Interaction of landscape variables on the potential geographical distribution of parrots in the Yucatan Peninsula, Mexico

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Abstract
Interaction of landscape variables on the potential geographical distribution of parrots in the Yucatan Peninsula, Mexico.— The loss, degradation, and fragmentation of forested areas are endangering parrot populations. In this study, we determined the influence of fragmentation in relation to vegetation cover, land use, and spatial configuration of fragments on the potential geographical distribution patterns of parrots in the Yucatan Peninsula, Mexico. We used the potential geographical distribution for eight parrot species, considering the recently published maps obtained with the maximum entropy algorithm, and we incorporated the probability distribution for each species. We calculated 71 metrics/variables that evaluate forest fragmentation, spatial configuration of fragments, the ratio occupied by vegetation, and the land use in 100 plots of approximately 29 km², randomly distributed within the presence and absence areas predicted for each species. We also considered the relationship between environmental variables and the distribution probability of species. We used a partial least squares regression to explore patterns between the variables used and the potential distribution models. None of the environmental variables analyzed alone determined the presence/absence or the probability distribution of parrots in the Peninsula. We found that for the eight species, either due to the presence/absence or the probability distribution, the most important explanatory variables were the interaction among three variables, particularly the interactions among the total forest area, the total edge, and the tropical semi–evergreen medium–height forest. Habitat fragmentation influenced the potential geographical distribution of these species in terms of the characteristics of other environmental factors that are expressed together with the geographical division, such as the different vegetation cover ratio and land uses in deforested areas.

Key words: Deforestation, Fragmentation, Land use, Parrots, Vegetation cover

Resumen
La interacción de las variables del paisaje sobre la distribución geográfica potencial de los loros en la península de Yucatán, México.— La pérdida, degradación y fragmentación de las zonas boscosas están poniendo en peligro a las poblaciones de loros. En este estudio se determinó la influencia de la fragmentación en relación con la cobertura vegetal, los usos del suelo y la configuración espacial de los fragmentos, sobre los modelos de distribución geográfica potencial de los loros en la península de Yucatán, México. Se utilizó la distribución geográfica potencial de ocho especies de loros, teniendo en cuenta los mapas publicados recientemente y obtenidos con el algoritmo de máxima entropía, y se incorporó el mapa de probabilidad de distribución de cada especie. Se calcularon 71 parámetros y variables que evalúan la fragmentación forestal, la configuración espacial de los fragmentos, la proporción ocupada por vegetación y los usos del suelo en 100 parcelas de aproximadamente 29 km² distribuidas al azar dentro de las zonas de presencia y ausencia predichas para cada especie. Además, se tuvo en cuenta la relación entre las variables ambientales y la probabilidad de distribución de las especies. Se empleó una regresión de mínimos cuadrados parciales para analizar la relación existente entre las variables empleadas y los modelos de distribución potencial. Ninguna de las variables ambientales analizadas determina por sí sola la presencia, la ausencia ni la probabilidad de distribución de los loros en la península. Se observó que para las ocho especies, ya sea debido a la presencia y la ausencia o a la proba-

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bilidad de distribución, las variables explicativas más importantes son la interacción entre tres variables, en especial la interacción entre la superficie forestal total, la longitud total de los perímetros de los fragmentos y la cantidad de bosque tropical subperennifolio de altura mediana. La fragmentación del hábitat influye sobre la distribución geográfica potencial de estas especies en combinación con otros factores ambientales asociados a la misma, como son la proporción de las diferentes coberturas vegetales y los usos del suelo que se desarrollan en las áreas deforestadas.

Palabras clave: Deforestación, Fragmentación, Uso del suelo, Loros, Cobertura vegetal

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Introduction

Forest loss and fragmentation are significant factors that contribute to extinction of species worldwide (Hanski et al., 2013). Different species respond differently to these anthropogenic perturbations, particularly those that are affected by the size of the remaining fragment and its connectivity with other fragments or the main forest mass (Donovan & Lamberson, 2001). A reduction in the average size of forest fragments will affect bird populations if these fragments are too small to satisfy species specific requirements (Bregman et al., 2014). It has been shown that the effect of fragment size depends on the characteristics of the surrounding forest–fragment mosaic (Brotons et al., 2002). In addition, in abandoned agricultural areas subject to secondary succession, or in areas where badly planned reforestation has taken place, some species of farmland birds are affected due to both habitat loss and an increase in forest edge density (Rey Benayas et al., 2008; Reino et al., 2009).

Few studies have examined the effects of forest fragmentation on parrots (*e.g.* Evans et al., 2005), one of the most threatened species in Mexico as their habitats face disappearance throughout their range of distribution (Norma Oficial Mexicana, 2010). In Mexico, current research on psittacines has focused on the potential distribution of several species (Monterrubio–Rico et al., 2010; Monterrubio–Rico et al., 2011), the effects of land use changes (Ríos–Muñoz & Navarro–Sigüenza, 2009), habitat loss, and the illegal trafficking of species (Marín–Togo et al., 2012). Eight of the twenty–two species of psittacines in Mexico are present in the Yucatan Peninsula (MacKinnon, 2005), and some of them still have high populations (*e.g.* Macías–Caballero & Iñigo–Elías, 2003; Plasencia–Vázquez & Escalona–Segura, 2014a). However, the loss of forest areas, together with degradation and fragmentation have intensified (Céspedes–Flores & Moreno–Sánchez, 2010) and are is endangering viable parrot populations in the region.

