | Without expert knowledge | With expert knowledge |
| Sensitivity | 0.958 | 0.937 | 1 | 0.847 | 0.947 | 0.942 |
| Specificity | 0.861 | 0.902 | 0.946 | 0.981 | 0.891 | 0.933 |
| True skills statistics | 0.82 | 0.839 | 0.946 | 0.828 | 0.838 | 0.875 |
| Kappa | 0.622 | 0.702 | 0.854 | 0.848 | 0.700 | 0.788 |

**Table 6** Percentage of true absences used for validation correctly predicted by potential and realized distribution models

| | *Ateles geoffroyi* | | *Alouatta palliata mexicana* | | *Alouatta pigra* | |
|---|---|---|---|---|---|---|
| | Without expert knowledge | With expert knowledge | Without expert knowledge | With expert knowledge | Without expert knowledge | With expert knowledge |
| Potential distribution | 0.55 | 3.31 | 100 | 100 | 16.90 | 59.16 |
| Realized distribution | 0.55 | 6.63 | 100 | 100 | 25.35 | 60.56 |

of the geographical regions from which they had experience, increasing the reliability of their judgments (Johnson et al. 2012). Here, we implemented an iterative process to include experts in three stages of the modeling process (Fig. 1); nevertheless, participation of experts could be different depending on the goals of the study. While for any study the inclusion of experts for building and cleaning occurrence datasets is crucial, in analyses aimed at identifying potential distribution areas (e.g., invasive species), the inclusion of experts may help guiding the selection of the environmental variables used in the modeling process, rather than delimiting realized distributions.

In our study, we used variables to model species' distributions that represent annual trends, seasonality, and extreme values of climatic factors that influence the distribution of species at broad scales. Some studies have integrated other factors that influence the distribution of species at finer scales or at the landscape level, for example land cover (Ramos-Fernandez et al. 2013) and human pressure (Junker et al. 2012). However, in order to include this type of dynamic information in the modeling process, it is necessary that the environmental data coincide with collection dates to avoid misleading relationships between the species' presence and environmental conditions. In our case, it was not possible to incorporate this information in the modeling process because we did not have collection dates for many of the occurrence records used; and for those that we did have, dates spanned for several decades and land cover has been so dynamic and uneven in the southern regions of Mexico (Turner II et al. 2001) that it was not possible to associate our primate records to a distinct vegetation stage.

We conclude that the explicit incorporation of expert knowledge may play an important role in niche/distribution modeling, particularly when the aim is to produce maps that approach the realized distribution of species. Access to high-quality public occurrence records of species is also crucial for building reliable ENMs. As illustrated by our study, experts can contribute in all stages of the modeling process:

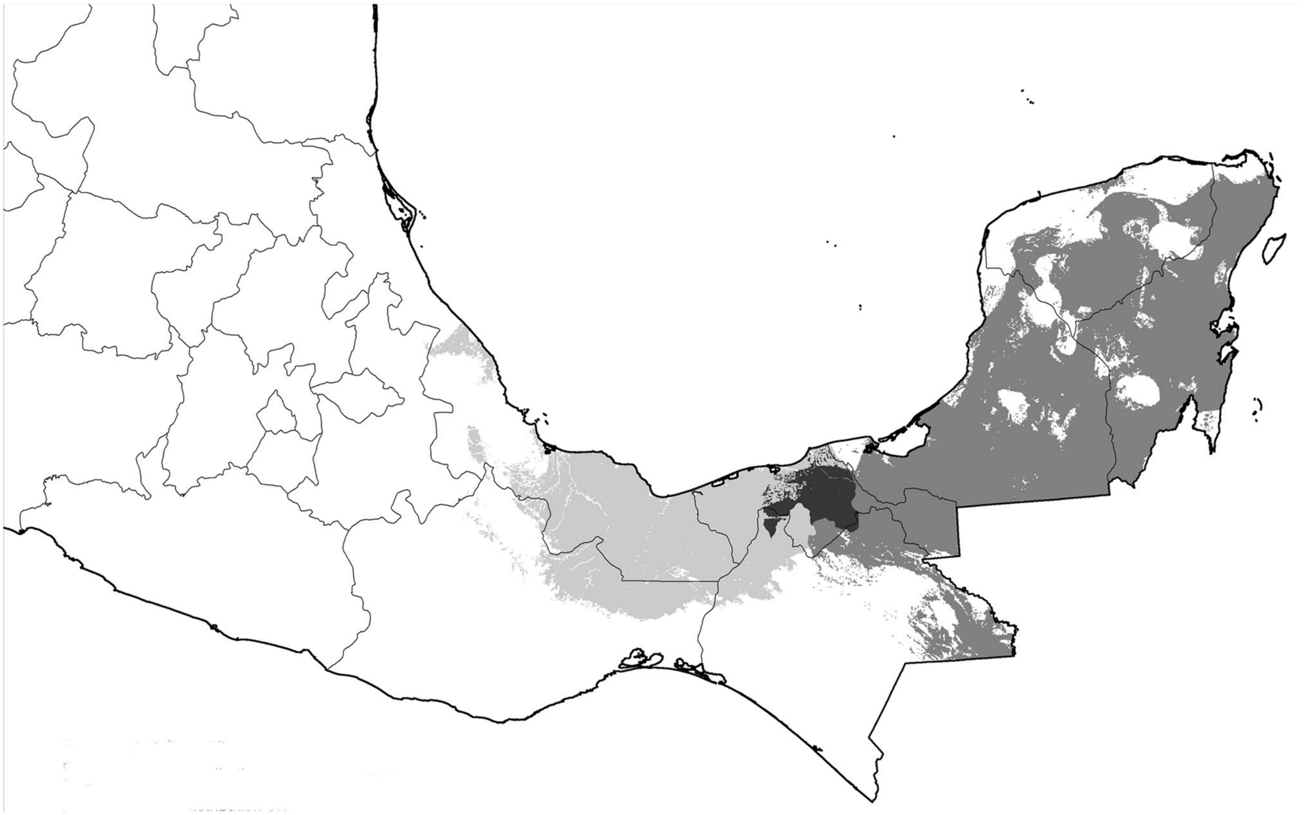

**Fig. 5** Contact zone (black area) for *Alouatta palliata mexicana* (dark gray) and *Alouatta pigra* (light gray) estimated with expert knowledge

reviewing data to providing reliable taxonomic identification and precise georeferencing; advising on critical environmental variables; providing ecological and historical information that is not explicitly included in ordinary modeling exercises; post-processing and validation of models. Finally, we recommend that expert knowledge is included in niche/distribution modeling in a systematic and rigorous fashion to reduce individual biases and perceptions.

**Acknowledgements** We are grateful to the 46 primatologists who participated in the elicitation process and shared their knowledge with us (Appendix 1). The elicitation workshop was funded by the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad and the Comisión Nacional de Áreas Naturales Protegidas, México. Sergio Díaz-Martínez provided support for the edition of images and helpful comments on earlier versions of this paper. GRF thanks the Instituto Politécnico Nacional and CONACYT (grant 157656). GPM thanks the colleagues of COBIUS A.C., the regional citizens who participated in the monitoring sessions and the directors of the natural protected areas: Selva El Ocote, Sepultura, Encrucijada, Sian Kaan, Yum Balam, Balam Kaax, UayMil, Cañón de Sumidero, Laguna de Términos, and Pantanos de Centla, from CONANP, for their sponsorship by the PROMOBI y PROCER 2013-2016 programs. ECP thanks the Posgrado en Ciencias Biológicas (PCB) at the Universidad Nacional Autónoma de México for logistic and academic support. This paper is part of the requirements for the PhD in Sciences at the PCB-UNAM. ECP was supported by a graduate scholarship from the Consejo Nacional de Ciencia y Tecnología, Mexico.

## Appendix 1. List of 19 bioclimatic variables used into the modeling

BIO1 = annual mean temperature
BIO2 = mean diurnal range (mean of monthly (max temp–min temp))
BIO3 = isothermality (BIO2/BIO7) (*100)
BIO4 = temperature seasonality (standard deviation *100)
BIO5 = max temperature of warmest month
BIO6 = min temperature of coldest month
BIO7 = temperature annual range (BIO5–BIO6)
BIO8 = mean temperature of wettest quarter
BIO9 = mean temperature of driest quarter
BIO10 = mean temperature of warmest quarter
BIO11 = mean temperature of coldest quarter
BIO12 = annual precipitation
BIO13 = precipitation of wettest month
BIO14 = precipitation of driest month
BIO15 = precipitation seasonality (coefficient of variation)
BIO16 = precipitation of wettest quarter
BIO17 = precipitation of driest quarter
BIO18 = precipitation of warmest quarter
BIO19 = precipitation of coldest quarter

## Appendix 2. Maxent default parameters

| | |
|---|---|
| Max number of background points | 10,000 |
| Maximum iterations | 500 |
| Convergence threshold | 0.00001 |
| Convergence threshold | 0.00001 |
| Default prevalence | 0.5 |

