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Por medio de la presente me permito informar a usted que en la reunión ordinaria del Subcomité de (Ecología y Manejo Integral de Ecosistemas), del Posgrado en Ciencias Biológicas, celebrada el día 28 de octubre del 2013, se acordó poner a su consideración el siguiente jurado para el examen de DOCTOR EN CIENCIAS del alumno **RIVERA ORTÍZ FRANCISCO ALBERTO** con número de cuenta **97362416,** con la tesis titulada: **"Genética de la conservación, pérdida y caracterización del hábitat de la Guacamaya Verde (*Ara militaris*) en México"**, bajo la dirección del **Dr. Alberto Ken Oyama Nakagawa.**

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Todo nos amenaza:

el tiempo, que en vivientes fragmentos divide

al que fui

del que seré,

como el machete a la culebra...

Octavio Paz

Ningún hombre es una isla,

algo completo en sí mismo;

todo hombre es un fragmento del continente,

una parte de un conjunto.

John Donne

ÍNDICE

RESUMEN

La Guacamaya Verde (*Ara militaris*) es una especie amenazada a nivel global y en peligro de extinción en México, principalmente por la perdida de hábitat y la caza por el comercio ilegal. Esta especie se distribuye en dos vertientes, la primera en el Pacifico y la segunda en el Golfo de México, asociado a los bosques tropicales caducifolios y subcaducifolios. Para evaluar esta asociación con los bosques tropicales secos, se realizó la caracterización del hábitat a lo largo de su distribución y se evaluaron los cambios y la pérdida de la cobertura vegetal a lo largo de su distribución en cuatro escenarios temporales (1970, 1996, 2000, 2010). También se evaluó el efecto de la fragmentación y la pérdida del hábitat sobre la diversidad genética en los tetrápodos (anfibios, reptiles, aves y mamíferos), por medio de un meta-análisis. Finalmente, se analizó la diversidad y la estructura genética de la Guacamaya Verde utilizando microsatélites con el fin de conocer el estado actual de la diversidad genética de la especie para futuras acciones de conservación. En esta tesis se muestra que la Guacamaya Verde requiere sitios con gran cobertura vegetal, con árboles mayores de siete metros de altura con diámetros a la altura del pecho (DAP) de 70 cm para poder anidar. Encontramos asimismo que la Guacamaya Verde tiene alta afinidad con ciertas especies de árboles de los géneros *Cyrtocarpa, Brosimum, Celtis, Hura, Bunchonsia, Lysiloma* y *Bursera*. Estas especies de árboles tienen una distribución similar a la de la Guacamaya Verde y son indispensables como recurso para su anidación y alimentación. Al analizar la pérdida de la cobertura vegetal, el área de distribución potencial de la Guacamaya Verde, se aprecia que ha disminuido en 30% en los últimos 40 años; además, los sitios más afectados por la fragmentación y pérdida del hábitat son los que presentan de cinco a ocho especies arbóreas importantes para la Guacamaya

Verde. Estos datos manifiestan la importancia de incrementar el área de las zonas protegidas de bosques naturales para preservar el hábitat potencial de la Guacamaya Verde en México. A través de los resultados del meta-análisis, se encontró que la fragmentación del hábitat reduce la diversidad genética global de las poblaciones de tetrápodos, detectándose efectos negativos significativos de la fragmentación para los anfibios, aves y mamíferos. Dentro de cada grupo taxonómico, las especies con tamaños corporales grandes fueron afectados significativamente por la fragmentación. El tiempo transcurrido en el estado de fragmentación fue también decisiva; poblaciones de tetrápodos que sobreviven en los sistemas fragmentados de más de 50 años mostraron una erosión genética significativa. Los resultados encontrados permiten identificar y determinar las probabilidades de los riesgos de extinción de las poblaciones silvestres y ayudar a generar criterios para priorizar los esfuerzos de conservación. La diversidad genética encontrada en la Guacamaya Verde fue moderada en comparación con otros psitácidos. La destrucción del hábitat y la caza furtiva son factores que afectan negativamente a las poblaciones naturales y que representan un amenaza para la supervivencia de esta especie. Se encontró estructura genética en las poblaciones de esta especie, lo cual indica la necesidad de proteger diferentes regiones con el fin de mantener su diversidad genética. En este sentido, la creación de un sistema de corredores naturales entre las poblaciones remanentes de la especie ayudarían al mantenimiento del flujo génico entre las poblaciones de la Guacamaya Verde y por lo tanto su sobrevivencia en la naturaleza.

ABSTRAC

The Military Macaw (*Ara militaris*) is a globally threatened species and endangered in Mexico primarily by habitat loss and hunting by illegal trade. This species is distributed in two versants, the first in the Pacific and the second in the Gulf of Mexico associated of the tropical deciduous forests and semi-deciduous. To evaluate this association with tropical dry forests, was conducted habitat characterization along its distribution and is evaluated the changes and the loss of vegetation cover along four temporal scenarios (1970, 1996, 2000, 2010). Also has assessed the effect of habitat fragmentation and loss of genetic diversity in tetrapods (amphibians, reptiles, birds and mammals) by performing a meta-analysis. Finally was analyzed diversity and structure genetic and of the Military Macaw by using of the microsatellite with molecular marker in order to determine the current status of the genetic diversity of the species for conservation future actions. In this thesis it was shown that the Military Macaw, requires sites with great cover, with trees over seven feet tall with Diameters at Breast Height (DBH) of 70 cm to be able nesting. In this thesis we discovered that the Military Macaw has a high affinity to certain species of trees such as: *Cyrtocarpa*, *Brosimum*, *Celtis*, *Hura*, *Bunchonsia*, *Lysiloma* and *Bursera*. These tree species are distributed similarly to the distribution of Military Macaw and are an indispensable resource for nesting and feeding. When analyzing the loss of forest cover, the potential range of Military Macaw has decreased by 30% and sites that presented 5 - 8 tree species important for Military Macaw are the sites most affected by fragmentation and habitat loss, so it is suggested that the natural forest protected areas must be increased to preserve habitat potential of the Military Macaw in Mexico. Through our meta-analysis results is showed that habitat fragmentation reduces overall genetic diversity of populations of tetrapods and

detected strong negative effects of fragmentation habitat to amphibians, birds and mammals. Within each taxonomic group, large body size species were strongly affected by fragmentation habitat. The elapsed time in the state of fragmentation was also decisive; tetrapod's populations surviving in fragmented systems over 50 years showed strong genetic erosion. The results that are found should help to identify and determine the probability of extinction risk in wild populations and help generate criteria to prioritize conservation efforts. The genetic diversity found in the Military Macaw was moderate compared to other psittacidae, the value of genetic diversity detected in the Military Macaw seems to not pose a threat to the survival of this species, but habitat destruction and poaching are factors adversely affecting wild populations. Individuals from two locations in the versant of the Gulf of Mexico are genetically distinct to nuclear level from rest of populations of Military Macaw, whereby is found a genetic structure in populations of this specie. The observed genetic structure does the need to protect different regions in order to maintain genetic diversity of the Military Macaw, in this sense, the creation of a system of natural corridors between remnant populations of the species ensures the maintenance of gene flow between Military Macaw populations and therefore their survival in nature.

1.0 Introducción general

Una de las principales amenazas para la persistencia de las especies son la pérdida y fragmentación de los ecosistemas que ocasionan una disminución en la diversidad biológica (Sutherland, 2000; Solórzano et al., 2003). Durante las últimas décadas, el problema de la fragmentación y la pérdida del hábitat de los ecosistemas es reconocida en el campo de la biología de la conservación como los efectos más devastadores sobre la biodiversidad (Saunders et al., 1991; Fahrig, 2003; Alcaide et al., 2009).

La fragmentación de los bosques es un proceso que divide el hábitat continuo en pequeños parches, el cual puede producirse por factores naturales. Sin embargo, la causa más importante del incremento a gran escala de la fragmentación es el cambio de uso de suelo por los seres humanos (Foster, 1980; Andren, 1994). Las actividades humanas han modificado el hábitat natural ocasionando la pérdida de la continuidad de los ecosistemas, cambios importantes en la estructura de las poblaciones y las comunidades, así como la reducción general en el tamaño de las poblaciones y la conexión entre las poblaciones naturales y los fragmentos remanentes de hábitat (Saunders et al., 1991; Fahrig, 2003; Alcaide et al., 2009), afectando las tasas de natalidad y mortalidad e incrementando la competencia intra e interespecífica (Primack, 1998). Las poblaciones fragmentadas tienden a reducir sus tamaños poblacionales, se aíslan disminuyendo el flujo genético y el tamaño efectivo de la población y, por consiguiente, se incrementa la probabilidad de los apareamientos entre congéneres (endogamia) ocasionando una reducción en la diversidad genética (Avise, 1989; Frankham, 1995; Reed y Frankham, 2003; Caizergues et al., 2003).

Los estudios en el campo de la biología de la conservación han contribuido con propuestas conceptuales y metodológicas para estandarizar criterios para conocer el estatus de conservación de cada especie y minimizar la pérdida de la diversidad biológica en todos sus niveles (Simberloff, 1988; Solórzano, 2003). Para conocer el estatus de conservación de las especies se requiere de un conocimiento detallado de su biología, ecología y genética (e.g. demografía, conducta reproductiva, diversidad genética). Además, es importante conocer los factores que han causado un declive poblacional y colocado en riesgo de extinción a varios taxas, como los procesos de fragmentación y la pérdida del hábitat (Fernández et al., 2003; Solórzano, 2003). Por lo tanto, es necesario determinar y evaluar el estado de conservación de los hábitats de las especies amenazadas.

1.1 Estructura, composición del hábitat y análisis de la cobertura vegetal

Entender los requerimientos de hábitat de las poblaciones de animales tiene un enorme valor para los esfuerzos por conservar especies amenazadas (Garshelis, 2000). Debido a que tales requerimientos son específicos para cada especie (James y Shugart, 1970), es importante determinar este tipo de relaciones para realizar predicciones acerca de la capacidad de la especie para responder a cambios en el tiempo y espacio. Además, es necesario obtener información para el manejo de las poblaciones, por lo cual una cuantificación rigurosa de los atributos de la vegetación ayuda a comprender detalladamente la composición y estructura de cada hábitat (Rotenberry, 1978; Brower et al., 1990; Bibby et al., 2000; Botero-Delgadillo et al., 2011). Los estudios de caracterización del hábitat y la composición florística de una localidad arrojan información muy útil para el manejo y conservación de aquellas

áreas que cuenten con las mismas características físicas y florísticas (e.g. altura, tipo de vegetación, cobertura vegetal, especies vegetales compartidas) y de esta manera tratar de conservar estas áreas adecuadas y útiles para las especies (Rue, 1967; Zamora-Crescencio et al., 2008).

Otra herramienta que permite evaluar diferentes aspectos relacionados con las características del hábitat es el uso de sistemas de información geográfica (SIG´s) (Martínez, 1994; Pinedo, 1995; Solórzano, 2003; Ríos-Muñoz y Navarro-Sigüenza, 2009), que permiten el modelaje cartográfico combinando una serie de datos procedentes de bases de datos digitalizadas (e.g. curvas de nivel, precipitación, tipos de vegetación, tipos de suelos) que ayudan a conocer los cambios en la distribución y en la cubierta forestal a diferentes escalas y tiempos, así como el mapeo de las características físicas y ambientales de los diferentes ecosistemas y permitir anticiparse a los cambios en el uso del suelo, para sugerir planes de manejo adecuado de los recursos naturales (Wadswhorth y Treweek, 1999; Solórzano, 2003; Ríos-Muñoz y Navarro-Sigüenza, 2009; Contreras-Medina et al., 2010), y así proponer acciones para la conservación del hábitat, que permiten la preservación de aquellas especies amenazadas.

En el presente trabajo, se caracterizó el hábitat de la Guacamaya Verde (*Ara militaris*) para determinar la estructura vegetal y la composición florística a lo largo de su distribución en México. También se utilizó el SIG para evaluar los cambios en la cubierta forestal de su distribución en México. *Ara militaris* está estrechamente asociada a los bosques tropicales caducifolios y subcaducifolios que son utilizados como un hábitat para reproducción, forrajeo y descanso (Forshaw, 1989; Rivera-Ortíz et al., 2008; Contreras-González et al., 2009). Estos ecosistemas son clasificados como bosques tropicales secos y se caracteriza por una marcada

estacionalidad y se localizan en zonas de los 0 a los 1900 metros de altitud aunque en los declives del Golfo de México no se le observa por arriba de los 800 metros de altitud. La temperatura promedio anual de estos bosques oscila entre 20 - 29 ºC. Este tipo de bosque es reconocido en todo el mundo por su estructura arbórea dominante el cual oscila generalmente entre los 5 y 15 metros de altura, pero frecuentemente entre 8 y 12 metros (Rzedowski, 1978; Bullock et al., 1995; Trejo y Dirzo, 2000). Las trepadoras y epifitas son escasas y solo se encuentran con cierta abundancia en cañadas o barrancas; entre las epifitas destacan bromeliáceas del género *Tillansia* (Rzedowsky, 1978). En cuanto a la dominancia, lo común en este tipo de vegetación son las pocas especies arbóreas o algunas veces puede ser una sola (Bullock et al., 1995).

Estos bosques tropicales secos son considerados prioritarios para su conservación por albergar una gran cantidad de especies endémicas de plantas y vertebrados (Trejo y Dirzo, 2000). En México se estima que el bosque tropical seco ocupa el 60% de la superficie del total de la región neotropical (Dirzo y García, 1992; Trejo y Dirzo, 2000) y presentan de acuerdo a datos de la FAO (2012), tasas de pérdida anual del 1.1 al 2%, principalmente debido a la industria del turismo, la agricultura y la ganadería (Trejo y Dirzo, 2000).

1.2 Genética de la conservación

La conservación de las especies con poblaciones fragmentadas y en peligro de extinción pasa por un conocimiento previo y profundo de su dinámica y estructura metapoblacional, lo cual supone la determinación de la variabilidad genética dentro y entre poblaciones. Los marcadores moleculares nos permiten identificar poblaciones

con una diversidad genética reducida y generalmente más vulnerables a un posible cambio ambiental, así como distinguir subpoblaciones genéticamente diferenciadas del resto para dirigir los esfuerzos de conservación hacia ellas. Del mismo modo, permiten descubrir genealogías genéticas y conocer el grado de parentesco entre individuos con el fin de determinar y conocer los procesos de consanguinidad (González, 2003).

