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Potential distribution of hybrids between *Crocodylus acutus* and *Crocodylus moreletii* on the Mexican Pacific coast outside the natural hybridisation zone

Gerardo J. Soria-Ortiz[1*], Patricia G. García-Navarrete[2], Leticia M. Ochoa-Ochoa[2] & Armando Rincón-Gutiérrez[3]

[1]Instituto de Ecología, Universidad Nacional Autónoma de México, Circuito exterior s/n anexo al Jardín Botánico, C.P. 04500, Ciudad de México, México

[2]Museo de Zoología, Departamento de Biología Evolutiva Facultad de Ciencias, Universidad Nacional Autónoma de México, Circuito exterior s/n, C.P. 04510, Ciudad de México, México

[3]Instituto de Biología, Universidad Nacional Autónoma de México, Tercer circuito s/n, Ciudad Universitaria, Alcaldía Coyoacán, 04510 México City, México

In Mexico, *Crocodylus acutus* is widely distributed along the Pacific coast, while *C. moreletii* occurs on the Gulf of Mexico. Both species converge in the Yucatán peninsula where natural hybridisation is reported, and later it was also reported in the Gulf of Mexico. Unfortunately, due to translocations and stochastic events, currently there are hybrids of both species on the coast of Oaxaca and Guerrero. In this study, we evaluated the potential colonisation areas of the hybrids on the Pacific coast through ecological niche analyses. The results indicate that the hybrid crocodiles and the parent species share preferences in at least three climatic variables: average temperature range, isothermality, and minimum temperature of the coldest month. Furthermore, it was found that the climatic niche of the hybrids is more similar to that of the *C. moreletii* leaving reminiscent areas for *C. moreletii* in Nuevo León, San Luis Potosí and small areas far from the coast in Veracruz, coinciding with what was previously reported by molecular analysis. On the other hand, the climatic niche of the hybrid crocodiles is also sufficiently similar to that of *C. acutus*, having the possibility to colonise the Pacific coast extensively, leaving reminiscent small areas for *C. acutus* on the northern coast of Sinaloa, southern of Sonora, central coast of Oaxaca and small inland areas of the Pacific coast.

Keywords: Crocodilians, ecological niche, hybrids, species model distributions, conservation, Mexico

INTRODUCTION

American crocodile *Crocodylus acutus* and Morelet's crocodile *C. moreletii* belong to the Crocodylidae family, both are included in the Official Mexican Standard (SEMARNAT, 2010) which aims to identify the species or populations of wild flora and fauna at risk in the Mexican Republic; under the category of Special Protection (Pr) and have a wide distribution in Mexico. In Mexico, the first one is distributed along the Pacific coast, from Sinaloa to Chiapas, reaching the coast of Quintana Roo and Yucatán (Thorbjarnarson, 2010), while *C. moreletii* occurs throughout the entire Gulf of Mexico coast, from Tamaulipas to Quintana Roo (Platt et al., 2010). Both species are highly dependent on water bodies; *C. acutus* prefers brackish water and *C. moreletii* prefers fresh water (Álvarez del Toro, 1974; Hekkala et al., 2015).

The natural zone of contact and hybridisation between *C. acutus* and *C. moreletii* in Mexico is found along the coast of Yucatán, Quintana Roo and Campeche (Cedeño-Vázquez et al., 2008; Escobedo-Galván & González-Salazar, 2011; Pacheco-Sierra et al., 2016; Pacheco-Sierra et al., 2018). It is suggested that this hybridisation zone began 2 to 3 million years ago (Pacheco-Sierra et al., 2018) and

currently hybrids have been able to colonise other areas beyond the natural contact zone, throughout the Gulf of Mexico, up to Tamaulipas (Pacheco-Sierra et al., 2016).

Regarding the presence of hybrid crocodiles on the Pacific coast, in the 1970s an unknown number of individuals with hybrid descent were translocated from the Yucatán area to the Chacahua crocodile farm within the Lagunas de Chacahua National Park (Parque Nacional Lagunas de Chacahua; PNLCH) (Soria-Ortiz, 2019). Several crocodiles from the farm escaped to the adjacent lagoons of the PNLCH and interbred with the native *C. acutus*, which has resulted in a set of hybrids in the PNLCH. Currently, the PNLCH is a focal point of hybridisation on the Pacific coast, with hybrids having even been reported outside the PNLCH in relatively near lagoons (~ 10 km away, Soria-Ortiz, 2019). It was reported that at least two hybrids are housed in Playa Linda at Ixtapa Zihuatanejo, Guerrero (Pacheco-Sierra et al., 2018). That hybrids exist in the PNLCH and wider Pacific coast poses a threat that the native species, *C. acutus*, will be displaced by hybrids, similar to what happened in the Gulf of Mexico with *C. moreletii* (Pacheco-Sierra et al., 2016).