## Appendix 3. List of experts who participated in the elicitation process

| Name | Institution | Group of participation | Assistance to workshop | Participation in the electronic survey |
|---|---|---|---|---|
| Gabriel Ramos Fernández | President of the Mexican Association of Primatology | Core group | X | X |
| Pedro Américo Duarte Dias | Instituto de Neuroetología, Universidad Veracruzana | Core group | X | X |
| Mónica Améndola Pimenta | Mexican Association of Primatology | Core group | X | X |
| Ariadna Rangel Negrín | Barcelona University | Core group | X | X |
| Víctor Arroyo Rodríguez | Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México | Core group | X | |
| Celene Espadas Manrique | Centro de Investigación Científica de Yucatán, A.C. | Consulting group | | X |
| Francisca Vidal | Instituto de Ecología A.C | Consulting group | | X |
| Juan Carlos Serio Silva | Instituto de Ecología A.C. | Consulting group | | X |
| Jurgi Cristóbal | Centro de Investigaciones Tropicales, Universidad Veracruzana | Consulting group | | X |
| Teresita de Jesús Ortiz Martínez | Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, Unidad Oaxaca. | Consulting group | X | X |
| Magali Bonilla | Instituto de Neuroetología, Universidad Veracruzana | Consulting group | X | X |
| Miguel Angel Gómez Gómez | Reserva de la Biosfera “Pantanos de Centla.” Comisión Nacional de Áreas Naturales Protegidas | Consulting group | X | |
| Patricia Oropeza Hernández | Comisión Nacional de Áreas Naturales Protegidas | Consulting group | X | |
| Griselda Pérez Sarabia | Procuraduría Federal de Protección al Ambiente | Consulting group | X | |
| Carlos Mario Burelos Jiménez | Chief of the Wildlife Department, Secretaría del Medio Ambiente y Recursos Naturales. | Consulting group | X | |
| Gilberto Pozo Montuy | Instituto de Neuroetología, Universidad Veracruzana | Consulting group | X | X |
| Fernando Winzig León | Secretaría del Medio Ambiente y Recursos Naturales. | Consulting group | X | |

| Name | Institution | Group of participation | Assistance to workshop | Participation in the electronic survey |
|---|---|---|---|---|
| Rosalía Pastor Nieto | Dirección General de Zoológicos de la Ciudad de México. | Consulting group | X | |
| Víctor Manuel O. Torres | Wildlife Department, Secretaría del Medio Ambiente y Recursos Naturales. | Consulting group | X | |
| Jose O. Molina | Centro de Estudios de Políticas Públicas y Desarrollo Sustentable, A.C. | Consulting group | X | |
| Rogelio Manríquez Martínez | Comisión Nacional de Áreas Naturales Protegidas | Consulting group | X | |
| Irma de J. Serrano Sánchez | Parque Nacional Cañón del Sumidero, Comisión Nacional de Áreas Naturales Protegidas | Consulting group | X | |
| Luis Arturo Álvarez Márquez | Comisión Nacional de Áreas Naturales Protegidas | Consulting group | X | |
| Patricia G. Robles Zenteno | Comisión Nacional de Áreas Naturales Protegidas | Consulting group | X | |
| Eduardo Rendón Hernández | Comisión Nacional de Áreas Naturales Protegidas | Consulting group | X | |
| Guillermo Islas Dondé | Facultad de Ciencias, Universidad Nacional Autónoma de México | Consulting group | X | |
| Juan Carlos Sánchez Olmos | Conservación Sin Fronteras | Consulting group | X | |
| Fernando Miranda Martínez | Conservación Sin Fronteras | Consulting group | X | |
| Cristina Domingo Balcells | Instituto de Biología, Universidad Nacional Autónoma de México | Consulting group | X | |
| Arturo Ramírez Ortiz | Conservación Sin Fronteras | Consulting group | X | |
| Sandra Flores Hernández | Área de Protección de Flora y Fauna “Otoch Ma’ax Yetel Kooh” | Consulting group | X | |
| Juan Manuel Cornelio Pérez | Secretaría del Medio Ambiente y Recursos Naturales. | Consulting group | X | |
| Rosa Olivia Rodríguez Reyes | Reserva de la Biosfera “Pantanos de Centla,” Comisión Nacional de Áreas Naturales Protegidas | Consulting group | X | |
| Katya Andrade Escobar | Comisión Nacional de Áreas Naturales Protegidas | Consulting group | X | |
| Carlos A. Guichard Romero | Reserva de la Biosfera “El Triunfo,” Comisión Nacional de Áreas Naturales Protegidas | Consulting group | X | |
| Francisco García Orduña | Instituto de Neuroetología, Universidad Veracruzana | Consulting group | X | |
| Alfredo Cuarón Orozco | Multicriteria S.C. | Consulting group | X | |

| Name | Institution | Group of participation | Assistance to workshop | Participation in the electronic survey |
|---|---|---|---|---|
| Eduardo García Frapolli | Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México | Consulting group | X | |
| Ernesto Rodríguez Luna | Universidad Veracruzana | Consulting group | X | |
| Armando Figueroa | Procuraduría Federal de Protección al Ambiente | Consulting group | X | |
| Francisco García Contreras | Procuraduría Federal de Protección al Ambiente | Consulting group | X | |
| Tamara Ortiz Ávila | Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México | Consulting group | X | |
| Mateo Pérez Ortiz | Conservación Sin Fronteras | Consulting group | X | |
| Diana Platas Neri | Instituto de Investigaciones Antropológicas, Universidad Nacional Autónoma de México | Consulting group | X | |
| Jorge Luis Cruz Rueda de León | Unidad de Manejo de Fauna Silvestre "Nueva Era de la Chontalpa" | Consulting group | X | |
| Bárbara Ayala Orozco | Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México | Consulting group | X | |

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