La genética de la conservación tiene como objetivo principal el conocer los patrones genéticos y la evaluación de los procesos evolutivos de las especies en peligro de extinción e identificar posibles amenazas que pongan en riesgo la sobrevivencia de éstas (Frankham, 2003; Solórzano, 2003; Martínez-Cruz, 2011).

Los aspectos que se evalúan con la genética de la conservación son principalmente la endogamia, la pérdida de la diversidad genética, la fragmentación de las poblaciones y la reducción del flujo de genes, la deriva génica, efectos fundador, cuellos de botella, la resolución de incertidumbres taxonómicas, definición de las unidades de manejo dentro de las especies, así como también el uso de análisis genéticos moleculares para entender aspectos de la biología de las especies importantes para la conservación (Hartl y Clark, 1997; Frankham, 2003; Martínez-Cruz, 2011). Así también se puede recurrir al enfoque filogeográfico para esclarecer los principios y procesos que gobiernan la distribución geográfica de la diversidad genética dentro y entre poblaciones o especies (Avise, 2000).

En genética de la conservación se utilizan marcadores moleculares cuyo desarrollo ha permitido realizar un análisis aleatorio del genoma (Avise, 1994; Lande, 1999; Frankham et al., 2002). Estos análisis genéticos proporcionan información para valorar el estado de conservación de las poblaciones de una especie que han permitido tomar decisiones adecuadas para su manejo y protección

(Lande, 1999; Solórzano, 2003). Los análisis de estructura genética permiten adjudicar la existencia de diferencias significativas en la composición genética de las distintas poblaciones de una especie y describir sus niveles de diferenciación (Hedrick, 1999; Martínez–Cruz et al., 2004).

Los microsatélites son uno de los marcadores moleculares más utilizados ya que son marcadores codominantes que consisten en secuencias cortas (1 a 6 bases núcleotidicas) repetidas en tándem y sufren pérdidas y ganancias de repeticiones, lo cual genera un gran número de polimorfismos (Schlötterer y Tautz, 1992; Amos, 1999). Los microsatélites tienen importantes ventajas; son abundantes, presentan niveles altos de polimorfismo y son neutros, por lo cual aportan información muy útil para resolver problemas tanto específicos como individuales (Bruford y Wayne, 1993; Jarne y Lagoda, 1996) permitiendo abordar problemas principalmente de análisis de la estructura genética poblacional (Paetkau et al., 1995; Valsecchi et al., 1997) y problemas de paternidad y parentesco (Dow y Ashley, 1996), entre otros,. Por ello se ha convertido en los últimos años en uno de los marcadores mas utilizados en estudios de conservación y manejo de especies en peligro de extinción (González, 2003).

Las razones por las cuales los microsatélites son utilizados en los estudios de especies en peligro de extinción y en planes de conservación se debe a que son fáciles de obtener en una gran cantidad de especies, y son de fácil comparación y automatización (Beaumont y Bruford, 1999; Goldstein y Schlötterer, 1999).

La toma de decisiones eficaz es crucial en el área de la genética de la conservación, donde los gestores de vida silvestre rigen la probabilidad de supervivencia de una especie. La genética de la conservación ayuda a los gestores proteger la biodiversidad mediante la identificación de una serie de unidades de

conservación que incluyen: Unidades Evolutivas Significativas (ESU's), Unidades de Manejo (MU`s), Unidades de Acción (AU`s) y las Unidades de Familias Anidadas (FN`s). La idea de proponer políticas de conservación en unidades por debajo del nivel de especie utilizando datos moleculares ha cobrado gran importancia cuando se acuñaron estos conceptos (Ryder, 1986; Qiu-Hong, 2004).

En esta tesis seguiremos bajo el concepto de las MU`s, debido a nuestro marcador molecular (microsatélites) proporciona una herramienta muy precisa para establecer vínculos con posibles poblaciones parentales. Las MU`s, son unidades de conservación que integran la demografía, la estructura y diversidad genética de distintas poblaciones (Domínguez–Domínguez y Vázquez–Domínguez, 2009). El criterio para establecer las MU´s se basa en frecuencias haplotípicas y alelos nucleares, es decir presencia de haplotipos no compartidos con otras poblaciones (Moritz, 2002).

Las MU´s están destinadas a ser un nivel de unidad de conservación por debajo de la ESU´s, antes de estableces una ESU´s, es evidente explorar la historia de la población para inferir las fuerzas demográficas, como las barreras geográficas, glaciaciones, cambios ecológicos y otros factores (Moritz, 1999). El enfoque de las MU`s esta en la estructuración poblacional contemporánea y el seguimiento a corto plazo, lo que requiere una determinación de la estructura genética reciente, los patrones de dispersión y migración de las poblaciones fragmentadas actualmente (Moritz, 1999; Qiu-Hong, 2004)

Sin embargo, encontrar un método que permita la identificación correcta de las unidades prioritarias para la conservación es hasta la fecha es casi imposible, por lo cual el proceso de identificación de estas unidades se debe tener clara la

división de la diversidad biológica en dos componentes: i) aquella resultante del aislamiento histórico y II) la que tienen que tiene que ver con la evolución adaptativa (Moritz, 2002; Vázquez–Domínguez, 2002; 2007; Domínguez-Domínguez y Vázquez-Domínguez, 2009). A pesar de esta discusión vigente en el campo de la biología de la conservación, estos conceptos han logrado precisar propuestas significativas de conservación y ha permitido la protección de varias poblaciones de especies amenazadas y en peligro (Frankham et al. 2002, Solórzano 2003).

Toda esta información expuesta sirve como marco teórico para entender el caso de la Guacamaya Verde, una especie que se encuentra amenazada a nivel mundial de acuerdo al Apéndice I de CITES (UNEP-WCMC, 2010) y en México debido a la reducción de sus poblaciones y la alta fragmentación de sus colonias. La SEMARNAT la incluye en la NOM-059-SEMARNAT-2010 como una especie en peligro de extinción. A pesar que es considerada en peligro esta especie, se tiene poco conocimiento que se limita principalmente a la biología básica y pocos estudios sobre su ecología.

2.0 Sistema de estudio

2.1 Clasificación

Las relaciones filogenéticas y de sistemática del orden Psitaciformes no están claramente establecida, y han sido áreas de estudio en los últimos veinte años. Joseph et al. (2012) realizo una revisión sustancial de las relaciones evolutivas a nivel supra-genérico, incorporando estudios tanto moleculares como morfológicos, presentando una clasificación mas normalizada que refleja la filogenética de este orden. Esta clasificación pone a el orden Psittaciforme como un grupo monofiletico

que se divide en tres familias: i) Cacatuidae (cacatúas) con seis géneros y 21 especies, ii) Strigopidae (loros de Nueva Zelanda) con dos géneros y tres especies, y iii) Psittacidae (Loros y Guacamayas verdaderas) que incluye 78 géneros y 330 especies distribuidas en las zonas tropicales y subtropicales de América, África - Asia y Australia (Forshaw, 1989; Joseph et al., 2012).

La familia Psittacidae está conformada por cinco subfamilias, la subfamilia Arinae esta constituida por 148 especies en 30 géneros, siendo uno de los más representativos el género *Ara* (guacamayas) (Forshaw, 1989; Collar, 1997). El género *Ara* está conformado por ocho especies y son exclusivas del Continente Americano, se distribuyen desde México hasta el norte de Argentina (Collar, 1997). *A. glaucogularis* y *A. rubrogenys* son endémicas de Bolivia; *A. ararauna* y *A. severa* se distribuyen en Panamá, Paraguay, Bolivia y Brasil; *A. macao* se encuentra desde el sur de México hasta Bolivia; *A. ambiguus* se localiza desde Honduras hasta Colombia; *A. chloroptera* se distribuye de Panamá hasta el norte de Argentina y *A. militaris* la cual tiene una distribución fragmentada en las regiones tropicales y subtropicales desde el norte de México hasta el norte de Venezuela, noroeste de Venezuela, noroeste e Bolivia y este - sur de Colombia, este de Ecuador, noroeste de Perú y noroeste de Argentina (Forshaw, 1989; Iñigo-Elías, 1999; 2000_1; Strewe y Navarro, 2003).

El Sistema Integrado de Información Taxonómica (consultado el 30 de Octubre del 2013) reconoce que *Ara militaris* se dividen en tres subfamilias, *A. m. militaris* (Liinaeus, 1766), *A. m. bolivianus* (Reichenow, 1908) y *A. m. mexicanus* (Ridway, 1915). Las diferencias entre las subespecies están más definidas por las áreas de distribución, *A. m. bolivianus* se encuentra restringida de Bolivia hasta el Norte de Argentina (Navarro et al., 2008), *A. m. militaris* se localiza de Venezuela al

sudeste de Perú (Desenne y Strahl, 1994) y *A. m. mexicanus* solo se localiza en México (Peterson y Chaliff, 1989; Howell y Webb, 1995).

La Guacamaya Verde en México se presenta de manera fragmentada en colonias aparentemente aisladas y se distribuye en dos áreas separadas, la primera en la vertiente del Pacífico en regiones tropicales secas, desde el sureste de Sonora pasando por Chihuahua hasta Chiapas (Peterson y Chaliff, 1989; Howell y Webb, 1995), y la segunda en la vertiente del Golfo donde se ha reportado en Tamaulipas, San Luis Potosí y Querétaro (Peterson y Chaliff, 1989; Howell y Webb, 1995; Iñigo-Elías, 1999; Arizmendi y Márquez, 2000; Iñigo-Elías, 2000a; 2000b$_2$). En el Interior del país la Guacamaya Verde se localiza en el Sótano del Barro en Querétaro y en la Cañada Cuicateca en Oaxaca (Gaucín, 1999; Rivera-Ortíz et al., 2008; Contreras-González et al., 2009) (Figura 1).

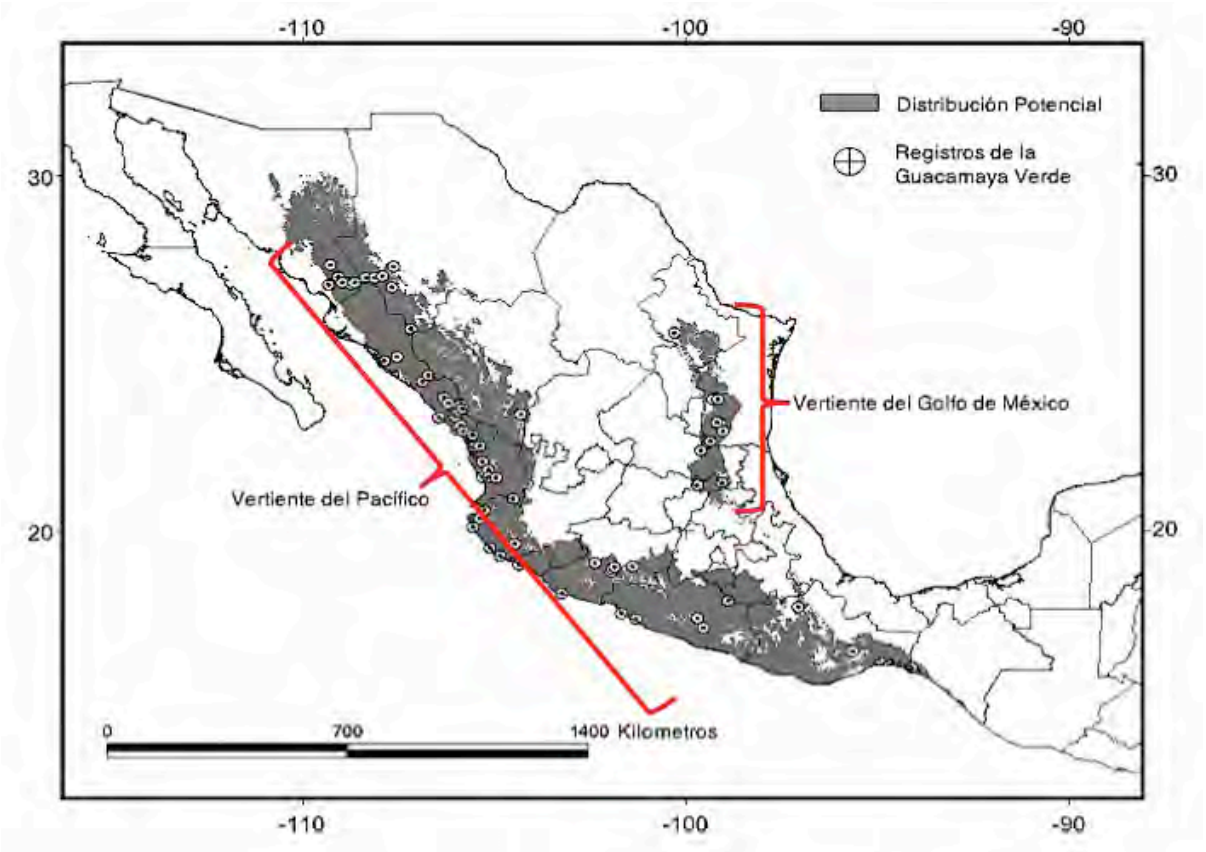

Fig. 1. Distribución potencial de la Guacamaya Verde (*Ara militaris*) en México. Los círculos blancos tachados nos muestran los registros históricos y actuales de la distribución de la Guacamaya Verde. La zona gris muestra el área de distribución potencial de la Guacamaya

2.2 Ciclo Reproductivo

La Guacamaya Verde en México se reproduce en los bosques tropicales caducifolios y subcaducifolios que se localizan entre los 200 y 1900 msnm (Forshaw, 1989; Collar y Juniper, 1992; Howell y Webb, 1995). Presentan dos formas de anidación, en el bosque tropical seco se les observa anidar en agujeros de riscos de piedra cárstica y en el bosque tropical subcaducifolio anida en agujeros de arboles vivos y muertos con un D.A.P. mayor a los 60 cm (Carreón, 1997; Gómez, 2004; Rivera-Ortiz et al., 2008, Rivera-Ortíz et al., en prensa).