Ecological niche studies used to determine the limiting environmental variables of a species are essential to

know the geographic space that species may occupy. Also, they allow us to estimate areas with high environmental suitability outside the natural range of the species and to project them geographically in areas where it is not distributed, to explore the potential invasion that a species might have (Peterson & Vieglais, 2001). Predicting and understanding the potential invasion processes of a species, combined with ecological niche models of native species, is fundamental for management and making effective conservation plans (Gallien et al., 2010).

In this article we aim to evaluate the risk of displacement that the species *C. acutus* may suffer due to the presence of hybrid crocodiles on the Pacific coast of Mexico, for which we intended to: i) estimate the ecological niche (only the climatic part) of *C. acutus*, *C. moreletii* and the hybrids between both species in Mexico, ii) to compare the climatic space of *C. acutus*, *C. moreletii* and hybrids, and finally, iii) identify the remaining distribution areas of *C. acutus* by evaluating the colonisation potential of hybrid crocodiles on the coast of the Pacific Ocean.

MATERIALS & METHODS

Obtaining and cleaning the primary data

Presence records of *C. acutus* and *C. moreletii* were obtained from SNIB (Sistema Nacional de Información sobre Biodiversidad), CONABIO (http://www.snib.mx/), GBIF (Global Biodiversity Information Facility, http://www.gbif.org) databases, and the iNaturalista platform (http://www.naturalista.mx). Presence records were restricted to Mexico, with dates from the decade 1970 to 2019, because in previous years the identification of these particular species was not adequate, and the records do not agree with their known distribution; fossil records and records outside the known range of these species were discarded. Finally, records of captures of both species were obtained from Pacheco-Sierra et al. (2016; 2018) and records of hybrid crocodiles from collection points reported by Pacheco-Sierra et al. (2016; 2018) and Soria-Ortiz (2019) where used. Records were cleaned by eliminating duplicates, and only one point per pixel (~1 km²) was kept. The records of hybrids were compared with those of the parental species and, in the event of a duplicate record between the two, we kept only the hybrid record. Finally, in the case of records located outside the environmental layers (e.g. the sea), they were moved to the closest environmental pixel to avoid information loss.

Study area and climatic variables

We used 19 climatic variables in ASCII format at a resolution of 1 km² developed by Cuervo-Robayo et al. (2014), which include information from the entire 20th century and the first decade of the 21st century, and the layers are also restricted to Mexico and southern United States of America. The climatic layers were trimmed based on the selection of the accessible area "M" (Peterson et al., 2011); that is, those areas where each species is or could be given the biological knowledge, its dispersal capacities, large barriers or environmental discontinuities that limit their establishment (Martínez-Méndez et al., 2016). The

area "M" was determined independently for *C. acutus*, *C. moreletii* and hybrids. The herpetofaunal provinces of Mexico was taken as a basis (Casas-Andreu & Reyna-Trujillo, 1990), these coincide with the main mountain ranges in which it is known that there will hardly be any crocodile species. For *C. moreletii*, the provinces of Petén, Tamaulipeca, Yucateca, and Veracruzana were used; for the area "M" of *C. acutus* the provinces used were Petén, Yucateca, Veracruzana, Mexicana del Oeste and Desierto de Colorado-Sonora; and for the hybrids the provinces of Petén, Tamaulipeca, Yucateca, Veracruzana and Mexicana del Oeste (see Fig. S1 and Table S1 in Appendix I).

To avoid overfitting in the niche models, the number of environmental variables used for each parental species and hybrids was reduced. Test runs were carried out with the MaxEntsoftware version 3.4.1 (Phillips et al., 2006) using the 19 climatic variables within the "M" used for each species. From the table of values of contribution to the model and individual importance of each climatic variable, those variables that in sum contributed at least 80 % of the variance of the model and the variables that alone contributed 10 % of permutation were selected. Additionally, a correlation analysis was carried out with the values from the 19 environmental variables that the locality records have. We eliminated one of the variables that presented collinearity, giving preference to the variable that could be more biologically relevant (r > 0.8). With the final selected variables, a final model was performed for each parental species and hybrid crocodiles.

Determination of the niche volume

From the selection of variables for each species, three environmental variables that coincided between *C. acutus*, *C. moreletii* and hybrids were chosen, in addition to analysing the 19 variables together. A principal component analysis (PCA) was performed for both sets of variables to identify the volume of the niche occupied by each of the parental species and the hybrids. Subsequently, a multivariate non-parametric analysis of variance (MANOVA) was performed to identify if there was a significant difference between the climatic niche for each species. Paired t tests were performed for each environmental variable to identify the variables that differ between *C. acutus*, *C. moreletii* and the hybrids. To compare the climatic niche of each species, box and whisker plots were made, and the distribution was observed as the relationships between the set of variables shared by the two crocodile parental species and the hybrids. The results were presented in a table containing minimum and maximum values, averages and standard deviation.