Ecological studies have tended to analyse the independent impact of environmental factors on psittacine distribution. Significantly, it has not been considered whether a series of concomitant environmental factors can modify the impact of forest fragmentation on species. Such factors include a loss of vegetation cover (Waltert et al., 2005) and types of land use (Ríos–Muñoz & Navarro–Sigüenza, 2009) within the habitat mosaic surrounding forest fragments. In addition, different levels of anthropogenic disturbance (Marín–Togo et al., 2012) and fragment degradation (Raman, 2004) can influence the impact of fragmentation on psittacines.

Psittacine distribution patterns may reflect the combined action of all these factors and would be established in association with the spatial configuration of the forest fragments. Thus, the aim of this study was to determine the influence of fragmentation in terms of vegetation cover, land use, and the spatial configuration of forest fragments, on the patterns of potential geographical distribution of parrots in the Yucatan Peninsula, Mexico.

Material and methods

Study area

The study was conducted in the three Mexican states that comprise the Yucatan Peninsula: Campeche, Quintana Roo, and Yucatán (17° 48' – 21° 35' N, 86° 43' – 92° 27' W), in southeastern Mexico (Barrera, 1962). The entire Yucatan Peninsula is a flat–lying karst landscape with few hills and little topographical variation (Lugo–Hubp et al., 1992). It is divided into two biogeographical regions, the first towards the northwest and the second towards the southeast. The vegetation of the Yucatan Peninsula changes gradually along an environmental gradient associated with rainfall distribution patterns that stretch from the semi–arid northwest to the wetter southeast. The changes in vegetation largely reflect rainfall patterns with dry low deciduous scrub and semi–deciduous forest dominating towards the northwest, and semi–wet and tropical semi–evergreen forest predominant towards the southeast (Pennington & Sarukhán, 1998).

Species and models of potential geographical distribution

Eight species of psittacines present in the Yucatan Peninsula were analysed: Olive–throated Parakeet (*Eupsittula nana),* White–fronted Amazon (*Amazona albifrons*), Yellow–lored Amazon (*Amazona xantholora*), Red–lored Amazon (*Amazona autumnalis*), White–crowned Parrot (*Pionus senilis*), Brown–hooded Parrot (*Pyrilia haematotis*), Yellow–headed Amazon (*Amazona oratrix*), and Southern Mealy Amazon (*Amazona farinosa*) (MacKinnon, 2005). Potential geographical distribution models obtained by Plasencia–Vázquez et al. (2014) were used for *A. xantholora* and *A. oratrix,* while potential geographical distribution models obtained by Plasencia–Vázquez & Escalona–Segura (2014b) were used for the remaining six species. The distribution models of the eight species were obtained using the MaxEnt program (Phillips et al., 2006), considered the most appropriate program when few records of species are available (Hernandez et al., 2006). The same methodology was used to obtain the models for all eight species.

Vegetation and land use

A land use and vegetation map from INEGI (National Institute for Statistics and Geography) Serie IV was used to describe the types of land use and vegetation present within the potential geographical distribution areas. These maps cover the Yucatan Peninsula and are the most up–to–date maps available. All vegetation types were taken into account: halophytic vegetation, hammocks, coastal dunes, tule vegetation, popal marshes, mangrove forest, halophytic pasture, induced pasture, tropical semi–evergreen medium–height forest (tree height 15–30 m, TSeMhF), tropical semi–deciduous medium–height forest (tree height 15–30 m, TSdMhF), tropical deciduous medium–height forest (tree height 15–30 m); tropical semi–deciduous low–height forest (tree height 4–15 m), tropical semi–evergreen low–height thorn forest (tree height 4–15 m), tropical deciduous low–height thorn forest (tree height 4–15 m), tropical deciduous low–height forest (tree height 4–15 m), tropical evergreen low–height forest (tree height 4–15 m), tropical semi–evergreen high–height forest (tree height + 30 m), tropical evergreen high–height forest (tree height + 30 m), riparian forest, savanna, oak forest, palm forest, and induced palm grove. The land use variables included: human settlements, urban zones, livestock raising (Liv), irrigated agriculture and rain–fed agriculture. Some types of agriculture could not be classified and were entitled N/C. Ground fresh water sources were also included.

Using the presence/absence map for each species, obtained from the potential geographical distribution models (Plasencia–Vázquez & Escalona–Segura, 2014b; Plasencia–Vázquez et al., 2014), 100 hexagonal plots, each with an approximate area of 29 km², were randomly selected. This area is consistent with the home range of similar psittacine species as presently there is no data on the home range of the studied species (Tamungang et al., 2001; White et al., 2005; Ortiz–Maciel et al., 2010). Plots with 50% or more of their area potentially occupied by the corresponding species were classified as presence and the remaining plots as absence. The numbers of plots classified as absence (A) or presence (P) for each species were the following: *E. nana* (14A, 86P), *A. albifrons* (11, 89), *A. xantholora* (22, 78), *A. autumnalis* (58, 42), *P. haematotis* (49, 51), *P. senilis* (42, 58), *A. farinosa* (57, 43), and *A. oratrix* (79, 21). The same procedure was followed for the distribution probability (DP) of each species, calculating the mean DP for each plot.