El inicio de la reproducción varía de acuerdo a las regiones donde se distribuye esta especie: Carreón (1997) y Gómez (2004) reportan que inicia la reproducción en octubre con el cortejo y termina en marzo con el vuelo de los primeros volantones en la zona de la vertiente del Pacífico. En la zona del centro del país y en la vertiente del Golfo de México, Gaucín (1999) y Rivera-Ortíz et al. (2008) reportan que el inicio de la reproducción empieza en diciembre – enero con el cortejo y termina en julio – septiembre con el vuelo de los volantones.

El comportamiento de anidación de la Guacamaya Verde es muy parecida a otras especies de psitácidos (e. g. Monterrubio et al., 2002; Seixas y Mourao, 2002). El ciclo reproductivo está representado por seis periodos: i) cortejo y formación de parejas, ii) selección de cavidades, iii) copulación, iv) incubación, v) crianza de pollos y vi) vuelos de los juveniles (Carreón, 1997; Gaucín, 1999; Gómez, 2004, Rivera-Ortíz et. al., 2008).

La formación de parejas y cortejo tiene una duración aproximadamente de dos meses, las parejas establecidas se separan del grupo y se dedican al cortejo. La selección de cavidades es realizada de manera conjunta por la pareja, en esta etapa

pueden existir interacciones antagonistas por competencia por las cavidades, esta etapa dura aproximadamente un mes y medio (Gaucín, 1999, Rivera-Ortíz et. al., 2008). La cópula se observa en los primeros meses del inicio de la reproducción (aprox. cuatro meses), en este periodo se observa una intensa actividad en las zonas de anidación (Carreón, 1997; Gaucín, 1999; Rivera–Ortiz et al., 2008). Al año se produce una sola puesta, de uno a dos huevos (Carreón, 1997). La incubación es realizada por la hembra y dura alrededor de 28 a 30 días, el macho sale a las zonas de forrajeo regresando para alimentar a la hembra, la hembra pasa cerca del 90% dentro y/o cerca del nido. La crianza de pollos se desarrolla por ambos padres y dura dos a tres meses, durante este periodo ambos padres se dedican a alimentar a los pollos y forrajean más cerca del nido (Carreón, 1997, Rivera-Ortíz et al., 2008). El vuelo de los juveniles se da al final de la temporada reproductiva, el primer vuelo se da un mes antes de que el alimento empieza escasear y alcanzan una madurez sexual hasta los cinco años (Rivera-Ortíz et al., 2008; Contreras-González et al., 2009). El éxito reproductivo de la Guacamaya Verde es bajo alrededor del 8.5 % al 23.3% de los pollos alcanzan hacer juveniles (Carreón, 1997; Gaucín, 1999; Gómez, 2002; Rivera-Ortíz et al., 2008).

2.3 Migración y alimentación

La Guacamaya Verde realiza migraciones altitudinales hacia diferentes tipos de bosques que se encuentran entre las latitudes de los 0 a los 2300 msnm. Los tipos de vegetación que son utilizados durante estos movimientos migratorios son el bosque tropical caducifolio, bosque tropical subcaducifolio y bosques de encino de tierras bajas (Gaucín, 2000; Contreras-González et al., 2009). La dinámica de la

migración para la especie es compleja y se desconoce totalmente, hasta la fecha no se cuenta con esta información y no hay estudios de telemetría, debido a que es una especie difícil de capturar, además que es muy sensible a la presencia humana (Gaucín, 2000).

El cambio en la abundancia del recurso alimenticio es el factor que se ha propuesto como la causa de los desplazamientos altitudinales en *A. militaris* como en otras especies de psitácidos y aves frugívoras, ya que las éstas son capaces de rastrear el alimento en escala espacial y temporal (Renton, 2001; Oliveira et al., 2002; Symes y Perrin, 2003; Codensio y Bilenca, 2004; Freifeld et al., 2004; Karubian et al., 2005; Contreras-González et al., 2009).

Las especies arbóreas que forman parte de la dieta de la Guacamaya Verde presentan una marcada estacionalidad entre estas especies se destaca: *Cyrtocarpa, Bursera, Celtis, Brosimum, Plumeria, Quercus, Lysiloma, Bunchonsia y Pseudobimbax*, las cuales presentan una gran cantidad de proteínas y lípidos, indispensables en la época reproductiva (Carreón, 1997; Gaucín, 2000; Contreras-González et al., 2009).

La Guacamaya Verde es considerada especialista ya que solo consume entre el 10 y el 20 % de los recursos florísticos para alimentarse y aunque es clasificada como frugívora al igual que otros psitácidos, ocasionalmente puede cambiar de la frugívora a la herbívora o insectívora debido a que los frutos no pueden proveer un balance nutricional adecuados en la dieta (Contreras-González et al., 2009).

2.4 Problemática de la Guacamaya Verde

Dentro de la familia Psitacidae se encuentran un total de 90 especies en riesgo de extinción. La situación es crítica en la región neotropical, donde el 31% del total presente se encuentra en riesgo de extinción (Bennett y Owens, 1997). La situación para los Psitácidos en México es muy alarmante, ya que del total (20 especies), 13 especies se encuentran en alguna categoría de riesgo (SEMARNAT, 2010). La Guacamaya Verde es considerada en peligro de extinción (SEMARNAT, 2010) y a nivel mundial es una especie amenazada de acuerdo al Apéndice I de CITES (UNEP-WCMC, 2010). Se ha propuesto que la fragmentación del hábitat y el cambio de uso de suelo de su hábitat son una amenaza para sus poblaciones y ha llevado al declive poblacional (Ríos-Muñoz y Navarro-Sigüenza, 2009; Rivera-Ortíz et al., en prensa). Otro factor que amenaza sus poblaciones es el saqueo de individuos en los sitios de reproducción para el mercado ilegal (Iñigo-Elías, 1999), aunque no hay un estudio donde evalúen la magnitud de este saqueo sobre las poblaciones silvestres.

Esta conjunción de factores (fragmentación y perdida de habita, saqueo de nidos) en las poblaciones silvestres, han colocado a la Guacamaya Verde, una de las especies mas llamativas del continente americano, en un estado de conservación amenazado pero poco documentado.

Con base en la información presentada y disponible, la presente investigación tuvo como objetivo estudiar las características y estado de conservación del hábitat de la Guacamaya Verde, así como la diversidad y estructura genética de esta especie para proponer estrategias de conservación.

3.0 Objetivos

General

Evaluar la perdida y las características del hábitat de la Guacamaya Verde, así como analizar la diversidad y estructura genética contemporánea de esta especie, para generar estrategias de conservación.

Particulares

1. Determinar el impacto provocado el cambio de uso de suelo sobre las áreas hipotéticas disponibles para la supervivencia de la Guacamaya verde y caracterizar los elementos fundamentales del hábitat de esta especie, con base a las medidas de la estructura de la vegetación.

2. Evaluar el efecto de la fragmentación sobre la diversidad genética de las poblaciones de vertebrados (tetrápodos), mediante un meta – análisis.

3. Analizar la estructura de la diversidad genética de las poblaciones de la Guacamaya verde (*Ara militaris*) en México, para proponer medidas de conservación prioritarias para México.

4.0 Presentación

Esta tesis esta conformada por tres capítulos. En el Capítulo I se presenta la caracterización del hábitat en ocho poblaciones de la Guacamaya Verde en México. Se evaluó con más detalle la composición florística en estos sitios y la relación de la presencia de la Guacamaya Verde con las especies arbóreas. También se estimó la pérdida de la cobertura forestal en cuatro escenarios de tiempo asociados a la distribución potencial de la Guacamaya Verde en México. Este capitulo es un artículo publicado por Rivera-Ortíz et al. (2013) en la Revista Mexicana de Biodiversidad.

En el Capítulo II se realiza una revisión bibliográfica, donde se evalúa cuantitativamente, los efectos de la fragmentación sobre los parámetros genéticos de las poblaciones de tetrápodos (anfibios, reptiles, aves y mamíferos), mediante un meta-análisis. Se analizan diferentes variables como: el tamaño del cuerpo, la calidad del fragmento, y se evaluó si estas variables determinan la capacidad de encontrar efectos de la fragmentación del hábitat sobre la variabilidad genética. Este capitulo los constituye un articulo de investigación el cual fue enviado a la revista Animal Conservation para su eventual publicación.

En el Capítulo III se analiza los niveles de variabilidad genética de siete poblaciones de la Guacamaya Verde a lo largo de su distribución en México y se evalúa los niveles de estructura genética y tasas de flujo génico entre poblaciones. Se utilizan como marcador molecular a los microsatélites nucleares y se analizaron los resultados bajo el criterio de la genética de la conservación. Este capitulo es un articulo que será enviado a la revista Conservation Genetics para su eventual publicación.

Finalmente, en la discusión general de la tesis se presenta una reflexión integral sobre los diferentes tópicos de este estudio. Se analizan también información de otros estudios con el fin de examinar las particularidades y se plantean algunas nuevas preguntas de investigación a partir de lo encontrado en los diferentes capítulos.

5.0 Capítulo I

Rivera-Ortíz, F. A., Oyama, K., Ríos-Muñoz, C. A., Solórzano, S., Navarro-Sigüenza, A. G. and Arizmendi, M. C.

Habitat characterization and modeling the potential distribution of the Military Macaw (*Ara militaris*) in Mexico

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Habitat characterization and modeling of the potential distribution of the Military Macaw (*Ara militaris*) in Mexico

Caracterización del hábitat y modelación de la distribución potencial de la guacamaya verde (*Ara militaris*) en México

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Abstract. Forest structure and composition have been used to assess the habitat characteristics that determine bird distributions. The patterns of distribution have been shaped by historical and ecological factors that play different roles at both temporal and spatial scales. The objectives of this research were to characterize the habitat of the endangered Military Macaw (*Ara militaris*) and evaluate the potential distribution of this species based on trends of land use changes in Mexico. We characterized the community structure and floristic composition of 8 forests that are currently used by the Military Macaw for breeding and feeding and compared the results with 6 similar forests characterized in other studies but without historical records of the presence of the Military Macaw. The Military Macaw preferred sites with high diversity of plant species dominated by trees from 4 to 15 m in height and from 5 to 90 cm in diameter at breast height. We identified 236 plant species in the 8 forests with 20 species (8.4%) used for nesting and feeding by the Military Macaw. The floristic composition is important for the presence of the Military Macaw because there were significant differences between forests with and without its presence. The potential area of distribution of the Military Macaw had decreased by 32% and the remnant areas are included in only 8 National Protected Areas. The protected areas of natural forests should be increased to preserve the sites of potential distribution and consequently the habitat of the Military Macaw in Mexico.

Key words*: Ara militaris*, bird conservation, ecological niche modeling, forest community structure, habitat characterization, habitat loss.

Resumen. La estructura y composición del bosque se ha utilizado para evaluar las características del hábitat que determinan la distribución de las aves. Los patrones de distribución han sido moldeadas por factores históricos y ecológicos que desempeñan diferentes papeles en ambas escalas temporales y espaciales. Los objetivos de esta investigación fueron caracterizar el hábitat de la guacamaya verde en peligro de extinción (*Ara militaris*) y evaluar su distribución potencial sobre las tendencias de los cambios de uso del suelo en México. Se caracterizó la estructura de la comunidad y la composición florística de 8 fragmentos remanentes de bosque que actualmente utiliza la guacamaya verde para reproducirse y alimentarse, y se compararon estos resultados con los obtenidos en bosques similares en otros estudios pero sin registros de la presencia de guacamaya verde. La guacamaya verde prefiere zonas con una alta diversidad de plantas, dominadas por árboles de 4 a 15 m de altura y de 5 a 90 cm de diámetro a la altura del pecho en las 8 localidades muestreadas. Ser identificaron 236 especies de plantas en los 8 sitios de bosque de las cuales 20 (8.4%) son utilizadas para la anidación y la alimentación de la guacamaya verde. La composición florística es importante para la presencia de estas aves, ya que hubo diferencias significativas en esta composición entre los bosques con y sin su presencia. El área de distribución potencial de esta guacamaya ha disminuido en un 32% y las áreas remanentes están incluidas únicamente en 8 Áreas Naturales Protegidas. Las áreas protegidas de bosques naturales deben de incrementarse para conservar los sitios de distribución potencial y en consecuencia el hábitat de la guacamaya verde en México.

Palabras clave: *Ara militaris*, conservación de aves, modelación de nicho ecológico, caracterización de hábitat, estructura de la comunidad del bosque, pérdida de hábitat.

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Introduction

Forest structure and composition have been used to assess the habitat characteristics that determine bird distributions (Gillespie and Walter, 2001). Forest structure, such as leaf structural diversity, canopy coverage, volume and density of plants, and species composition, has been significantly correlated with bird distribution patterns (Gillespie and Walter, 2001; Warketin et al., 2003). These patterns of distribution have been shaped by historical and ecological factors that play different roles at both temporal and spatial scales (Vuilleumier and Simberloff, 1980; Hutto et al., 1986; Cherril and McClean, 1997; Gaston and Fuller, 2009). Food availability and habitat type determine the geographic distribution of bird species (Hutto, 1985; Orians and Wittenberger, 1991; Luke and Zack, 2001) because habitat selection by birds must ensure the availability of resources for food, nesting areas, and refuge against natural predators (Márquez-Olivas et al., 2002; Canales-del-Castillo et al., 2010; Emrick et al., 2010).

Characterization of preferred habitat of bird species could facilitate the prediction of the species' ability to respond to changes over time and space (Rotenberry, 1978), and eventually, this information may serve to support conservation policies if populations become threatened (Brower et al., 1990).

Moreover, recording the distribution and changes in forest coverage at different scales and times and mapping the physical and environmental characteristics of different ecosystems, allow conservationists to anticipate changes in land use and to suggest plans for appropriate natural resource management (Wadsworth and Treweek, 1999; Ríos-Muñoz and Navarro-Sigüenza, 2009; Contreras-Medina et al., 2010), that enable animal preservation in species threatened with extinction.