To quantify niche overlap of *C. acutus*, *C. moreletii* and hybrids, we calculated the average pairwise Czekanowski niche overlap. This metric is bounded between zero and one, with zero indicating no overlap, and one indicating complete overlap between all species pairs; to test the significance we compared the observed overlap vs the mean of simulate index. If the simulated index is higher than observed there is niche difference. Results were

considered significant if they were < 0.05. All analyses were performed in R 3.6.2 using ade4, vegan, stats, MNOVA.RM, and EcoSimR packages (Stéphane et al., 2020; Oksanen et al., 2017; R Core Team, 2013; Friedrich et al., 2019; Gotelli et al., 2015).

Distribution ranges overlap

From the suitability models resulting from *C. moreletii*, *C. acutus* and hybrids, binary presence-absence maps were generated using two threshold values, one was 0 % omission (strict scenario) of the test records (minimum training presence), and the second in which 10 % of omission (relaxed scenario) of the test records was allowed (10th percentile). To estimate the remaining geographic areas that *C. acutus* could occupy on the Pacific coast, the distribution model of *C. acutus* was compared, projecting the potential distribution of hybrids in the geographic space of the province Mexicana del Oeste and Desiertode Colorado-Sonora along the Pacific coast. To compare this result, the same procedure was performed with *C. moreletii* and the hybrids in the Gulf of Mexico, hoping that the reminiscent areas of *C. moreletii* distribution would coincide with the non-hybrid and isolated populations determined by Pacheco-Sierra et al. (2016; 2018).

RESULTS

The species more represented was *C. moreletii* (2,362 records) while *C. acutus* and the hybrids presented a similar number of records (285 and 277, respectively). In the case of hybrids, information was only taken from literature since these were records genetically validated (Table S2 in Appendix I). For each species and hybrids, eight important climatic variables were identified, of which three coincide: average temperature interval (Bio2), isothermality (Bio3) and minimum temperature of the coldest month (Bio6) (Table 1). For the niche volume analyses, 231 environmental values were used for *C. acutus*, 584 for *C. moreletii*, and 219 for hybrid crocodiles.

Niche volume

We found that the climatic niche volumes, determined as the climatic environmental spaces for hybrids and *C. moreletii* are very similar, unlike the climatic niche volume occupied by *C. acutus*. PCA with 19 climatic variables and three shared variables, respectively, show that the polygons that include 95 % of the climatic data between hybrids and *C. moreletii* widely overlap, while the ellipse for *C. acutus* shifts from the trainers (Figs. 1 & 2). The relationships between the shared climatic variables show the same observed pattern as in the PCAs, in which *C. acutus* differs from both hybrids and *C. moreletii* (Fig. 3). It can also be observed that the distribution of the mean diurnal range (Bio2) is extremely similar between *C. moreletii* and hybrids, while the distribution of the values for *C. acutus* is different (Table S3 in Appendix I). Likewise, the variation of the minimum temperature of the coldest month (Bio6) in *C. acutus* is greater compared to the restricted variation presented by *C. moreletii* and

Table 1. Climate variables selected for each species of crocodile and hybrids. Shared variables (among the three groups) are shown in bold.

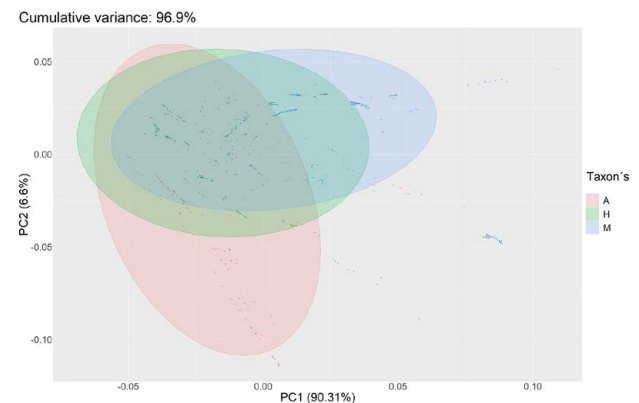| *C. acutus*	*C. moreletii*	Hybrids
Bio2	**Bio2**	**Bio2**
Bio3	**Bio3**	**Bio3**
Bio5	Bio5	Bio4
Bio6	**Bio6**	**Bio6**
Bio10	Bio7	Bio7
Bio13	Bio9	Bio13
Bio14	Bio18	Bio14
Bio15	Bio19	Bio18

Figure 1. Principal Component Analysis (PCA) using all 19 climatic variables. In blue the variables for *C. moreletii* **(M)** are shown, in red the variables for *C. acutus* **(A)**, and in green the variables for the hybrid crocodiles **(H)**.
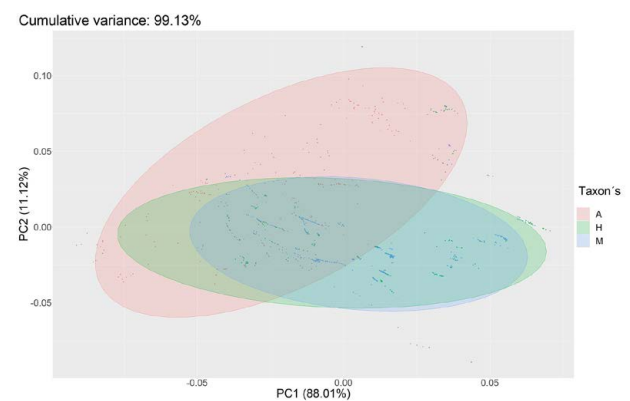