The same 100 plots that were used in the aforementioned procedures were delineated on the land use and vegetation maps. The area within each plot occupied by the different land uses, water bodies, and vegetation types was then calculated. All these calculations and procedures were carried out using the ArcView 3.2 program (ESRI, 1999).

Forest fragmentation in the Yucatan Peninsula

The land use and vegetation map from Series IV of the National Institute of Statistics and Geography in Mexico (INEGI, 2010) was also used to measure the levels of forest fragmentation within the potential geographical distribution areas of psittacines in the Yucatan Peninsula. Only forested areas (including mangrove forest, hammocks, tropical forest, and oak forest) that are potential habitat for the parrot species were selected; all other vegetation types, ground fresh water sources, and land uses were eliminated. All these forest areas were grouped together in order to obtain one map that represented the total forest mass in the Yucatan Peninsula. The ArcView 3.2 program (ESRI, 1999) was used for the above procedures.

Using the Patch Analyst extension in ArcView 3.2 (ESRI, 1999), a series of indexes were calculated for the plots defined for each species. These indexes were then superimposed onto the forest mass map. Indexes that describe fragmentation over the whole landscape were selected, as suggested by Fahrig (2003). The following variables were calculated: total forest area (TFA), number of patches, mean patch size, median patch size, patch size coefficient of variance, patch size standard deviation, total edge (TE), edge density, mean patch edge (MPE), mean shape index, area–weighted mean shape index, mean perimeter–area ratio (MPAR), mean patch fractal dimension, area–weighted mean patch fractal dimension, Shannon's diversity index, and Shannon's evenness index.

In addition, the distance between fragments (DF) and their spatial configuration were calculated. For distances, the shortest distance between the edge of one fragment to another and the distance between the centroids of all the fragments were calculated for each plot. The sum of the crossed multiples of the matrixes of distances between the fragment edges and their centroids was then calculated to obtain a distances summary variable. Moran's I Index for four neighbours (Moran, 1950) with the ROOKCASE for Excel 97/2000 complement (Sawada, 1999) was calculated using the matrix of distances between fragment edges in each plot in order to obtain a measure of the spatial distribution of fragments in the landscape.

Statistical analysis

To reduce the co–linearity between fragmentation, spatial configuration, land use, and vegetation type variables, Pearson correlations between all variables were calculated and those with coefficient values of $|r| < 0.7$ were selected (Dormann et al., 2012). Based on the natural history, habitat and knowledge obtained through field observations of these species (Fitzpatrick et al., 2013), one of variables that possibly presents a strong relationship with psittacine distribution patterns in the Yucatan Peninsula was selected from the pairs of strongly correlated variables. Land use and resultant vegetation variables that were represented in less than 10% of the 100 plots were eliminated.

A partial least squares regression (PLS) was performed to determine the possible relationship between the matrix of fragmentation, spatial configuration, land use and vegetation variables and the potential geographical distribution of the species of psittacines, based on the distribution probability (DP) and presence/absence (P/A). The PLS regression is a statistical method with great potential for ecological studies, and it is appropriate for analyses that endeavour to explain complex phenomena defined by the combination of a variety of explicative variables (Carrascal et al., 2009). The dependent presence/absence and distribution probabilities, with two and three categories respectively, were used as qualitative variables during the PLS regression analysis. The probability of presence values, obtained for each species in the study plots, were converted into three percentage intervals of equal width (high, medium and low probability).

The automatic mode was used as the stop condition and the third level interactions between the explicative variables were taken into account. The Q^2 index, which measures the total goodness of fit and the predictive quality of the models, was calculated.

Lost data were disregarded and the correlation matrix was considered to determine the type of relationship established between explicative and dependent variables. The variable importance in projection (VIP) was also considered. Regarding the PLS regression, after eliminating several variables that were highly correlated or represented in less than 10% of the plots, the number of explicative variables fluctuated between 13 and 15, depending on the specific species of psittacine. The XLSTAT (2014) complement for Excel was used for the above analyses.

Results

Urban zones, irrigated agriculture, and non–classified agriculture N/C were discarded from the total of six land use variables. Human settlements were only taken into account during the analysis of *A. albifrons* and *E. nana*. The vegetation variables that presented the highest percentages of representation in plots were tropical semi–deciduous medium–height forest (22–31%), tropical semi–evergreen medium–height forest (52–74%), and tropical semi–evergreen low–height thorn forest (35–52%). The mangrove forest vegetation type was used for the analysis with the species *A. albifrons*, *A. oratrix* and *P. senilis*. Tule vegetation was taken into account for the three aforementioned species and *E. nana*.