The Military Macaw (*Ara militaris*) is a species of conservation concern in Mexico, with a current estimated population size of less than 10,000 individuals and a clearly declining trend in that number (Collar, 1997; Snyder et al., 2000; Bird Life International, 2011). This species is included in the Appendix I of the Convention on International Trade of Endangered Species of Fauna and Flora (CITES, 1998) and is considered to be globally vulnerable (Bird Life International, 2011). In Mexico, the species is considered endangered according to federal regulations (Norma Oficial Mexicana, Nom-059-Semarnat-2010). Habitat destruction and illegal trade have been recognized as the main threats for survivorship of the Military Macaw (Íñigo-Elías, 2005).

The distribution of the Military Macaw ranges from Mexico (Sonora to Oaxaca states) to South America, with a major distribution gap in Central America (Collar, 1997; Bird Life International, 2011) that is occupied by the great Green Macaw (*Ara ambigua*). The Military Macaw lives in dry to semi-humid, warm sub-humid (Carreón, 1997; Rivera-Ortíz et al., 2008), and temperate (Juniper and Parr, 1998; Cruz-Nieto et al., 2006; Nocedal et al., 2006) climates with summer rains. During the reproductive season, the species distribution ranges from 0 to 2 500 m in altitude (Carreón, 1997; Rivera-Ortíz et al., 2008; Contreras-González et al., 2009).

The Military Macaw nests in holes in cliffs and in living or dead trees with a diameter at breast height (DBH) from 67 to 205 cm (Carreón, 1997). Locally, the species is considered a specialist feeder because it consumes few plant species (13 to 20) of the total species richness of a forest (Loza, 1997; Gaucín, 2000; Flores and Sierra, 2004; Contreras-González et al., 2009).

Despite its endangered status, a habitat characterization of sites for breeding, foraging and roosting of the Military Macaw has yet to be conducted. This information and a record of the distribution range of this bird species are critical in Mexico to design conservation actions. In this paper, we characterized the habitat of the Military Macaw based on composition and structural traits of forests used by the Military Macaw for feeding and reproduction. We also modeled the potential distribution of the Military Macaw based on its ecological niche traits and the geographic distribution of associated tree species that are considered suitable habitats for the species. We conducted this study to provide information to support conservation efforts for the Military Macaw in Mexico.

Materials and methods

Study areas. This study was carried out in 8 sites in Mexico. The selected sites contained some of the largest populations reported for the Military Macaw and covered most of the distribution range of the species in Mexico (Gaucín, 2000; Gómez, 2004; Rubio et al., 2007; Rivera-Ortíz et al., 2008; Jiménez-Arcos et al., 2012). Five of the sites were located on the Pacific slope: La Sierrita, Sonora; La Reserva de Nuestra Señora del Mineral, Sinaloa; El Mirador del Águila, Nayarit; El Tuito, Jalisco, and Papalutla, Guerrero. Two other areas were located on the Gulf of Mexico slope: El Cielo, Tamaulipas and Santa María de Cocos, Querétaro, and another site was located in central Mexico: Santa María Tecomavaca, Oaxaca (Table 1; Fig. 1).

Habitat structure: characterization. Sampling was conducted in the 8 sites where the Military Macaw was observed nesting, roosting, or foraging in 2010 and 2011. We recorded the tree coverage and the density of plant species, growth form, total plant density, leaf strata

Table 1. Sampling sites for the habitat characterization of *Ara militaris*

Locality (state)	*Location*	*Altitude* (m)	Precipitation *(mm)*	*Temperature (ºC)*	*Estimated area (km^2)*	*Vegetation*	*Estimated population size of the Military Macaw*	*References*
La Sierrita (Sonora)	26 °52'48" N 108 °34' 12" W	800-1 200	60	22	928	Tropical deciduous forest	38 individuals	Rivera-Ortiz F. A., unpublished results
Nuestra Señora del	24°24'44" N	500-1 800	250	24	512	Tropical deciduous forest	25-40 individuals	Rubio et al., 2007
Mineral (Sinaloa)	106°41'22" W							
El Mirador del	21°30'28" N	600-1 200	1 121	21	524	Tropical subdeciduous forest	50 individuals	Rivera-Ortiz F. A., unpublished results
Águila (Nayarit)	104°55'47" W							
El Tuito (Jalisco)	20°17'35" N 105°23'6.4" W	0-400	800	26	1 001	Tropical subdeciduous forest	14-24 individuals	Rivera-Ortiz F. A., unpublished results
Papalutla (Guerrero)	18°01'20.3" N 98°54'16.1" W	630-1 600	1 200	30	600	Tropical deciduous forest	25-35 individuals	Jiménez-Arcos et al., 2012
Santa María	17°51'43" N	660-820	400	22	41	Tropical deciduous forest	76 individuals	Rivera-Ortiz et al., 2008
Tecomavaca (Oaxaca)	97°02'40" W							
El Cielo	23°04'22" N	700-1 400	1 800	18	1 445	Tropical subdeciduous forest	35-40 individuals	Rivera-Ortiz F. A., unpublished results
(Tamaulipas)	99°09'24" W							
Santa María de	21°18'37" N	700-1 800	400	22	731	Tropical deciduous forest	70 individuals	Gaucín, 2000
Cocos (Querétaro)	99°40'4" W							

diversity (LSD), plant species richness (S), plant diversity (H'), and importance-values index (IVI) (Krebs, 1985; Brower et al., 1990). The sampling included all woody trees with stems with a diameter at breast height (DBH) of 10 cm or more and shrubs taller than 1.5 m, because the Military Macaw uses different layers of the canopy forests (Forshaw, 1989).

We conducted sampling efforts directed to specific zones of nesting, roosting, or feeding the Military Macaw in each site. In these specific areas, we corroborated the presence of the species and measured vegetation cover using transects covering representative areas of vegetation used by the Military Macaw (Fig. 1). In each site, 16 transects of 50 m^2 were divided into 4 transects of 25 m^2 each, and oriented to the 4 cardinal points. The plant density was obtained by placing a rod vertically on the forest floor every 1.5 m to record the total number of plants with which the rod made contact. This procedure was repeated until 16 records were obtained along the 4 transects of each plot. For each of the trees, the name, the number of contacts with the rod as well as the height, coverage, and DBH were recorded. Plant specimens were deposited at the Herbarium of FES Iztacala (IZTA) at the Universidad Nacional Autónoma de México (UNAM).

The density of trees and shrubs (total individuals / area) and species coverage (coverage= (π x major diameter x minor diameter) / 2) according to each growth form were estimated. To estimate the LSD, the heights of the contacted plants were grouped in 16 strata of 2 m in height (0-2 m stratum, 2.1-4 m stratum and so on, up to the 26.1-28 m stratum) and the LSD based on the Shannon-Wiener diversity index was calculated within each stratification (MacArthur and MacArthur, 1961). Using the abundance, frequency, and vegetation coverage data of each species, we calculated the importance value index (Ar + Fr + Cr= 0 to 3) for plant species and growth forms.

An analysis of similarity of structure and composition of plant species between sites with and without presence of the Military Macaw to date was conducted. Information of sites without record of the Military Macaw was obtained from available reports (Table 2).

Statistical analyses: comparison of structure and floristic composition. Data were tested for statistical normality using Shapiro-Wilk test and Levene's homogeneity of variance using SPSS software (SPSS, 2003). The data were $\log_{10}$ transformed when comparisons were made using parametric tests (Sokal and Rohlf, 1979). The differences in height, coverage, and DBH were compared using an Anova (Siegel and Castellan, 2003).

Comparisons of values of plant density and diversity by sampling area were performed using a permutational analysis of variance (Permanova) (Anderson, 2001, 2005).

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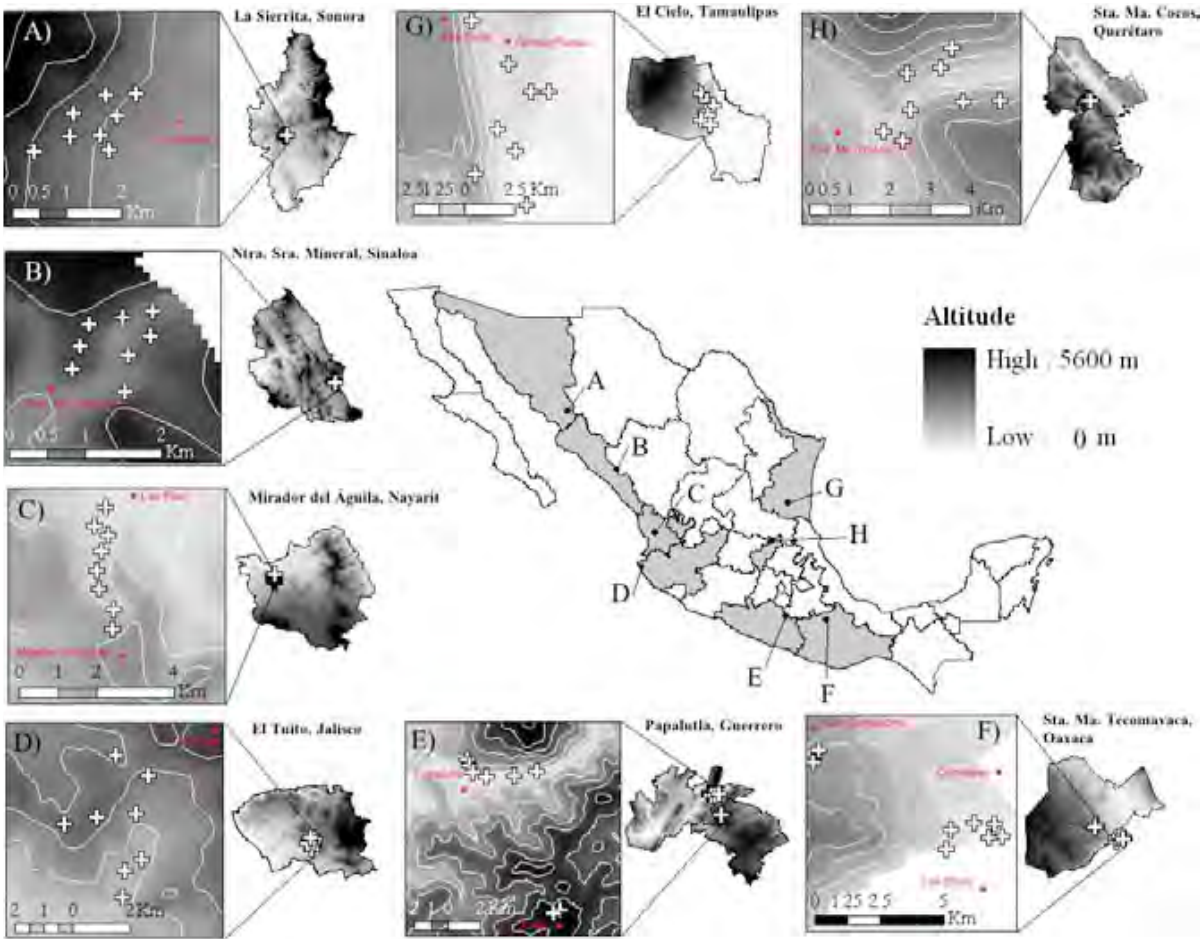

Figure 1. Sampling areas of *Ara militaris* along its distribution in Mexico. A, La Sierrita, Sonora; B, Nuestra Señora del Mineral, Sinaloa; C, Mirador del Águila, Nayarit; D, El Tuito, Jalisco; E, Papalutla, Guerrero; F, Santa María Tecomavaca, Oaxaca; G, El Cielo, Tamaulipas, and H, Santa María de Cocos, Querétaro. White crosses indicate the vegetation transects for habitat characterization of *Ara militaris*.

We used the Euclidean distance measure as recommended by Vázquez (2007). All of the tests were subjected to 9 999 permutations (α= 0.005) and the outcomes were analyzed using a t test based on an equal probability of significance.

The leaf structural diversity among localities was compared using the chi-square test (Siegel and Castellan, 2003). We used a t-test to compare the similarities in vegetation structure between the locations with and without records of Military Macaw (SPSS, 2003). In addition, the floristic composition between the localities with and without records of the Military Macaw was compared using the Sorensen's similarity index (PAST 2.12, 2001). *Distribution models, vegetation cover changes, and environmental overlap.* The models were constructed using the Genetic algorithm for rule-set production (Garp) through the desktop garp interface (Scachetti-Pereira, 2001), which has proved to be a useful tool in understanding the ecological and evolutionary processes that explain the distribution of organisms (Peterson and Navarro-Sigüenza, 1999; Anderson et al., 2002; Nakazawa et al., 2004). Garp works in an iterative process where there are formation of rules that are evaluated and then considered to pass, or not, to the next generation (Stockwell and Noble, 1992, Stockwell and Peters, 1999).

We generated models of potential distribution of the Military Macaw, the potential distribution of the most important tree plant species that are used by the Military Macaw for feeding or nesting and 4 scenarios of land cover changes as follows.

Potential distribution models were created using 19 environmental variables derived from weather climatic stations stored in the Worldclim Project 1.4 (Hijmans et al., 2005) and 3 topographic layers derived from the Hydro 1k project (http://edcdaac.usgs.gov/gtopo30/hydro). Although it has been stated that the inclusion of all 19 bioclimatic variables will be prone to overfitting (Peterson and Nakazawa, 2008), the use of all variables represents a conservative and a more reliable approach to estimate the potential distribution of the species (Jakob et al., 2009).

The pixel spatial resolution was set as 0.02° by 0.02° (*ca*. 4 km^2). The biological information used for each explanatory and response species was obtained from bibliographic sources. The geographical coordinates of the historical records for Military Macaw were obtained from the "Atlas of the birds of Mexico" (Navarro-Sigüenza et al., 2003), which is the largest collection of specimens contained in Mexican and foreign collections, as well as records taken directly from fieldwork. The records obtained in the field were sightings of nesting sites, roosting, and feeding.

For plants, the geographical coordinates were obtained from the Global Biodiversity Information Facility (GBIF, http://www.gbif.org) and specialized references (Gordon, 1981; Mitchell and Daly, 1991; Gale and Pennington, 2004; Pennington and Sarukhán 2005; Rzedowski et al., 2005; Espinosa et al., 2006).