Figure 2. Principal Component Analysis (PCA) using shared climatic variables. Annual Mean Diurnal Range (Bio2), Isothermality (Bio3) and Min Temperature of Coldest Month (Bio6). In blue the variables for *C. moreletii* **(M)** are shown, in red the variables for *C. acutus* **(A)** and in green the variables for hybrid crocodiles **(H)**.

hybrids (Fig. 3).

One of the crocodilian groups analysed was found to be different statistically (MANOVA, F = 60.411, gl = 2, p = 0.0001) and the paired comparisons between the shared environmental variables (Bio2, Bio3, Bio6) shows that *C. acutus* is the one which differs from both *C. moreletii* and hybrids (Table 2). In all niche overlap comparisons between *C. acutus* x hybrids, *C. acutus* x *C. moreletii* and *C. moreletii* x hybrids, the observed index (Oi) was always higher than expected under the random model (simulated index, Si) (Oi = 0.8512 vs Si = 0.2979; Oi = 0.8684 vs Si = 0.2979; Oi = 0.8957 vs Si = 0.2977, respectively, p < 0.05), which means that their environmental niche overlap in all cases is larger than expected under a null hypothesis scenario (p < 0.05, Fig. S2 in Appendix I). We can also observe that there is more niche overlap between *C. moreletii* and hybrids than between *C. acutus* and hybrids.

In the box-and-whisker plot (Fig. 4) the differences between the values of the shared climatic variables are represented; in which it can be observed that *C. acutus* differs considerably from *C. moreletii* in Bio2 and Bio6, while in Bio3 it can be observed that the hybrids present intermediate values between the parental species. In general, *C. acutus* differs from *C. moreletii* and hybrids mainly in the precipitation variables, particularly at the lowest values (Bio12–Bio14, Bio16–Bio19), except for Bio15 (seasonality of precipitation) which presents the highest value (Table S3 & Fig. S3 in Appendix I). In summary, regarding the climatic variables of temperature, the hybrids have a similar pattern to that of *C. moreletii*, while, in the precipitation variables, the hybrids show an intermediate pattern between the two parental species (Fig. 4, Table S3 & Fig. S3 in Appendix I).

Geographical space

The modelled distribution of *C. acutus* is mostly restricted to the Pacific coast, from southern Sonora to Chiapas (Fig. 5, in red). In the Yucatán peninsula the modelled distribution is greater inland than the known distribution, however, on the coast the suitability values are higher (Fig. S4 in Appendix I); also in Tabasco and Veracruz there are suitable climatic values for its presence. The modelled distribution of *C. moreletii* coincides with the known distribution, which goes from Tamaulipas to Quintana Roo on the Atlantic coast of Mexico (Fig. 5, in blue). Likewise, it can also be observed that there are suitable climatic conditions in the coastal plains of the Gulf of Mexico, without being so restricted to the coastal zone (Fig. S5 in Appendix I). The hybrid crocodiles have a modelled distribution in the Gulf of Mexico and Mexican Caribbean that is somewhat more restricted to the coast (Fig. 5, in green), but with greater climatic suitability. Moreover, it can be observed that the modelled distribution of hybrids on the Pacific coast is limited to the coast, ranging from Sinaloa to Chiapas (Fig. S6 in Appendix I).

The suitable zones for *C. acutus*, due to the possible potential distribution of the hybrid crocodiles on the Pacific and Atlantic coasts of Mexico, in the strict scenario (0 % omission) are the southern area of the Sonora and the northern of Sinaloa, central Oaxaca and inland areas

Table 2. Result of multivariate variance analysis (MANOVA) and t-paired tests between climatic variables: Annual Mean Diurnal Range (Bio2), Isothermality (Bio3) and Min Temperature of Coldest Month (Bio6). At *** significant p-values between comparisons.