The number of components that were automatically selected by the PLS regression varied according to species and the P/A and DP data analysis. The following list presents psittacine species and the number of PLS regression components for the P/A and DP data presented in parenthesis: *A. albifrons* (7 P/A and 2 DP), *A. autumnalis* (4 and 6), *A. farinosa* (3 and 3), *E. nana* (4 and 2), *A. oratrix* (5 and 5), *A. xantholora* (4 and 5), *P. haematotis* (3 and 2), and *P. senilis* (4 and 3). The Q^2 index attained low values for the eight psittacine species, including the cumulated value for the total obtained components (table 1). The DP data presented lower Q^2 cumulated (Q^2cum) values than the P/A data. *A. albifrons* presented the highest Q^2cum.value using the P/A data (table 1).

In summary, with respect to the confusion matrix and the reclassification of the observations, the P/A data presented the highest percentage of observations of well–classified species (table 2). The percentages of well–classified observations coincided for both P/A and DP data only in the case of *A. Oratrix*.

For all eight species of parrot, the most important explicative variables for both P/A and DP data were third level interactions (table 3). Using P/A and DP data, the most frequent effect was the interaction between total forest area, total edge, and tropical semi–evergreen medium–height forest. This effect contributed to the models of six species. The most frequent variables in the third level interactions that had the greatest influence on the models were total edge, total forest area and distance between fragments (appendix 1). In the matrixes of the correlation coefficients between the different fragmentation variables and the species P/A and DP, it was possible to distinguish which independent variables had a positive or negative influence (tables 4, 5).

Table 1. Accumulated predictive quality (Q^2cum) of the models performed with the presence/absence and distribution probability data of eight parrot species found in the Yucatan Peninsula, Mexico: P/A. Presence/Absence; DP. Distribution probability distribution.

Tabla 1. Calidad predictiva acumulada (Q^2cum) de los modelos realizados con los datos de presencia y ausencia y de probabilidad de distribución de las ocho especies de loros presentes en la península de Yucatán, México: P/A. Presencia/Ausencia; Pd. Probabilidad de distribución.

Species	P/A Q^2cum	DP Q^2cum
Amazona albifrons	0.62	0.14
Amazona autumnalis	0.18	–0.03
Amazona farinosa	0.14	0.05
Eupsittula nana	0.49	0.08
Amazona oratrix	0.43	0.42
Amazona xantholora	0.09	0.14
Pyrilia haematotis	0.22	0.11
Pionus senilis	0.30	0.38

Table 2. Confusion matrix with the total percentage of presence/absence (P/A) observations and well–classified distribution probability (DP) for eight parrot species in the Yucatan Peninsula.

Tabla 2. Matriz de confusión con el porcentaje total de observaciones de presencia y ausencia (P/A) y de probabilidad de distribución (DP) bien clasificada, para las ocho especies de loros de la península de Yucatán.

Species	Correct P/A (%)	Correct DP (%)
A. albifrons	91	56
A. autumnalis	74	70
A. farinosa	55	46
E. nana	92	51
A. oratrix	80	80
A. xantholora	84	65
P. haematotis	65	60
P. senilis	79	77

Table 3. Variables with greater importance during the projection (VIP) for the components automatically generated during the PLS regressions made with the presence/absence and distribution probability data of eight parrot species found in the Yucatan Peninsula: TFA. Total forests area; TE. Total edge; MPAR. Mean perimeter–area ratio; MPE. Mean patch edge; DF. Distance among the fragments; TSeMhF. Tropical semi–evergreen medium–height forest; TSdMhF. Tropical semi–deciduous medium–height forest; Liv. Livestock raising.

Tabla 3. Variables con mayor importancia durante la estimación (VIP) de los componentes generados automáticamente durante las regresiones de mínimos cuadrados parciales realizadas con los datos de presencia y ausencia y de probabilidad de distribución de las ocho especies de loros presentes en la península de Yucatán: TFA. Superficie forestal total; TE. Longitud total de los perímetros de los fragmentos; MPAR. Media de la proporción entre la superficie y el perímetro; MPE. Media del perímetro de fragmento; DF. Distancia entre los fragmentos; TSeMhF. Bosque tropical subperennifolio de altura mediana; TSdMhF. Bosque tropical subcaducifolio de altura mediana; Liv. Ganadería.

Species	VIP Presence/Absence	VIP Distribution of probability
A. albifrons	TFA*TE*TSeMhF	TFA*TE*TSeMhF
A. albifrons	TFA*TE*TSdMhF	TFA*TE*DF
E. nana	TE*MPAR*DF	TE*MPAR*DF
E. nana		TFA*TE*TSeMhF
A. xantholora	TFA*TE*TSeMhF	TFA*TE*TSeMhF
A. xantholora		TE*MPAR*DF
A. autumnalis	TE*Liv*DF	TE*Liv*DF
A. autumnalis	TFA*TE*MPAR	TFA*TE*MPAR
A. farinosa	TE*Liv*DF	TFA*TE*TSdMhF
A. farinosa	TFA*TE*MPAR	TFA*TE*TSeMhF
A. oratrix	TE*MPAR*DF	TE*MPAR*DF
A. oratrix	TFA*TE*TSeMhF	TFA*TE*TSeMhF
P. haematotis	TE*Liv*DF	TE*Liv*DF
P. haematotis	TFA*TE*TSeMhF	TFA*TE*TSeMhF
P. senilis	TFA*MPE*TSeMhF	TFA*TE*MPE
P. senilis	TFA*MPE*TSdMhF	TE*Liv*DF
P. senilis	MPAR*Liv*DF	