The biological information of each species was divided into training (50% of the data) and validation points (the remaining 50% of the data). In total, 100 replicates for each species were generated using a limit of convergence such that the model rules could not improve in more than 1% or 1 000 iterations. The validation of the models was made using a X^2 and using the training and testing data to evaluate the predictive capacities of the replicates (Peterson and Shaw 2003; Ríos-Muñoz and Navarro-Sigüenza, 2009). Then, we selected the 10 best models as suggested by Anderson et al. (2002) based on minor errors of omission and values of commission close to the median. These distribution models were summed to obtain only one final consensus model. The consensus model was used to establish a threshold of presence/absence for all the species, which accounted for at least 90% of the biological data (Ríos-Muñoz and Navarro-Sigüenza, 2009). Once the threshold was established, we created binary models to represent the presence/absence of the species.

The resulting distribution models were linked to watersheds and biogeographical provinces where the Military Macaw and plant species have been recorded. Hence, based upon the biogeographic history of each taxon, potential distribution models were obtained (Illoldi-Rangel and Escalante, 2008; Ríos-Muñoz and Navarro-Sigüenza, 2009). The resulting distribution scenarios were overlapped to depict coincident areas, and the final model considered as the potential distribution of the Military Macaw was the intersection with the plant species potential distributions.

To evaluate the change in vegetation cover, we used 4 databases of land use change in the country, the first for 1973-1976 was based on serial photographs (Peterson et al., 2006, Ríos-Muñoz and Navarro-Sigüenza, 2009), and the series II (1990's), III (2005), and IV (2010) of land use change in Mexico (Inegi, 2000, 2005, 2010). The use of the database linkage permitted an identification of the Military Macaw habitat loss assessment (Ríos-Muñoz and Navarro-Sigüenza, 2009). In this sense, the 4 databases were reclassified and were considered unsuitable zones for the distribution of the plant species and the macaw. These zones were urban, agricultural, forestry, livestock, grassland, and non-vegetated areas (Sánchez-Cordero et al., 2005; Peterson et al., 2006; Contreras-Medina et al., 2010). Finally, we calculated the percentage of the area occupied in each temporary stage to obtain the pattern of habitat loss for the area associated with tree species richness. For this calculation, we considered the areas remaining in the year 2011 that were contained in the Natural Protected Areas system (NPAs) and the Important Bird Areas (IBAs) for Mexico.

Data from the same climatic layers used in the creation of the models of potential distribution for each recording site were extracted to construct a matrix to determine

Table 2. Community structure of deciduous and subdeciduous tropical forests reported without the presence of *Ara militaris*

Locality	*Type of vegetation*	*Coverage* (m^2 ha^{-1})	*Height* (*m*)	*DBH* (*cm*)	*Source*
El Limón, Morelos	Tropical deciduous forest	34.7	5.7	5.35	Trejo (1998)
Región Costa, Oaxaca	Tropical deciduous forest	23.4	5.53	6.58	Salas-Morales (2002)
La Trinitaria, Chiapas	Tropical deciduous forest	46.5	7.8	6.14	Trejo (1998)
Papantla, Veracruz	Tropical subdeciduous forest	152.95	27.0	50.75	Basañez et al. (2008)
Sayil, Yucatán	Tropical deciduous forest	36.7	7.9	3.3	Trejo (1998)
Tzucacab, Yucatán	Tropical subdeciduous forest	—	8.7	4.31	Zamora et al. (2008)

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the environmental overlap between the Military Macaw and the most important associated tree species. With this matrix, the variation of 19 environmental parameters and altitude were subjected to Principal Component Analysis (Pca) (Novak et al., 2010; Janzekovic and Novak, 2012) and to a discriminant analysis to identify if there was a separation between species (Military Macaw and tree species). Ellipses at 95% confidence for each species were estimated (Novak et al., 2010; Janzekovic and Novak, 2012). The overlap between the areas of the ellipses was calculated using the Jacquard index ranging from 0-1 (Real and Vargas, 1996). The statistics were performed in R 3. 0. 1. (R Development Core Team, 2008).

Results

Habitat characterization. A total of 236 plant species were recorded in the 8 sampled sites. We quantified a total of 1 353 trees and 424 shrubs in the 8 sampling sites. The sites with the highest plant density were Salazares (297 ind/ha) and El Tuito (291 ind/ha). In contrast, the sites with the lowest densities were La Sierrita (177 ind/ha) and Papalutla (121 ind/ha). However, no significant differences among sites were detected ($F_{7, 56}$= 0.95, p> 0.05). The tree growth form prevailed in all the sites (Table 3).

The vertical forest structure composed of 16 strata showed significant differences among the 8 sampled sites (X^2= 36.124, D. F.= 15, p< 0.001); the height strata varied from 0 to 28 m across the sites (Table 3). Trees and shrubs ranging from 2 to 10 m in height dominated the vertical forest stratification in the 8 sites; however, in the localities of El Mirador del Aguila and El Cielo, the tallest trees reached over 26 m (Fig. 2).

The highest species richness was documented in El Tuito (63 species), followed by Papalutla (59 species) and Nuestra Señora del Mineral (46 species); the site with the lowest species richness was Santa María de Cocos (22 species) (Table 3). The sites with the highest plant diversity were Papalutla (H' = 3.8) and El Tuito (H' = 3.5), while Santa María de Cocos had the lowest diversity (H'= 2.2). The analysis of permutational variance indicated that the diversity of plant communities was not significantly different among the sampling sites ($F_{7, 40}$= 0.83, p> 0.05) (Table 3).

The tree coverage significantly differed among the sites ($F_{7, 38}$= 0.56, p< 0.001) (Table 3). The sites with the greatest tree coverage were Mirador del Águila (162.85 m^2) and El Cielo (118.28 m^2). In contrast, the lowest tree coverage was documented in Papalutla (39.26 m^2) and Santa María de Cocos (50.73 m^2). The tree growth form had the highest coverage values in all of the sampling sites. The areas with plant species with greater height and larger DBH were Mirador del Águila, El Cielo, and El Tuito (Table 3). We found significant differences in height ($F_{7,38}$= 20.17, p< 0.001) and DBH ($F_{7, 38}$= 5.63, p< 0.001) among the sites.

The IVI values showed that plants sampled in all of the sites were highly variable (Appendix 1, supporting information). A total of 14 tree species (*Brosimum alicastrum*, *Bursera simaruba*, *Ceiba aescutifolia*, *Ceiba pentandra*, *Cyrtocarpa procera*, *Guaiacum coulteri*, *Guazuma ulmifolia*, *Hura polyandra*, *Haematoxylon brassileto*, *Ipomea arborences*, *Lysiloma divaricata*, *Lysiloma microphylla*, *Plumeria rubra*, and *Taxodium mucronatum*) had an IVI above 0.20 and were used for modeling their distribution in association with the modeling of the Military Macaw (see the corresponding section below).

The plants that showed the highest values of IVI were *Lysiloma divaricata, L. microphyla, Brosimum alicastrum, Hura polyandra*, and *Cyrtocarpa procera*. Important plant species that were present in more than one site were: *L. divaricata, B. alicastrum, H. polyandra, Taxodium mucronatum, Bursera simaruba*, and *Guazuma ulmifolia*. With the results of structure and composition obtained, it was observed that plant species with highest IVIs are those that the Military Macaw uses for feeding and nesting (Appendix 1).

Comparison of structure and floristic composition. In the vegetation structure, no significant differences were found comparing the cover height and DBH between sites with and without the Military Macaw [coverage ($t_{(11)}$= 0.987, p> 0.05), height ($t_{(12)}$= 1780, p> 0.05) and DBH ($t_{(12)}$= 15, p> 0.05)], indicating that the forests were structurally similar. A comparison of Sorensen´s similarity index among the sites confirmed 2 clearly separated groups; one contained those sites with records of the presence of the Military Macaw, and a second group formed by sites without the bird (Fig. 3).

Distribution models, land cover changes, and environmental overlap. All the models obtained presented predictions above the expected by random (X^2 test, all models: p< 0.01, D. F.= 1), Also, the potential distribution of the Military Macaw showed low levels of omission (i.e., the model was successful in predicting most of the primary source data), indicating a predictive power above 90%. Figure 4 shows the modeled distribution potential map of the Military Macaw and the most important plant species for feeding and nesting.

We analyzed the potential distribution and species richness of the important plants associated with the Military Macaw under 4 scenarios of land use change for the country (Fig. 4). In the potential distribution map without land use, the sites located in the Pacific slope had greater availability

Table 3. Habitat characteristics of *Ara militaris* in Mexico

Locality	*LSD*	*H´*	*S*	*Coverage* (m^2 ha^{-1})	*Height* (*m*)	*Density* (*Ind./ ha*)		*DBH* (*cm*)
						Trees	*Shrubs*	
La Sierrita	1.78	3.1	36	68.44 ± 14.11	16.41 ± 4.93	107	70	7.35 ± 0.74
Nuestra Señora del Mineral	1.90	3.2	46	81.44 ± 10.46	17.10 ± 1.16	179	90	8.88 ± 0.63
Salazares	2.57	2.7	37	162.85 ± 22.83	27.23 ± 3.00	149	48	140.50±1.7
El Tuito	2.13	3.5	63	96.24 ± 16.21	18.79 ± 2.36	245	46	74.70± 0.38
Papalutla	1.52	3.8	59	39.26 ± 6.74	10.66 ± 2.30	90	41	4.52 ± 0.74
Santa María Tecomavaca	1.19	3.2	38	58.82 ± 14.93	13.82 ± 2.42	166	21	2.93 ± 0.20
El Cielo, Tamaulipas	2.43	2.8	35	118.28 ± 22.40	23.91 ± 3.95	199	69	123.10±1.1
Santa María de Cocos, Querétaro	1.54	2.2	22	50.73 ± 4.52	9.78 ± 1.25	218	39	5.62 ± 0.39

LSD= leaf strata diversity; H´= plant diversity; S= plant richness; DBH= diameter at breast height.
General values of coverage, DBH and height are the averages of each sampling site ± standard deviation.

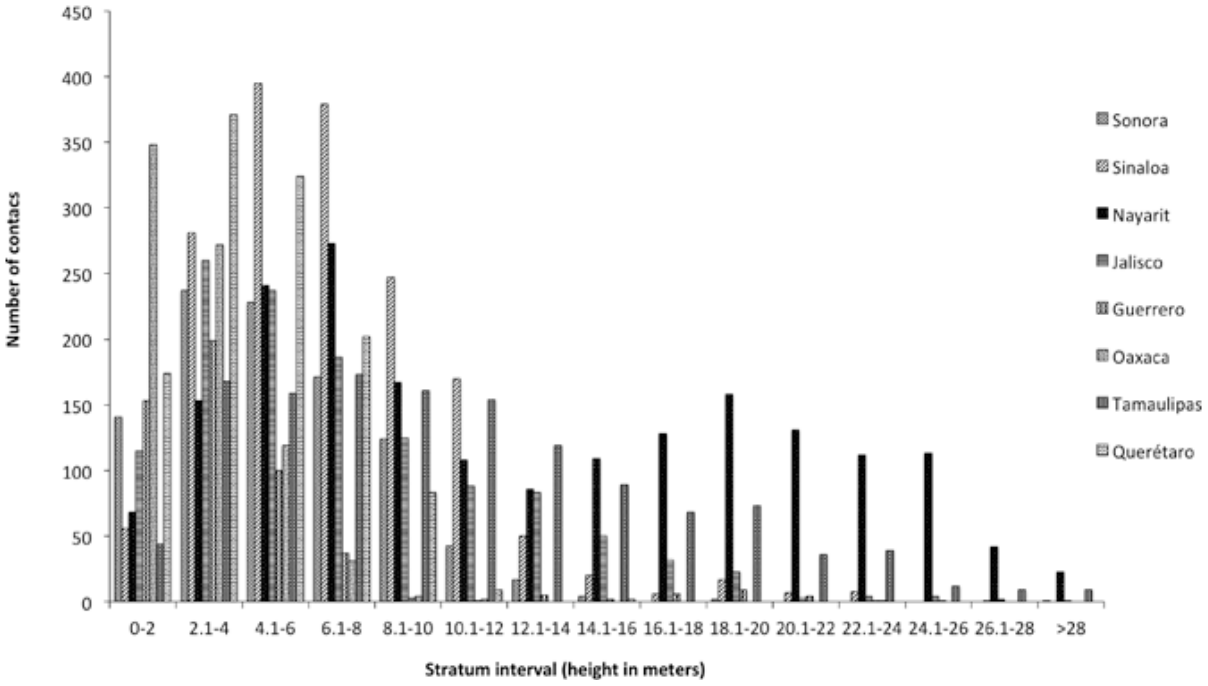

Figure 2. Vertical structure of the habitat of *Ara militaris* in Sonora, Sinaloa, Guerrero, Oaxaca, Querétaro, Jalisco, Nayarit, and Tamaulipas.

of resources (plant richness) compared with sites in eastern Mexico (Fig. 4). The highest number of species (12 to 14 species) was found scattered from Nayarit to Oaxaca in forest fragments that occupied less than 7% of the potential range of the Military Macaw habitat (Fig. 5). The 4 species that the Military Macaw predominantly relies on for food resources occupied slightly more than 28% of the potential distribution (Fig. 5).

Analyzing the changes in land use from those observed in the original map (without land use) in the 1976 scenario indicated that areas with 2 to 6 species have been the most affected by the change in land use, with a reduction of 32% to 48% of their original distribution. In the Series III and Series IV, it is shown that the areas with 4 and 6 species have had a decrease of 2% and 3% respectively with respect the Series II, showing a decrease of 50%-51% of the potential distribution in comparison with the original distribution. This finding is in contrast to other areas that had 7 and 14 plant species, which were not significantly affected by land use changes, with only 10%

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of the original distribution reduced under the 4 scenarios (1976, 2000, 2005, 2010) (Figs. 4, 5).

The potential distribution of Military Macaw in Mexico suggests the existence of 226 000 km^2 of suitable climatic area without considering any impact caused by changing land use. When changes were considered, the estimated remaining area was 182 000 km^2, a 21.12% reduction of the original area in the 1976 scenario. For Series II, the estimation was 160 000 km^2 (28.82% reduction) and for Series III, the estimated remaining habitat was 158 000 km^2 (30.23% reduction), similar to Series IV with an estimated potential distribution of 154 000 km^2 (32%) (Fig. 4). This pattern showed a drastic decrease in the percentage of forest cover reaching up to 32% for the species. In 2011, the calculation of protected areas available for the Military Macaw in NPAs and IBAs only accounted for 5% and 15%, respectively, of 100% (154 000 km^2) of the area distributed in 26 NPAs and 43 IBAs, along the Sierra Madre Occidental and 5 NPAs and 19 IBAs in the Sierra Madre Oriental. In the western zone, the potential area was in Sinaloa, Durango, and Guerrero, and did not include any NPAs. In the eastern zone, the NPAs and IBAs were well represented through the potential distribution of the Military Macaw.