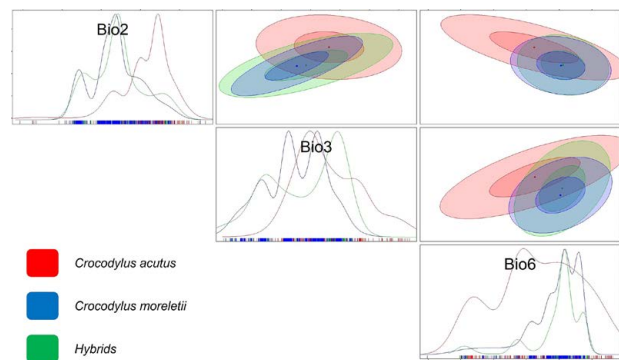| MANOVA (19 Bios)	F = 60.411	P < 0.0001***
	C. moreletii	*C. acutus*
C. acutus	Bio2 - 0.0001*** Bio3 - 0.0001*** Bio6 - 0.0001***	
Hybrids	Bio2 - 1 Bio3 - 0.66 Bio6 - 1	Bio2 - 0.0001*** Bio3 - 0.0001*** Bio6 - 0.0001***

Figure 3. Matrix of relationship between shared climatic variables: Annual Mean Diurnal Range (Bio2), Isothermality (Bio3), and Min Temperature of Coldest Month (Bio6). The diagonal shows the distribution of each climatic variable, while above the diagonal the relationship between them is shown.

far from the Pacific coast (Fig. 6A). While in the case of *C. moreletii* it is evident that the only suitable areas would be found between Nuevo León, San Luis Potosí, and small inland areas far from the coast in Veracruz, Chiapas, and Quintana Roo (Fig. 6B).

DISCUSSION

Niche volume

At first glance it can be observed that the climatic niche or climatic space occupied by *C. acutus* is different from that occupied by *C. moreletii* and hybrid crocodiles (Figs. 1 & 2). This may point to two possibilities: 1) that the climatic conditions on the Pacific coast, and the Gulf of Mexico and Mexican Caribbean may be different or 2) that in geographic spaces occupied by *C. acutus* on the Pacific coast, where *C. moreletii* is absent, and vice versa on the coast of the Gulf of Mexico where *C. moreletii* occurs but *C. acutus* is absent (Thorbjarnarson, 2010; Platt et al., 2010). In this sense, *C. acutus* occupies an important extension
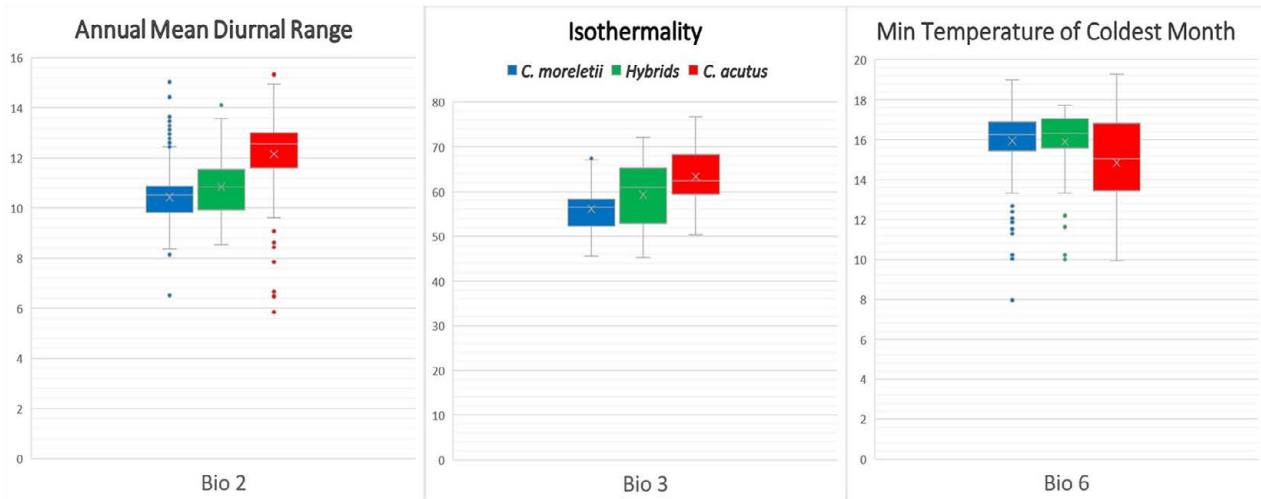
Figure 4. Box-and-whisker graphs between shared climatic variables: Annual Mean Diurnal Range (Bio2), Isothermality (Bio3), and Min Temperature of Coldest Month (Bio6).
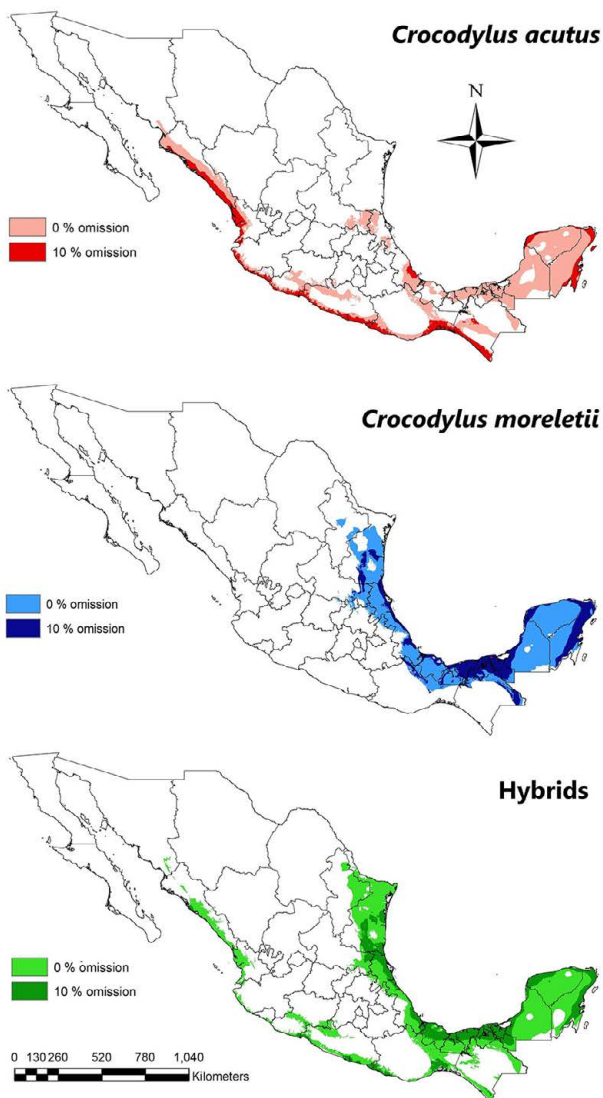