The potential presence of *A. albifrons* was favoured in those areas where the landscape is dominated by tropical semi–evergreen medium–height forest and tropical semi–deciduous medium–height forest. The distribution probability of this parrot was lower in areas with small forest fragments that are separated by large distances. *Eupsittula nana* was present mainly in areas with large forest fragments that were close together and which tended to be compact and simple (few irregularities). If, in addition to these characteristics, the fragments were composed of tropical semi–evergreen medium–height forest, then the distribution probability of this species was even higher. *Amazona xantholora* was present in landscapes characterized by large fragments of tropical semi–evergreen medium–height forest, and its distribution probability decreased with an increase in fragment irregularity and distances between forest fragments.

Amazona autumnalis was potentially found in areas where forest fragments tended to be irregular, separated by larger distances, where most of the total landscape area is not forested and agricultural activity is low. *Pyrilia haematotis* was mainly found in areas with similar characteristics to those inhabited by *A. autumnalis*, although the probability of finding this species was higher in areas where tropical semi–evergreen medium–height forest fragments were in close proximity. Regarding *P. senilis*, its potential distribution was favoured in those areas where the landscape was dominated by proximate regular tropical semi–evergreen medium–height forest. This particular species was less abundant in sites with agricultural activity or where tropical semi–deciduous medium–height forest was the dominant vegetation.

A. farinosa preferred landscapes characterized by clustered, regular forest fragments where there was very little or zero agricultural activity. This distribution probability of this species was higher at sites dominated by tropical semi–evergreen medium–height forest, while at sites where tropical semi–deciduous medium–height forest dominated there was a medium probability of occurrence. *Amazona oratrix* was potentially found in areas

Table 4. Coefficient of correlation matrix between fragmentation variables integrated to third level interactions, and the presence of eight species of parrots living in the Yucatan Peninsula: 1. *A. albifrons;* 2. *A. autumnalis;* 3. *A. farinosa;* 4. *E. nana;* 5. *A. oratrix;* 6. *A. xantholora;* 7. *P. haematotis;* 8. *P. senilis*. (For abbreviations of variables see table 3.)

Tabla 4. Matriz con los coeficientes de correlación entre las variables de fragmentación integradas en interacciones de tercer orden y la presencia de las ocho especies de loros presentes en la península de Yucatán. (Para las abreviaturas de las especies ver arriba y para las de las variables ver tabla 3.)

	Presence of species							
Variables	1	2	3	4	5	6	7	8
TFA	0.15	–0.14	0.21	0.26	–0.47	0.36	–0.10	0.12
MPE	–	–	–	–	–	–	–	0.05
TE	0.16	0.17	0.20	0.13	–0.12	0.07	0.20	–
MPAR	–	0.02	–0.06	–0.16	0.24	–0.30	0.13	–0.19
Liv	–0.01	–0.04	–0.14	–0.32	0.16	–0.37	–0.01	–0.19
TSdMhF	0.03	–0.23	0.02	0.13	–0.21	0.02	–0.05	–0.29
TSeMhF	0.08	0.26	0.06	0.00	–0.29	0.33	0.01	0.44
DF	0.04	0.25	0.00	–0.45	0.29	–0.20	0.13	–0.17

where small forest fragments predominated, separated by larger distances. The distribution probability of this psittacine species increased in landscapes characterized by very irregular forest fragments and few areas of tropical semi–deciduous medium–height forest.

Discussion

There is no precise information on the distribution areas of psittacines in the Yucatan Peninsula, and the information in the literature varies considerably (*e.g.* Howell & Webb, 1995; Peterson & Chalif, 1998; Forshaw, 2006). Thus, the use of the potential geographical distribution models developed by Plasencia–Vázquez et al. (2014) and Plasencia–Vázquez & Escalona–Segura (2014b) was crucial. However, these models are only a hypothesis on environments similar to those where these parrot species have been observed and are probably between the limits of the fundamental and occupied niche (Peterson et al., 2011). Consequently, the results on the influence of different environmental factors on potential geographical distribution of psittacines are only an approximation and therefore may represent information that does not entirely equate with reality.

Although the distribution of species is determined by a variety of factors, it is always important to know which variables are responsible for most of the observed variation (Carrascal, 2004). In the Yucatan Peninsula, the eight species of parrot that remain in the region are generally associated with tropical forest and for the majority, the potential presence and distribution probability are associated with the most preserved areas characterized by little anthropogenic alteration, a finding which has been found for species of psittacines in other areas and regions of Mexico (Morales–Pérez, 2005). In general, most parrot species are associated with forest areas as these provide food resources such as fruit, seeds, leaves, and flowers in addition to arboreal nesting sites (Morales–Pérez, 2005). Therefore, a reduction in forests would imply a loss of trophic resources and tree cavities for nesting that would lead to a decrease in psittacine populations (Rice, 1999; Berovides & Cañizares, 2004). Currently, tropical semi–evergreen medium–height forest covers the largest area within the Yucatan Peninsula and is the vegetation type that exerts most influence on the potential distribution of most psittacines in the region, coinciding with results obtained by Plasencia–Vázquez & Escalona–Segura (2014b).