In the PCA, component 1 explained 37.8% and component 2 explained 25.8% of the total variance of 19 environmental variables and altitude; PCA showed a single group (Fig. 6). In the discriminant analysis, the component LD1 explained 53.0 % and LD2 component explained 18.0 %; there was a clear overlap of environmental requirements of the Military Macaw with the 14 most important tree species associated to its distribution (Fig. 6). The projections of the environmental dimensions of Military Macaw and the 14 tree species are represented by ellipses in Figure 6. According to the Jacquard index, tree species distributions that showed the highest overlap with those of the Military Macaw were: *Lysiloma microphylla* (0.64), *Lysiloma divaricata* (0.53), *Guaiacum coulteri* (0.50), *Ipomea arborences* (0.50), *Hura polyandra* (0.46), *Plumeria rubra* (0.45), *Guazuma ulmifolia* (0.39), *Haematoxylon brassileto* (0.37), and *Ceiba aescutifolia* (.36). Species that showed lower overlap with Military Macaw were: *Cyrtocarpa procera* (0.27), *Taxodium mucronatum* (0.26), *Ceiba pentandra* (0.22), *Bursera simaruba* (0.16), and *Brosimum alicastrum* (0.14)

Discussion

Habitat characterization. The structural variables of the Military Macaw habitat indicated that the type of vegetation influenced the habitat selection. The Military Macaw is considered a canopy species (Íñigo-Elías, 1996; Loza,

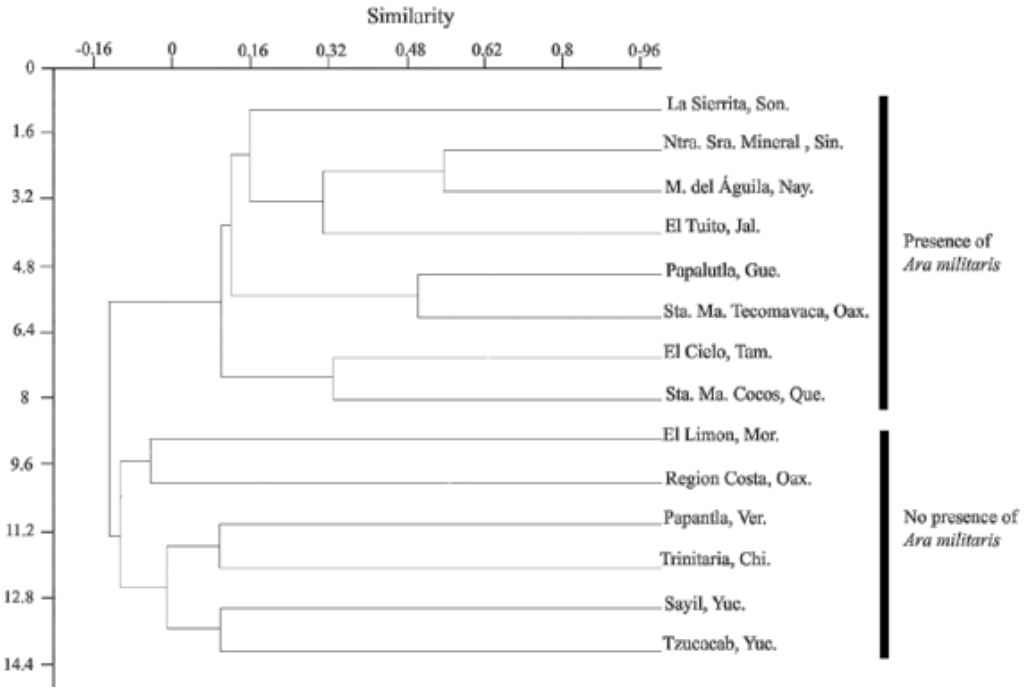

Figure 3. Cluster analyses using the Sorensen's similarity values of sites with and without presence of *Ara militaris*.

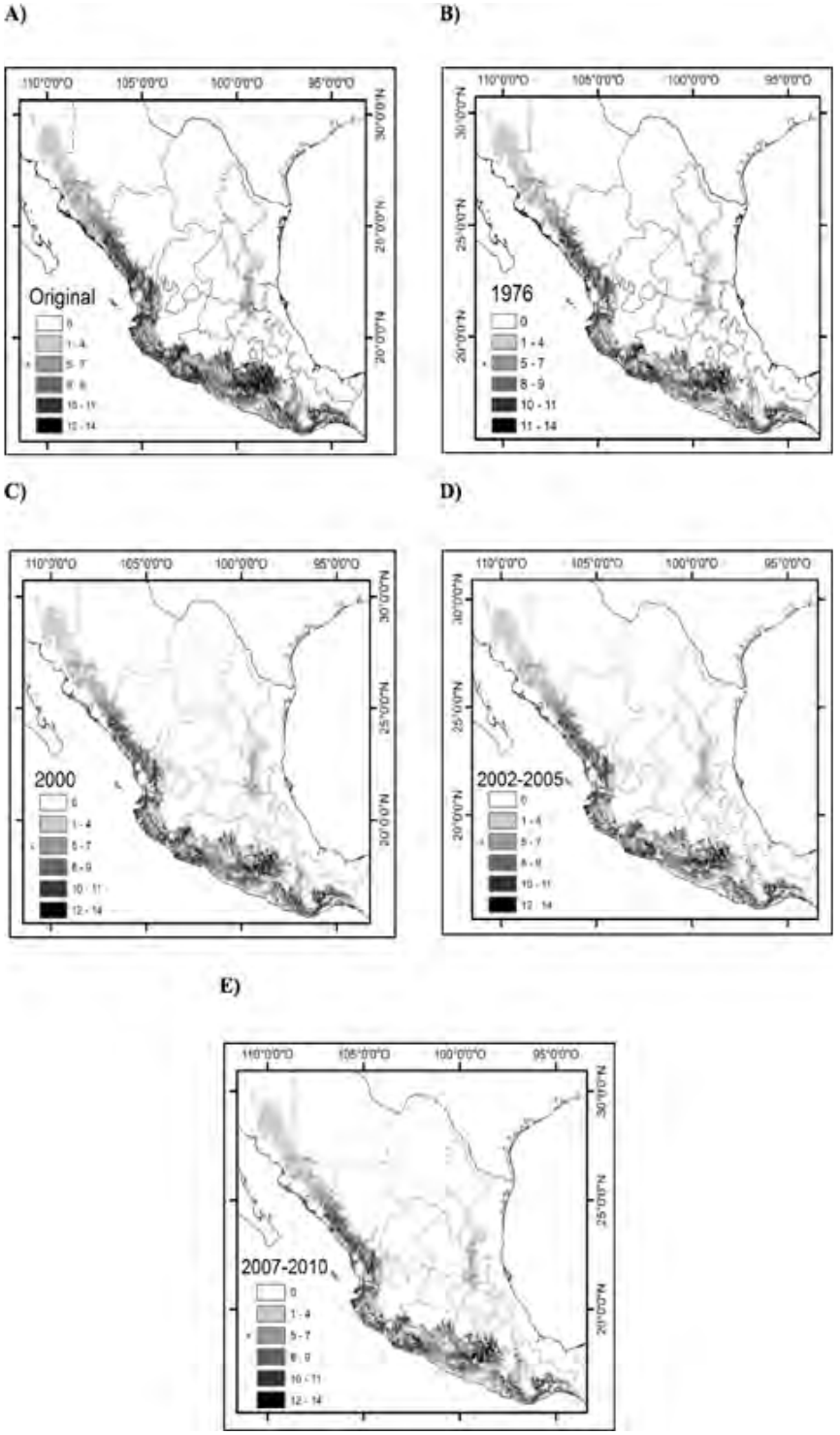

Figure 4. Models of potential geographical distribution of *Ara militaris* in Mexico. A, regardless of changing land use; B, scenario of changing land use of 1976; C, scenario of changing land use of year 2000 (Series II); D, scenario of changing land use of 2005 (Series III), and E, scenario of changing land use of 2010 (Series IV).

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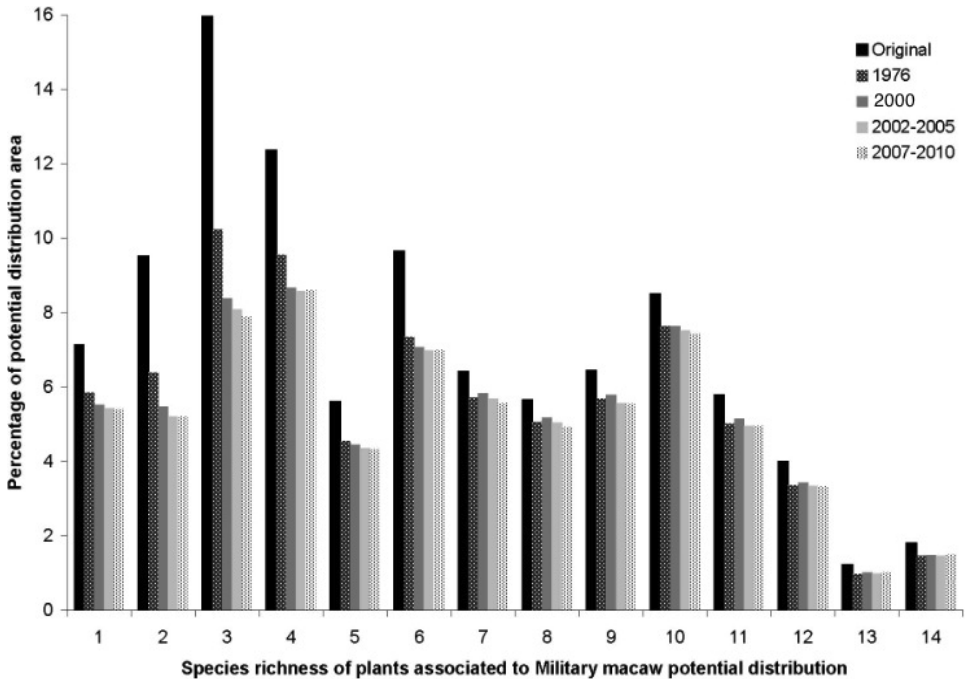

Figure 5. Patterns of plant species richness associated with the hypothetical distribution of *Ara militaris* in Mexico. They represent the conditions of the original vegetation and its amendments considering vegetation cover assessments for 1976, 2000 (Series II), 2005 (Series III), and 2010 (Series IV).

1997; Gómez, 2004) because it requires large canopy trees of deciduous and subdeciduous forests for feeding, breeding, and nesting behavior as well as protection against predators and thermal cover (Forshaw, 1989; Collar and Juniper, 1992; Collar, 1997; Loza, 1997; Íñigo-Elías, 1999; Salazar, 2001; Peterson et al., 2004; Rivera-Ortiz et al., 2008; Contreras-González et al., 2009). This species nests in trees of at least 15 m in height and the nests are 90 cm wide. In the nesting sites of El Mirador del Aguila, El Tuito, and El Cielo, the trees had the required structural characteristics for nesting (Collar, 1997; Loza 1997). The Military Macaw has the ability to shift its nesting sites to inaccessible sites such as steep cliffs in well-preserved areas: in La Sierrita, Papalutla, Santa María Tecomavaca, and Santa María de Cocos (Carreón, 1997; Gómez, 2004; Rivera-Ortiz et al., 2008).

The suitability of habitats for the Military Macaw requires the presence of certain genera of trees, such as *Brosimum*, *Cyrtocarpa*, *Celtis*, *Hura*, *Quercus*, *Bunchonsia*, *Lysiloma*, and *Bursera*; plant species of these genera have been reported in the distribution of the Military Macaw in Mexico as important sources either for nesting or as food supply by different authors (Carreón, 1997; Loza, 1997; Gaucín, 2000 and Contreras-González et al., 2009). In populations of Colombia and Peru, species of *Hura* and *Bursera* are also reported as important trees for feeding (Flores and Sierra, 2004); these plant species contain a large amount of nutrients, such as lipids, carbohydrates, and proteins, that are important for egg laying and the development of chicks (Contreras-González et al., 2009)

Comparing the vegetation structure and floristic composition in sites with and without presence of the Military Macaw, we found significant differences in the floristic composition but structural similarities. These findings indicate the reliance of the Military Macaw on specific floristic composition, commonly found in bird specialists (such as the Military Macaw). This pattern is due to the close relationship between the availability of food resources and reproductive effort (Saunders, 1977; Saunders, 1990; Collar and Juniper, 1992) with significant implications for the conservation of this species (Ruth et al., 2003).