Figure 5. Modelled distribution areas of *C. acutus* (red), *C. moreletii* (blue), and hybrid crocodiles (green), with two threshold values, 0 % omission (clear tonality) and 10 % record omission (darker tonality).

of the environmental-geographical space throughout the Pacific coast that it does not share with hybrids or with *C. moreletii*, which suggests that *C. acutus* could have a distinctive evolutionary and ecological imprint, such as it has been seen with other species (Martínez-Méndez et al., 2016). However, it is necessary to carry out analysis from a perspective of conservatism or divergence of climatic niche and combine them with phylogeographic analyses. Luna-Aranguré et al. (2020) analysed the *Ursus* genus and found that the most derived branches of each species coincided with the extreme environmental values, and that although there were species with great environmental space overlap, they occupy different geographical spaces.

According to what we obtained, the shared geographic space is mainly concentrated in the Yucatán Peninsula (Escobedo-Galván & Gonzales-Salazar, 2011; Sánchez-Méndez, 2016), where there is a presence of the three studied groups (Pacheco-Sierra et al., 2016). According to Pacheco-Sierra et al. (2018), the first contact between *C. acutus* and *C. moreletii* was in the Yucatán Peninsula, and later hybridisation between these species occurred, hence, the climatic niche similarity between the three taxa studied is because they occupy the same geographical space in south-eastern Mexico (Figs. 1 & 2 and Figs. S4, S5 & S6 in Appendix I). Furthermore, it was found that the climatic niche between *C. moreletii* and hybrids is very similar as they shared similar geographic space, corroborated by the modelled distribution overlap (Fig.6). This is mainly due to the fact that the hybrids managed to move from the Yucatán Peninsula to the Gulf of Mexico (Pacheco-Sierra et al., 2018). In the PCA (Figs. 2 & 3) the environmental ellipse of the hybrids completely encompasses the environmental space used by *C. moreletii*, even the observed index overlap was the largest (Oi = 0.8957). Due to the similarity of the environmental niche, the hybrid taxon would have the possibility of occupying the entire geographic space of *C. moreletii*, leaving few geographic areas for the unique presence of *C. moreletii*, which coincides with the existing
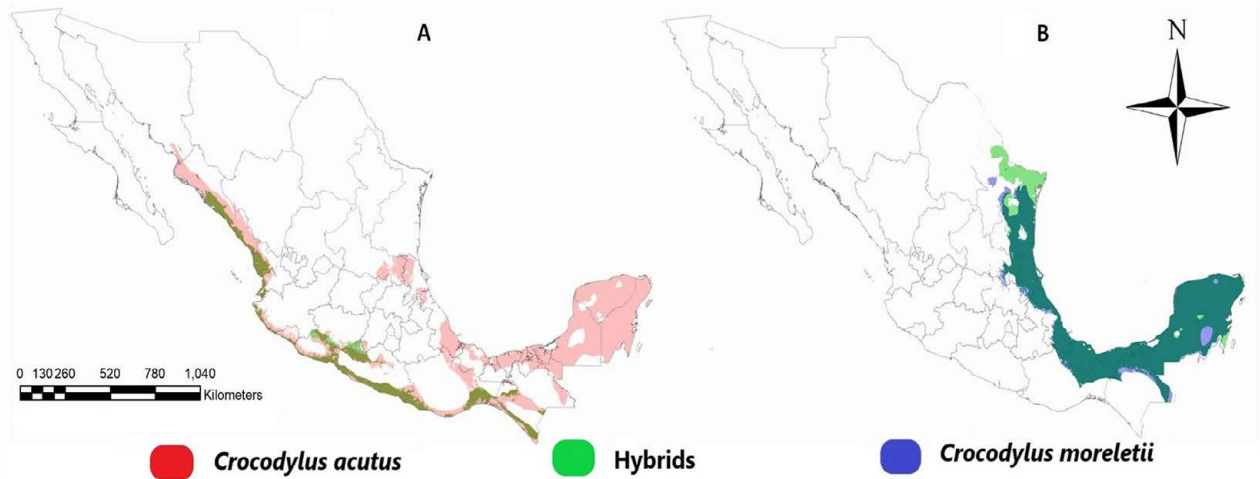
Figure 6. Reminiscent areas for *C. acutus* in the Pacific versant **(A)**, and for *C. moreletii* in the Gulf of Mexico and Mexican Caribbean **(B)**. Binary maps with 0 % omission.