In areas subject to forest loss and fragmentation, a decrease in reproductive success, due to an increase in egg predation and nest parasitism, has been observed at the edges of forest fragments (Willson et al., 2001). The structural characteristics of forest edges result in an increase in nest predation rates, so reproductive success rates increase towards the forest interior where vegetation is much denser (Hartley & Hunter, 1998). Furthermore, at the forest edge, parrot nests are more easily found and removed by poachers that participate in the illegal trafficking of parrot species. In the forests of the Calakmul Biosphere Reserve, in the state of Campeche, Mexico, larger frugivorous species are more likely to be found in areas with mature and senescent vegetation than in forests comprising younger successional stages of vegetation (Weterings et al., 2008). In general, these mature forests are found in well conserved natural areas or are secondary forests that have not been managed or disturbed over a long period of time, thus resembling mature primary forests (Guariguata et al., 1997). Most areas with younger stages of vegetation have been subject to recent anthropogenic modifications, such as *acahuales* (fallow agricultural land undergoing secondary

Table 5. Coefficient of correlation matrix between fragmentation variables integrated to third level interactions, and distribution probability of eight species of parrots living in the Yucatan Peninsula: DP. Distribution probability (H. High; M. Medium; L. Low). (For abbreviations of species see table 4 and for abbreviations of variables see table 3.)

Tabla 5. Matriz con los coeficientes de correlación entre las variables de fragmentación integradas en interacciones de tercer orden y la probabilidad de distribución de las ocho especies de loros presentes en la península de Yucatán: DP. Probabilidad de distribución (H. Alta; M. Media; L. Baja). (Para las abreviaturas de las especies ver tabla 4 y para las de las variables ver tabla 3.)

		Species							
Variables	DP	1	2	3	4	5	6	7	8
TFA	H	–0.06	–0.01	0.15	0.12	–0.37	0.10	0.07	0.17
	M	0.13	–0.15	0.05	0.15	–0.28	0.07	–0.08	0.02
	L	–0.10	0.15	–0.17	–0.25	0.49	–0.13	0.05	–0.14
TE	H	0.06	0.05	0.01	0.02	–0.27	0.10	0.00	–0.08
	M	0.23	0.15	0.19	0.06	0.14	–0.15	0.11	0.01
	L	–0.25	–0.17	–0.18	–0.08	0.06	0.08	–0.11	0.05
MPE	H	–	–	–	–	–	–	–	0.03
	M	–	–	–	–	–	–	–	0.05
	L	–	–	–	–	–	–	–	–0.06
MPAR	H	–	–0.04	–0.01	–0.11	0.09	–0.11	–0.05	–0.09
	M	–	0.03	0.03	0.08	0.17	–0.11	0.02	–0.06
	L	–	0.00	–0.02	0.01	–0.21	0.17	0.00	0.11
Liv	H	–0.11	–0.08	–0.17	–0.10	0.16	–0.17	–0.07	–0.13
	M	–0.19	–0.01	0.06	–0.22	0.07	–0.22	–0.04	–0.18
	L	0.24	0.05	0.08	0.31	–0.17	0.32	0.07	0.24
TSdMhF	H	–0.18	–0.04	–0.19	–0.19	–0.08	–0.10	–0.09	–0.14
	M	0.00	–0.23	0.30	0.01	–0.15	–0.16	–0.18	0.00
	L	0.10	0.24	–0.11	0.15	0.18	0.21	0.21	0.10
TSeMhF	H	0.23	0.09	0.17	0.21	–0.21	0.21	–0.10	0.16
	M	0.05	0.22	–0.12	0.03	–0.25	0.22	0.17	0.10
	L	–0.17	–0.27	–0.03	–0.21	0.35	–0.34	–0.13	–0.19
DF	H	0.25	–0.01	–	–0.09	0.08	–0.09	–0.05	–0.08
	M	–0.08	0.24	–	–0.17	0.30	–0.12	–0.01	–0.09
	L	–0.05	–0.23	–	0.25	–0.31	0.17	0.03	0.13

succession, initially characterized by tall herbaceous species), and have been undergoing regeneration for only a short period of time. Younger early stage vegetation may not provide the conditions required by psittacines for their development; there is a marked absence of large older trees with cavities that are required by the parrots for nesting and large tree species that provide the fruit and seeds that parrot species feed on are absent or have not grown sufficiently. Therefore, in certain areas, the presence of parrot species could be determined by the amount of time that *acahuales* have been regenerating.

This study showed that in the Yucatan Peninsula, the effect of habitat loss and fragmentation depends on the species of parrot and varies according to the sensitivity of each species to these changes, their habitat requirements and biology (Gurrutxaga, 2006). Several of the studied species are capable of exploiting some of the resources present in the landscape matrix surrounding the forest fragments and even degraded environments, such as agroecosystems, can support viable populations of certain psittacine species (Romero–Balderas et al., 2006). The effectivity of the matrix as a habitat depends on the interaction between its structural characteristics and the ecological requirements of the species (Antogiovanni & Metzger, 2005). The lesser the structural contrast between the matrix and the native habitat of the species, the more favourable the conditions for providing suitable habitat (Antogiovanni & Metzger, 2005).