The information available to establish conservation strategies for the Military Macaw has been based mainly on the effects of illegal traffic and other biological and ecological aspects, such as abundance, demography, and reproduction (Carreón, 1997; Loza, 1997; Gaucin, 2000; Íñigo-Elías, 2000; Rivera-Ortíz et al., 2008; Contreras-

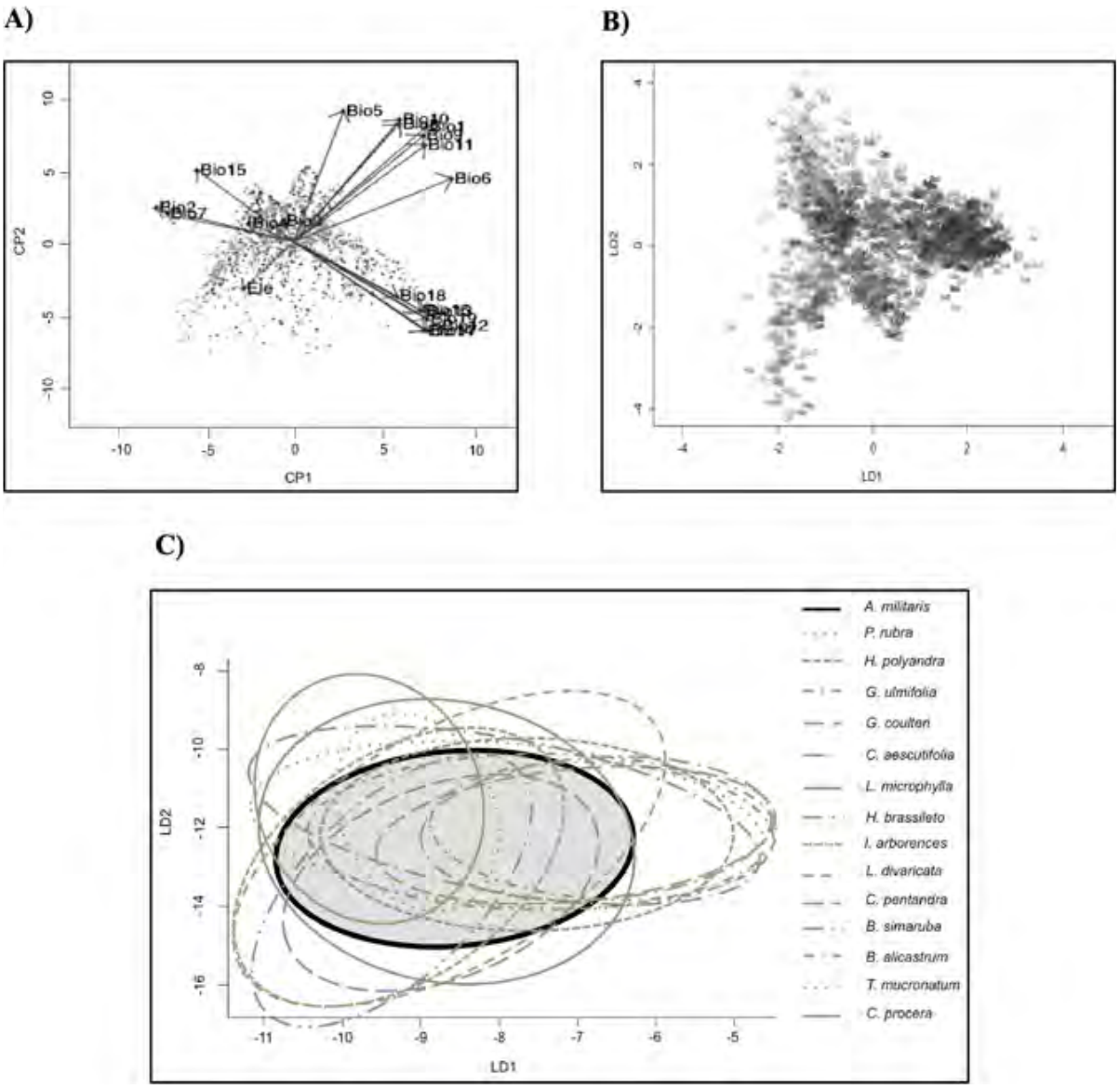

Figure 6. Environmental overlap. A, Pca of the 14 tree species and *Ara militaris* associated to 20 variables ecological (arrows) in the correlation circle; B, discriminant analysis of the 14 tree species and *Ara militaris*; C, ordination of the 19 environmental variables and altitude in 1st and 2nd LD axes. Ellipses (95% confidence) represent spatial overlap in the 14 tree species and *Ara militaris*.

González et al., 2009). Feeding and reproductive habitat modification has not taken into account in the analysis of land-use changes (Jetz and Rahbek, 2002).

The Military Macaw is not adequately protected in Mexico because only 5% of the potential distribution for the species is covered by the NPAs and 15% by IBAs. Of the 8 studied sites, 3 are located within a Biosphere Reserve (El Cielo, Santa María de Cocos, and Tecomavaca); one site is considered subject to ecological conservation (Cosalá), and la Sierrita Alamos is considered an area under the Protection of Flora and Fauna, while the other sites (El Tuito, Papalutla, and Salazares) are not protected (<htpp:/ www.economiadgm.gob.mx/ecologia /lista_ecolog.htm> November 18, 2010). We suggest that at least 30% of forests of the potential distribution should be protected to guarantee specific areas of nesting and feeding of the

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Military Macaw.

Distribution models, vegetation cover changes, and environmental overlap. Ecological niche modeling represents a conceptualization of the distribution of favorable environmental conditions in which a species could be found (Peterson, 2001). Our models indicate that Military Macaw and 14 arboreal plant species are found in areas with similar characteristics, at least in a coarse environmental space; this is reinforced by the high overlap environmental found in the discriminant analysis. The reciprocal prediction of environmentally based overlap could indicate few ecological differences between the Military Macaw and tree species.

It is important to identify and preserve the habitats of endangered species with particular requirements such as the Military Macaw. We estimated a reduction of 32% in the potential distribution of the Military Macaw comparing 4 land-use change scenarios since 1976 to 2010. These changes were particularly dramatic when only 6 of the plant species that the Military Macaw relies on were present *(Lysiloma microphylla*, *Lysiloma divaricata*, *Hura polyandra*, *Ceiba aescutifolia*, *Guaiacum coulteri*, and *Ipomea arborences*). These findings indicated the potential negative impacts on the survival of the Military Macaw if reductions of available habitats occur as land-cover changes continue in the future (Peterson et al., 2006; Ríos-Muñoz and Navarro-Sigüenza, 2009; Contreras-Medina et al., 2010). This is supported by previous studies. Ríos-Muñoz and Navarro-Sigüenza (2009) reported a reduction of 28.5% in the available habitat of the Military Macaw by the year 2000. Marin-Togo et al. (2011) and Monterrubio-Rico et al. (2010) declared the Military Macaw locally extinct in the Mexican Pacific Coast (i.e., Michoacán, Guerrero, and Oaxaca states) and in coastal areas of more than 400 m in altitude, with a decrease of 16% of the distribution as of 2000.

The land-cover change in tropical rain forests has caused the highest rates of deforestation in the country (Trejo and Dirzo, 2000), and as a consequence, Mexican parrots have suffered severe habitat declines. Specifically, a drastic decrease has been reported in habitat occupied by *Ara macao* (Scarlet Macaw) (86% reduction), *Aratinga astec* (Aztec Parakeet) (48%), and *Pionus senilis* (White-crowned Parrot) (49%) (Ríos-Muñoz and Navarro-Sigüenza et al., 2009; Marín-Togo et al., 2011). Renton and Salinas-Melgoza (2004) found that fragmentation and climatic variations of habitats in seasonally dry forests could adversely affect the reproductive success of *Amazona finschi* (Liliac-crowned Parrot).

According to our results, the habitat of the Military Macaw in tropical dry forests has already been reduced drastically by almost 32%, endangering the viability of its populations. In addition, the illegal international trade of wild species has also seriously affected populations of the Military Macaw and this directly affects the loss of species distribution (Gaucín, 2000; Marín-Togo et al., 2011). Although models based on the intended habitat are very important to detect changes in the potential distribution of the Military Macaw in different scenarios, we must take into account the use of updated cartographic information of land-cover change and factors such as hunting and illegal capture to make better predictions for this species (Marin-Togo et al., 2011; Monterrubio-Rico et al., 2011).

Conservation implications. The present study provides information regarding the type of vegetation and species composition that is critical for the preservation of the Military Macaw. Our findings suggest the importance of knowing the floristic composition of the habitat of endangered species and the impact of land-use variation over time on the potential distribution of those species as a tool to direct conservation efforts. It is worth noting that the use of ecological niche models and geographic data of land-use change are fundamental tools to be considered in the conservation efforts of the Military Macaw. Therefore, the protection of suitable habitats and the implementation of sustainable activities should be prioritized in conservation strategies for the Military Macaw. Habitat degradation and capture of the Military Macaw for illegal trade must be stopped and the size and number of natural protected areas must be increased.

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6.0 Capítulo II

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Habitat fragmentation and the genetic variability of tetrapod populations

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Fragmentation and genetic variability

Habitat fragmentation and genetic variability of tetrapod populations

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Abstract. In the last two centuries, the development of human civilization has transformed large natural areas into anthropogenic landscapes, making habitat fragmentation a pervasive feature of modern landscapes. In vertebrate populations, habitat fragmentation may alter their genetic diversity and structure due to limited gene flow and dispersion and reduced effective population sizes, potentially leading to genetic drift in small habitat patches. We tested the hypothesis that habitat fragmentation affects genetic diversity of tetrapod populations using a meta-analysis. We also examined life history and ecological traits that may determine differential susceptibility to genetic erosion in fragmented habitats. Our results showed that habitat fragmentation reduces overall genetic diversity of tetrapod populations. Stronger negative fragmentation effects were detected for amphibians, birds, and mammals. Within each taxonomic group, species with large body size were more strongly affected by fragmentation. The extent of habitat loss was also important; as expected, studied ecosystems with extreme habitat loss showed stronger negative effects on genetic diversity irrespectively of taxonomic groups. The information gathered in this review also highlights research bias and gaps in the literature. The results found here should help to identify and determine the probability of risk of extinction of wild populations to prioritize conservation efforts.

Key works: Amphibians, Birds, Conservation genetics, Habitat fragmentation, Genetic variability, Mammalians, Reptiles, Tetrapods.

Resumen. En los últimos dos siglos, el desarrollo de la civilización humana ha transformado grandes áreas naturales en paisajes antropogénicos, por lo que la fragmentación del hábitat en un aspecto dominante de los paisajes modernos. En los vertebrados, la fragmentación del hábitat puede afectar la diversidad y estructura genética de sus poblaciones, debido a limitaciones en el flujo de genes y reducción del tamaño efectivo poblacional, lo que puede llevar a procesos de deriva genética en pequeños parches de hábitat. Pusimos a prueba la hipótesis de que la fragmentación del hábitat afecta a la diversidad genética de las poblaciones de tetrápodos usando un meta-análisis. También examinamos rasgos ecológicos y de historia de vida que pueden determinan susceptibilidad a la erosión genética en hábitats fragmentados. Nuestros resultados muestran que la fragmentación del hábitat reduce la diversidad genética global de las poblaciones de tetrápodos. Se detectaron fuertes efectos negativos de la fragmentación para anfibios, aves y mamíferos. Dentro de cada grupo taxonómico, las especies con un gran tamaño corporal fueron más fuertemente afectados por la fragmentación. El grado de pérdida de hábitat también fue importante; como era de esperar, en estudios en los ecosistemas con pérdida de hábitat extrema mostraron mayores efectos negativos sobre la diversidad genética, independientemente de los grupos taxonómicos. La información recogida en este estudio también pone de relieve sesgos y ausencias de investigación. Los resultados encontrados sirven para identificar y determinar rasgos susceptibles de probabilidad de riesgo de extinción de las poblaciones silvestres, lo permitirá generar criterios para priorizar los esfuerzos de conservación.

Palabras claves: Anfibios, Aves, Conservación genética, Fragmentación del hábitat, Variabilidad genética, Mamíferos, Reptiles, Tetrápodos.

Introduction

Human activities have changed natural habitats into anthropogenic landscapes, resulting in a loss and fragmentation of originally continuous ecosystems. Such processes impose important changes in the structure and distribution of natural communities, which often results in the reduction of both the size and connectivity of plant and animal populations surviving in fragmented habitats (Saunders *et al.,* 1991; Fahrig, 2003; Alcaide *et al.,* 2009). Such rapid and drastic changes in land use across the globe represent the main driving forces behind current biodiversity loss and will continue to do so throughout the present century (Sala *et al.,* 2000). Although not always properly acknowledged, genetic diversity represents one of the three forms of biodiversity. The amount of genetic diversity is crucial in determining the potential of animal populations to adapt and evolve in changing environments. Thus, it is important to assess the effects of habitat fragmentation on tetrapod population genetic diversity in order to help to develop tools and strategies for the conservation of wild populations (Ouborg *et al.,* 2006; Pertoldi *et al.,* 2007).

After nearly three decades of research, considerable attention has been given to the effects of habitat fragmentation on population abundance and distribution of different groups of tetrapods (e.g. Stauffer & Best, 1980; Catan *et al.,* 1994; Vickery *et al.,* 1994; Kolozsvary & Swilhart, 1999; Férnandez-Juricic, 2004). Within the last 15 years, however, there has been a growing interest in assessing the genetic consequences of habitat fragmentation (Triggs *et al.,* 1989; Cunningham & Moritz, 1998; Lindsay *et al.,* 2008; Meyer *et al.,* 2008). Changes in landscape configuration imposed by habitat fragmentation can affect the genetic characteristics of tetrapod populations by limiting gene flow and dispersion, reducing the effective population sizes and increasing the effects of genetic drift in small habitat patches (Reed & Frankham, 2003; Caizergues *et al.,* 2003). As a result, the distribution patterns of genetic diversity within and among populations (i.e., genetic structure) can change drastically.

The immediate effects on genetic composition depend mainly on three factors: 1) the effective size of remaining populations, 2) the pattern of genetic diversity of the original population before fragmentation and 3) the rate of migration of individuals among patches (Bates, 2000; Young *et al.*, 1996; Meyer *et al.*, 2008).

Current evidence shows that not all fragmentation scenarios result in genetic erosion of vertebrate populations. Certain characteristics of species may confer differential susceptibility to lose genetic diversity in fragmented habitats. For example, degree of vagility of tetrapod species can be an important susceptibility trait. In this regard, amphibians and reptiles would be more likely to lose genetic diversity due to their low vagility, high philopatry and greater susceptibility to changes in the environment, compared to birds and mammals that may be able to move across matrices of unsuitable habitat (Wind, 1996; Moore *et al.*, 2008; Dixo *et al.*, 2009; Allentoft & O'Brien, 2009). Moreover, the size of mobile organisms determines the spatial scale of their habitat requirements. Tetrapod species with large body size require large foraging and reproductive areas and usually make use of different habitat types (Gurrutxaga & Lozano, 2006), which can be strongly limited in the remaining fragmented habitats. Thus, within the same taxonomic group, large-body species would be more susceptible to lose reproductive and genetic connectivity, being more likely to suffer genetic erosion compared to small-body species.

In addition to the potential susceptibility of particular life-history traits of species to suffer rapid genetic erosion in fragmented landscapes, other external drivers such as the degree of habitat loss and fragmentation can determine the magnitude of fragmentation effects on genetic diversity of tetrapod populations. Because patch size tends to be correlated with genetic diversity (Frankham, 1995), we might expect that studies evaluating genetic consequences of fragmentation in tetrapod populations surviving in extremely fragmented

habitats will show stronger effects than studies selecting less extreme or more moderately fragmented systems (Holmes *et al.,* 2013).