pure populations of *C. moreletii* reported for the Gulf of Mexico (Pacheco-Sierra et al., 2016; 2018).

The similarity of the environmental niche used in the Yucatán Peninsula by the three crocodiles taxons may cause a competition for geographic space (see Figs. S4, S5 & S6 in Appendix I), which, in theory, is a problem ecologically, since species with similar niches cannot occupy the same geographic space due to competition (Hardin, 1960). Therefore, the consequence would be that one of the species will be displaced. In this case, due to our findings and those from previous works, it seems that hybrids are the taxon that has managed to displace the parental species. The evidence points out that although there could be competitive coexistence, hybrids have achieved a large presence in the Yucatán Peninsula, Mexico (Cedeño-Vázquez et al., 2008; Rodriguez et al., 2008; Pacheco-Sierra et al., 2016), displacing non-admixed *C. acutus* to the islands of Banco Chinchorro and Cozumel (MacHkour-M'Rabet et al., 2009; Pacheco-Sierra et al., 2016), and non-admixed *C. moreletii* to remote areas of the Gulf of Mexico (Pacheco-Sierra et al., 2016).

Species distribution models
The geographically projected models agree with the potential distribution of *C. acutus* and *C. moreletii*, which are widely known (Platt et al., 2010; Thorbjarnarson, 2010). Regarding the geographic projection of *C. acutus*, it can be observed that, in the northern zone of Veracruz in the Gulf of Mexico, there are suitable conditions for the presence of this species, as suggested by Escobedo-Galván & Gonzales-Salazar (2011). However, these areas are not continuous, so it can be assumed that the state of Veracruz has not the most adequate environmental suitability for *C. acutus*. It can also be observed that in the state of Tabasco and the Yucatán Peninsula there are areas with suitable conditions for the presence of this species; however, between Veracruz, Tabasco, and Campeche there are less than 10 records, which means that there are probably no established populations of *C. acutus* in that area. Without the presence of geographic barriers between Tabasco and

Veracruz, probably the main cause of the absence of *C. acutus* is due to competition of *C. moreletii* and the hybrids that exist in these areas (Escobedo-Galván & González-Salazar, 2011; Pacheco-Sierra et al., 2016). Hypothetically *C. acutus* would have the ability to move to these areas and gradually colonise them; however, there must first be some type of interaction with *C. moreletii* or a hybrid crocodile with great possibilities of hybridisation, causing the displacement of *C. acutus* to be ineffective. Thus, for *C. acutus* what may exist is a biological barrier to its movement through the Gulf of Mexico coast. Regarding the Pacific coast, the distribution of *C. acutus* is restricted to the coast, but it is wide and continuous from Chiapas to southern Sonora, with the northern coast of Sinaloa and southern Sonora being possible areas of invasion, since according to the locality records, there are only presence records of *C. acutus* up to the central coast of Sinaloa.

The modelled distribution of *C. moreletii* coincides with the known distribution for this species (Platt et al., 2010). The areas with high suitable conditions for the presence of *C. moreletii* are found from Tamaulipas to Quintana Roo, and these are not restricted to the coast, unlike what was found for *C. acutus* in the Pacific coast. This remoteness from the coastal zones may be due to the preferences of *C. moreletii* for "fresh" water bodies (Álvarez del Toro, 1974; Hekkala et al., 2015), allowing this species to invade inland areas (Fig. 5). Also, the topography in the Gulf of Mexico is very different from that of the Pacific coast. In the Gulf of Mexico, the slope is much lower and there is a huge plain between the coast and the Sierra Madre Oriental (27 km in the central zone of Veracruz to 200 km in Tamaulipas), whereas in the Sierra Madre del Sur there are certain accessible zones (126 km in Oaxaca), the Chiapas highlands and the entire Yucatán Peninsula, as accessible areas for *C. moreletii*.