Although all the species analysed in this study are found in areas that have been modified to a greater or lesser extent by different factors, the effect on their potential geographical distribution varies considerably. Widely–distributed species such as *A. albifrons*, *A. xantholora* and *E. nana*, which present extensive areas of distribution within the Yucatan Peninsula, were not expected to be affected by fragmentation and would be found even within agricultural and urban matrixes. However, this study showed that these species display a greater preference for more conserved sites

Many species of parrot occupy agricultural areas simply because they provide large and easily accessible concentrations of food, spending little time and energy on foraging. In some areas, these anthropogenic resources are exploited to such an extent that parrots are considered agricultural pests (Bucher, 1992). Nevertheless, the fact that these species take advantage of these modified areas does not mean they always prefer them to natural areas. Due to the destruction of their natural habitat, reproduction and feeding areas, combined with the illegal capture and trafficking for the pet trade, wild parrot species currently experience relentless human pressure, leading to a reduction in their areas of distribution and forcing them to occupy new habitats which generally lack the appropriate ecological characteristics for their successful development.

For *A. farinosa* and *P. senilis,* the present study showed that most of their potential distribution areas are still found within well–preserved areas, and their distribution probability is greater in less fragmented sites, as observed for most psittacines in Mexico (Morales–Pérez, 2005). Contrary to their habitat characteristics described in the literature (*e.g.* Howell & Webb, 1995; Peterson & Chalif, 1998; Forshaw, 2006), *P. haematotis* and *A. autumnalis* were potentially found in more fragmented areas. Given its sensitivity to habitat modifications, we expected to find *P. haematotis* within extensive areas of conserved forest with low levels of fragmentation. However, it was evident that both species avoided areas where agricultural activities take place, thus supporting the view that these particular species are sensitive to the effects of human activities (Ríos–Muñoz & Navarro–Sigüenza, 2009). The present potential presence areas of these species are a consequence of years of intense modifications to their natural habitats. Some species have adapted better than others to these changes and still persist in modified areas or are simply concentrated in remaining forest fragments. As these results are based on potential species distributions only, empirical corroborations in the field are essential.

Amazona oratrix is in a critical situation as its potential distribution is in the southwest of the Yucatan Peninsula, an area that has suffered a high level of modification due to extensive cattle ranching (Villalobos–Zapata et al., 2010). According to the obtained results, this species is found in very fragmented areas and its probability of occurrence is greater at sites with a high degree of anthropization, contradicting the existing literature on the ecology of this parrot species (Enkerlin–Hoeflich, 2000). Macías–Caballero & Iñigo–Elías (2003) established that one of the most abundant populations of *A. oratrix* in Mexico was found in this region of the Yucatan Peninsula and this has been confirmed by previous visits to the area (Plasencia–Vázquez & Escalona–Segura, 2014a).

It is interesting that *A. oratrix*, characterized by a low reproductive rate and a preference for high and medium tropical forest, is present in large numbers within an area of significant human activity, making it highly vulnerable to illegal trafficking and deforestation (Enkerlin–Hoeflich, 2000). The historical component was not taken into account during this study and may be a determining factor in explaining the observed patterns. Very little is known about this species in the Yucatan Peninsula and there are no data on its abundance prior to the deforestation of most of the forest that dominated the distribution area of this species. Many parrots have high longevity (Munshi–South & Wilkinson, 2006), thus many of the individuals observed in this region of the Yucatan Peninsula are adults that have managed to survive in a suboptimum environment. Furthermore, adult parrots normally remain in the forest canopy, making them difficult to capture, while parrot chicks suffer the highest capture rates by poachers as they are more easily found and removed from their nests. Therefore, despite low reproduction rates and high predation, large numbers of *A. oratrix* individuals continue to be observed (Plasencia–Vázquez & Escalona–Segura, 2014a). Unfortunately, in the near future, the *A. oratrix* population will be composed of mainly old individuals, with very low productivity and on the verge of a potentially catastrophic population crash.

In general, the present study revealed that the existing potential geographical distribution of psittacine species in the Yucatan Peninsula is determined by the interaction between variables that represent forest fragmentation, vegetation cover, and land uses. At present, the areas occupied by the parrot species are determined by the combined effect of natural and anthropogenic factors. As forest perturbation in the Yucatan Peninsula increases, anthropogenic factors become increasingly determinative in psittacine distribution.

At the scale of this study, many human activities carried out within the Yucatan Peninsula do not occupy extensive areas and therefore do not appear to affect psittacine populations. Smaller scale studies are required to assess how and to what extent activities such as agriculture or the expansion of urban areas and human settlements impact parrot populations. The results presented in this study on parrot species present in the Yucatan Peninsula are just an approximation of reality, analysed under determined conditions. There is therefore a need for future research conducted at a smaller, more local scale and including other environmental variables.

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Appendix 1. Descriptive statistics of the variables comprising the third level interactions that had greatest influence on presence/absence and distribution probability of psittacine species in the Yucatan Peninsula (mean ± standard error, minimum–maximum, sample size in brackets: TFA. Total forest area; TE. Total edge; MPE. Mean patch edge; MPAR. Mean perimeter–area ratio; Liv. Livestock raising; TSdMhF. Tropical semi–deciduous medium–height forest; TSeMhF. Tropical semi–evergreen medium–height forest; DF. Distance between fragments.

	Species			
Variables	*A. albifrons*	*A. autumnalis*	*A. farinosa*	*E. nana*
TFA (km²)	19.89 ± 0.90	19.11 ± 0.86	20.37 ± 0.81	18.26 ± 0.91
	0–29.40	0–29.33	0–29.33	0–29.27
	(100)	(100)	(100)	(100)
TE (km)	25.97 ± 0.96	27.95 ± 1.01	28.40 ± 1.02	27.11 ± 1.09
	0–59.70	0–53.60	0–56.53	0–53.74
	(100)	(100)	(100)	(100)
MPE (km)	19.48 ± 0.90	16.96 ± 0.91	17.70 ± 0.89	17.08 ± 0.94
	3.29–41.23	2.42–43.24	2.42–43.24	2.42–43.24
	(98)	(99)	(99)	(98)
MPAR (km)	6.58 ± 1.21	9.14 ± 1.96	10.98 ± 2.39	9.28 ± 1.84
	0.69–62.57	0.69–125.25	0.69–130.47	0.69–125.25
	(97)	(94)	(94)	(94)
Liv (km²)	6.16 ± 1.01	8.59 ±1.20	7.94 ±1.20	9.26 ± 1.21
	0.01–27.67	0.01–28.97	0.01–28.97	0.01–28.97
	(52)	(50)	(50)	(52)
TSdMhF (km²)	21.44 ± 1.48	18.50 ± 1.92	18.23 ± 1.80	17.66 ± 1.87
	1.91–29.04	0.003–29.21	0.18–29.21	0.003–29.21
	(32)	(28)	(27)	(30)
TSeMhF (km²)	17.81 ± 1.33	17.33 ± 1.07	18.16 ± 1.07	16.31 ± 1.22
	0.01–29.21	0.70–29.33	0.67–29.33	0.56–29.22
	(55)	(69)	(66)	(62)
DF (km)	8.34 ± 1.98	22.22 ± 6.22	18.29 ± 5.80	19.26 ± 4.69
	0–109.09	0–466.80	0–466.80	0–295.18
	(98)	(99)	99	(98)

Apéndice 1. Estadísticos descriptivos de las variables integradas en interacciones del tercer orden que más influyeron en la presencia y la ausencia y en la probabilidad de distribución de las especies de loros de la península de Yucatán (media ± error estándar, mínimo–máximo, tamaño de muestra entre paréntesis). TFA. Superficie forestal total; TE. Longitud total de los perímetros de los fragmentos; MPE. Media del perímetro de los fragmentos; MPAR. Media de la proporción entre la superficie y el perímetro; Liv. Ganadería; TSdMhF. Bosque tropical subcaducifolio de altura mediana; TSeMhF. Bosque tropical subperennifolio de altura mediana; DF. Distancia entre los fragmentos.

Species			
A. oratrix	*A. xantholora*	*P. haematotis*	*P. senilis*
17.08 ± 0.98	19.09 ± 0.89	19.26 ± 0.87	20.04 ± 0.81
0–29.27	0–29.27	0–29.33	0–29.33
(100)	(100)	(100)	(100)
25.49 ± 1.17	26.80 ± 1.04	27.68 ± 1.00	28.28 ± 0.98
0–53.60	0–53.60	0–53.60	0–53.60
(100)	(100)	(100)	(100)
15.66 ± 0.94	17.86 ± 0.94	16.98 ± 0.90	17.71 ± 0.93
1.42–43.24	2.42–43.24	2.42–43.24	2.78–48.24
(98)	(98)	(99)	(99)
11.73 ± 2.36	8.76 ± 1.82	9.17 ± 1.96	8.50 ± 1.96
0.69–133.12	0.69–125.25	0.69–125.25	0.69–125.25
(94)	(95)	(94)	(93)
8.65 ± 1.11	8.63 ± 1.21	8.55 ± 1.21	7.45 ± 1.16
0.01–28.97	0.01–28.97	0.01–28.97	0.01–28.97
(56)	(51)	(50)	(48)
17.65 ± 1.91	17.98 ± 1.84	18.50 ± 1.92	17.94 ± 2.16
0.003–29.21	0.003–9.21	0.003–29.21	0.003–29.21
(27)	(31)	(28)	(24)
15.92 ± 1.32	17.69 ± 1.17	17.05 ± 1.11	17.98 ± 1.02
0–29.22	0.70–29.22	0.67–29.33	0.67–29.33
(58)	(61)	(68)	(74)
20.46 ± 6.13	13.87 ± 3.75	22.54 ± 6.22	19.88 ± 5.92
0–487.26	0–295.18	0–466.80	0–466.80
(98)	(98)	(99)	(99)