The potential hybridisation zone had previously been reported using the ecological niche approach; however, this was restricted to the Yucatán Peninsula due to the hybrid records at that time (Escobedo-Galván & González-Salazar, 2011). In this work, the records of hybrids

(genetically identified) from all of Mexico were collected (Pacheco-Sierra et al., 2016; Soria-Ortiz, 2019) and a projection of the potential distribution of hybrids to all of Mexico was performed. According to our models, suitable environmental conditions were found for the hybrids to invade the coast of the Pacific Ocean, the Gulf of Mexico and the Yucatán Peninsula, even with the ability to cross the Isthmus of Tehuantepec unlike what is known found for *C. acutus* (Fig. 5). Based on the potential distribution of the hybrids, it is estimated that they could colonise sites from Sinaloa to Chiapas along the Pacific Ocean coast, with a discontinuity in central Oaxaca. In the Gulf of Mexico and the Yucatán Peninsula, it is observed that the hybrids present a distribution that practically reaching the border with the United States; therefore, like *C. moreletii*, they have capacity to invade the plain of the Gulf and the Yucatán Peninsula.

Considerations in conservation

There are only two antecedents focused on modelling the ecological niche of crocodiles in Mexico (Escobedo-Galván & Gonzales-Salazar, 2011; Sánchez-Méndez, 2016). Studies trying to identify the potential invasion that a species could have when it is mobilised to a new area using ecological niche modelling have been useful and effective in the implementation of conservation measures (Zambrano et al., 2006; Ramírez-Albores et al., 2016; Suárez-Mota et al., 2016). In Mexico, the situation is the following: hybrids from the Yucatán Peninsula and the Gulf of Mexico appeared due to natural contact between *C. acutus* and *C. moreletii* (Pacheco-Sierra et al., 2018). Nevertheless, hybridisation in the Pacific is a different story, if hybridisation had occurred naturally, it would be expected that the geographic hybridisation pattern would be clinal, from the Yucatán Peninsula to the Pacific coast, expecting to find a lower degree of hybridisation in areas further away from the Yucatán Peninsula, such as what happened in the Gulf of Mexico with *C. moreletii* (Pacheco-Sierra et al., 2016). However, it is known that hybridisation in the Pacific was caused by human-mediated movement of individuals from Yucatán to Oaxaca(Soria-Ortiz, 2019), and evidence of hybrid individuals in Guerrero of unknown origin, with two independent points of hybridisation in Guerrero and Oaxaca that are not continuous.

Thanks to the species distribution model for hybrids in the Pacific versant, it can be observed that there are suitable environmental conditions for hybrids to invade and colonise practically the entire Pacific coast, except for the northern Sinaloa and part of central Oaxaca, these being the only reminiscent areas for *C. acutus* (Fig. 6). In the case of *C. acutus* it is related to marine or estuarine areas (Taplin et al., 1982; Thorbjarnarson, 2010) and when competing or being displaced by hybrids it could have ecological consequences due to the need to adapt to new environments, and that might not necessarily happen. It has been reported that hybrids have managed to have an important presence in the PNLCH in the wild in a short time (Serrano-Gómez et al., 2016; Soria-Ortiz, 2019), that hybrids may have a greater suitable space

(climatic niche volume) than parental species (Hekkala et al., 2015), and that hybridisation in the Yucatán Peninsula resulted in the only populations of pure *C. acutus* being isolated on the islands of Banco Chinchorro and Cozumel (MacHkour-M'Rabet et al., 2009). Furthermore, in the Gulf of Mexico, hybrids displaced *C. moreletii* to small isolated populations of pure lineages in Tabasco and San Luis Potosí (Pacheco-Sierra et al., 2016).

The aforementioned (in the absence of more ecological studies, reproduction, mobility, connectivity, among others),points to that *C. acutus* may be displaced by hybrids soon, promoting that isolated *C. acutus* populations may remain. Thus, it is essential that the potential invasion of hybrids on the Pacific coast - where *C. acutus* would be affected - is not taken lightly and preventive actions should be implemented.One option could be the containment and extraction of hybrid crocodiles in Oaxaca (PNLCH) and Guerrero (Ixtapa Zihuatanejo, in the absence of extensive local analysis) where hybrids are already known to be found in the wild. Design policies to reduce anthropogenic hybridisation (Allendorf et al., 2001), to avoid making movements of crocodiles to areas where they are not naturally distributed (e.g. *C. acutus* to the Gulf of Mexico or *C. moreletii* to the Pacific). Even make a proper genetic identification of crocodiles, because they could be handling hybrids without knowing it. In the absence of the option to do molecular analysis, morphological identification has proven to be effective (Pacheco et al., 2016; Soria-Ortiz, 2019). Therefore, implementing conservation actions at an early stage of hybridisation is advisable before it becomes an even more difficult problem.

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Authors' Contribution
G.J.S-O, P.N.G-N and A.R-G designed the research; G.J.S-O, P.N.G-N, A.R-G, and L.M.O-O performed the statistical analyses; G.J.S-O analysed the results and drafted the manuscript with the help of P.N.G-N, A.R-G, and L.M.O-O. All the authors corrected and approved the final version of the manuscript. The authors declare that they have no conflicts of interest.

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