In this work, we conducted a quantitative review to evaluate the overall effects of habitat fragmentation on genetic diversity of vertebrate (tetrapod) populations by testing some of predictions on conservation genetics paradigms. Specifically we aim (i) to determine the overall magnitude and direction of habitat fragmentation effects on genetic variability of tetrapod populations, (ii) whether the magnitude of fragmentation effects on genetic diversity is driven by vagility of different taxonomic groups (amphibians, reptiles, birds and mammals) and body size of species within the same taxonomic group, and (iii) whether the level of habitat fragmentation also guides the magnitude on of the observed effects.

Methods

Literature search

We conducted a systematic literature search comprising the period 1989-2013 through several databases such as Cambridge Scientific Abstracts, Science Citation Index, Searchable Ornithological Research Archive and databases of Biological Abstracts, and major publishers (Blackwell Science, Springer-Verlag and Elsevier) and scientific societies that group the most relevant journals in ecology, biology and conservation genetics. For this review, we only used the group of tetrapod vertebrates (amphibians, reptiles, birds, and mammals). We used a combination of the following keywords for conducting the literature search: (fragment* or "habitat loss") and ("genetic diversity" or "inbreeding") and ("vertebrate*" or "amphibian*" or "reptile*" or "bird*" or "mammal*"). We obtained 462 studies that were examined to determine whether they met the requirements for entry into the meta-analysis.

Because the process of habitat fragmentation produces habitat loss, reduces population size, and increases isolation between populations, our review allowed the inclusion of studies

analyzing any of these measures of fragmentation. We later evaluate the relative effects of each of these fragmentation parameters on genetic diversity. We only excluded articles that analyzed correlations between population size and genetic variability with no explicit mentions to the effects of habitat fragmentation.

The measures of genetic variability considered were: expected heterozygosity (*He*), number of alleles (*A*) and inbreeding coefficient (F_{IS}). In studies using dominant markers (RAPDs and AFLPs) we used molecular variance or gene diversity as alternative measures. These four genetic parameters were not necessarily evaluated altogether within the same study, so the sample sizes for each of these genetic parameters in the meta-analyses were different. In studies that did not provide the inbreeding coefficient, it was calculated using the expected (*He*) and observed (*Ho*) heterozygosity (F_{IS} = *He* - *Ho* / *He*).

For each vertebrate species studied, we collected information on body sizes and classified them into discrete categories (large or small) to compare their relative effect of size within each taxonomic group (i.e., large *vs*. small amphibians, etc.). All this information was obtained from the original paper or from other publications on the same species, but not all features of all species were available; therefore, the predictor variables in the meta-analyses did not share the same sample size. Finally, because the studies differed in their extent of fragmentation extreme values encompassed, we created two categories (moderate and extreme habitat loss) to compare the magnitude of effect sizes. Following Winfree et al. (2009), we categorized as ‘‘extreme habitat loss’’ to studies in which most fragmented site was < 5 Ha in area, surrounded by < 5% natural habitat or was > 5km from the nearest natural habitat. ‘‘Moderate habitat loss’’ refer to study systems where all these landscape parameters were less extreme.

Some authors assessed habitat fragmentation effects on genetic parameters in more than one species within the same paper and we included all these species in our meta-analysis.

Because the magnitude and sometimes the direction of genetic responses to habitat fragmentation in each species within the same study were quite different, it is reasonable to assume that the effects are independent for each species (Gurevitch & Hedges, 2001; Aguilar *et al.*, 2008).

Data analysis

We used a categorical meta-analysis approach to assess population genetic parameters of tetrapods in two contrasting habitat conditions (fragmented vs. continuous forest), thus we obtained the average and standard deviations of each of the genetic parameters (*He*, *A*, and F_{IS}) across tetrapod populations (*n*) in each of the two habitat conditions and these data were taken from the text, tables or graphs. The magnitude of fragmentation effects on each genetic parameter was quantified by calculating Hedge's *d* (Gurevitch & Hedges, 2001). The effect size (*d*) can be interpreted as the difference between the genetic diversity of the vertebrate groups in fragmented and continuous habitats measured in standard deviation units (Gurevitch & Hedges, 2001).

We run separate meta-analyses for each of the different genetic parameters assessed in each study. Negative values for the effect size (*d*) of *He* and *A* imply negative effects of habitat fragmentation on these parameters, while positive values of *d* imply positive effects of fragmentation. The interpretation of the direction of effect size for inbreeding coefficient (F_{IS}) is exactly the opposite; positive values of *d* imply negative effects of habitat fragmentation (high inbreeding), while negative values of *d* indicate positive effects of fragmentation (low inbreeding).

MetaWin software version 2.0 (Rosenberg *et al.*, 2000) was used to run the analyses and bootstrap resampling procedures as described in Adams *et al.* (1997) and to calculate confidence intervals of effect sizes. The effects of habitat fragmentation were considered

significant if the 95% biased-corrected bootstrap confidence intervals (CI) of the effect size (*d*) did not overlap zero (Rosenberg *et al.,* 2000). Confidence intervals based on resampling IC estimates are more conservative (Adams *et al.,* 1997). The data were analyzed with random effects model, assuming that differences between studies is due to sampling errors and also to random variation (Raudenbush, 1994). The heterogeneity of effect sizes was evaluated with *Q* statistics (Gurevitch & Hedges, 2001). Specifically, we examined the *P* values associated with $Q_{between}$ statistics, which describe the variation in effect sizes attributed to differences between the categorical predictors (*e.g*., life history and ecological traits).

Publication bias

Different methods were used to detect potential publication bias, first graphically (funnel plots and weighted histograms), and secondly by weighted calculation of the failsafe numbers (Rosenberg *et al.,* 2000; Rosenberg, 2005). If the calculated failsafe number was greater than 5n + 10, where n is the number of studies, then publication bias can be ignored because the results are robust regardless of publication bias (Rosenberg, 2005).

Phylogenetic Meta-analysis

In any meta-analysis involving multiple species it is crucial to consider the phylogenetic relationships among them, since more closely related species may share similar response to the same factor (Rifkin *et al.,* 2012). We used phyloMeta software version 1.3 to conduct a phylogenetically independent meta-analysis (Lajeunesse, 2011). Before running the analysis we constructed a phylogenetic tree for all tetrapod species included in this review (Appendix S1) using cytochrome b sequences for each species, retrieved from the GenBank database and aligned using the ClustalW algorithm (Thompson *et al.,* 1994). We used 720 bp to estimate the length of the tree branches covering all species included in this study using PAUP 4 beta 10 (Swofford, 2003), which is based on a model of a nucleotide substitution

GTR + 1 + G (Meunier *et al.*, 2011). Trees were obtained using ultrametric length branches, adjusted to one (Sanderson, 2002) using R 2.9.2 (Paradist *et al.,* 2004). Sub-trees were obtained trough pruning of species for each class of tetrapods, these sub-trees were used depending on the genetic parameter measured (Meunier *et al.*, 2011). Some the tetrapod species were evaluated by more than one author (see Appendix S2). For the phylogenetic meta-analysis we pooled these multiple effect sizes per species using a traditional meta-analysis with a fixed effects model (Koricheva *et al*., 2013), so that we used one effect size per species.

We used the AIC (model selection criteria) to compare model fit between the conventional meta-analysis and the phylogenetic-independent meta-analysis (Lajeunesse, 2011). The model with the smallest AIC was selected as the best fitting the data (Hedges & Olkin, 1985; Hedges, 1992).

Results

Conventional and Phylogenetic Meta-analyses

The conventional meta-analysis provided a significantly better-fit model than the phylogenetically corrected meta-analysis (*He*: AIC = 296.23 vs. 335.21, *A*: AIC = 229.11 vs. 245.52 and F_{IS}: AIC = 139.97 vs. 174.15), suggesting that the phylogenetic structure is not influencing the variation among effects sizes and thus we only show the results from the conventional meta-analyses.

Sample of studies

We obtained a total of 101 scientific publications that evaluated the effect of habitat fragmentation on genetic diversity of tetrapod populations. These studies measured at least one genetic parameter in 93 species of vertebrates, of which 15.4% were amphibians, 19.0% reptiles, 33.6% birds and 32.0% mammals. Some species were studied more than once by

different authors, thus we obtained a total of 99 data points for the traditional meta-analysis for the expected heterozygosity (*He*), 77 for the number of alleles (*A*), and 52 for the inbreeding coefficient (F_{IS}). Most of the studies used microsatellites (93%) as genetic markers to assess the effect of habitat fragmentation on genetic variability, and the 7% of the remaining studies with sequences.

The weighted histograms of *He*, *A* and F_{IS}, showed unimodal distributions, with the highest frequency around zero and the graph of effect size vs. sample size, showed a symmetric funnel shape, indicating no publication bias in our sample (Figures not shown). Similarly the fail-safe numbers calculated for each meta-analysis were always greater than 5n + 10 (*He* 4668.8 > (5 * 99) + 10 = 505, *A*: 4103.1 > (5 * 77) + 10 = 395; F_{IS}: 839.3 > (5 * 52) + 10 = 260), reinforcing the robustness of these results.

Overall, the average weighted effect sizes of habitat fragmentation on *He* and *A* were negative and significantly different from zero (Fig. 1). In contrast, habitat fragmentation had no significant effect on F_{IS}, but there was a slight trend of increased inbreeding in populations living in fragmented conditions (Fig. 1).

When looking separately at each vertebrate group we found that fragmentation effects on *He* were significantly negative for amphibians, mammals and birds, whereas for reptiles overall mean effect was non-significant (Fig. 2). Overall effects on *A* were significantly negative for all four taxonomic groups (Fig. 2). Fragmentation effects on inbreeding coefficient (F_{IS}) were consistently non-significant for all vertebrate groups (Fig. 2).

The evaluation of body size within each tetrapod group revealed that fragmentation effects on *He* were significantly different for amphibians and birds (amphibians: $Q_{between}$ = 9.9873, p = 0.0015; birds: $Q_{between}$ = 2.8681, p = 0.0503; Fig. 3), with larger-sized species of birds and amphibians showing significantly stronger mean effect sizes than their smaller-sized counterparts on He. When analyzing *A*, all tetrapod groups showed significant differences

between small versus large sized species (amphibians: $Q_{between}$ = 12.2179 p = 0.00004; reptiles: $Q_{between}$ = 4.2532, p = 0.0391; birds: $Q_{between}$ = 4.4264, p = 0.0353) with the exception of mammals ($Q_{between}$ = 3.6570, p = 0.0558). The response patterns remain as before, with significantly larger mean negative effect sizes in large-bodied species (Fig. 3). In particular for amphibians and reptiles, only large-sized species showed significant negative effects in *A*, while small-sized species show no significant fragmentation effects in *A* (Fig. 3).

We also detected that populations found in extremely fragmented habitats have significantly stronger effects in *A* ($Q_{between}$ = 3.6983, p = 0.007). Although with a similar trend, no significant differences were observed in *He* ($Q_{between}$ = 2.3649, p = 0.501) and F_{IS} ($Q_{between}$ = 0.2689, p = 0.634) (Fig. 4).

Discussion

In this study, we showed that habitat fragmentation reduces overall genetic diversity of tetrapod populations. The four groups of tetrapods showed similar negative fragmentation effects in allelic richness. Although a relatively fewer effect sizes were calculated for amphibians and reptiles, we still detected lower genetic diversity in fragmented habitats. Such decrease in allelic richness is likely to be the immediate result of sudden population reductions due to habitat loss and fragmentation, generating genetic bottlenecks. The impact of bottlenecks in genetic variation depends primarily on two factors: the effective size of the population and the time during which the population is kept small. Drastic reduction in the effective size of populations caused by habitat fragmentation reduces the genetic variation of remaining populations and will also affect the genetic variation of the following generations that remain in the fragments should gene flow is interrupted (Hoelzel, 1999).

We also observed negative fragmentation effects on the expected heterozygosity in amphibians, birds and mammals but not in reptiles. Reduced expected heterozygosity in

fragmented populations can be the result of genetic drift. When populations remain small and isolated for some generations, reductions in genetic variability occur by random elimination of heterozygous genotypes, affecting the number and frequencies of alleles (Reed & Frankham, 2003; Caizergues *et al*., 2003).

In contrast to the genetic diversity parameters, we did not observe significant changes in the inbreeding coefficients in fragmented habitats. The vast majority of the studies included here, the inbreeding coefficients were estimated on adults, not on progeny, thus, reflecting mating patterns of long-lived adult individuals, which may precede fragmentation events. It would be very interesting to determine inbreeding on progeny generated in fragmented habitats, as new habitat configurations may be causing changes in mating patterns towards increased biparental inbreeding (Aguilar et al., 2008).

We observed that amphibian populations surviving in fragmented conditions showed a stronger decreased in genetic diversity, especially in expected heterozygosity. Because their inherent high philopatry and low vagility, amphibian populations can be especially affected by decreased connectivity in fragmented habitats, strongly limiting gene flow between populations (Gibbs, 1998, Saunders et al., 1991; Couvet, 2002, Bowne & Bowers, 2004; Allendorf & Luikart, 2007; Allentoft & O `Brien, 2010). Moreover, amphibians are comparatively shorter-lived, thus individuals living in fragmented conditions expressed stronger effects on expected heterozygosity than the rest of the tetrapods (Cushman 2006). The loss of genetic diversity in amphibian populations has been little recognized as a potential factor in the overall decline of their populations. Our results suggest that genetic erosion imposed by habitat fragmentation can play an important role in the rate of species loss of amphibians (*e.g*., Allentoft & O `Brien, 2010).

In reptiles, we only observed fragmentation effects in allelic richness. No significant decrease in expected heterozygosity of fragmented reptile populations may be due to their

relative longer life spans, which imply that individuals surviving in fragmented conditions may have been there before fragmentation occurred. Thus, genetic diversity measured as expected heterozygosity in such adult populations would simply reflect the pre-fragmented situation, because not enough time has yet elapsed to reveal genetic drift effects (Cunningham & Moritz, 1998; Ciofi *et al*., 2002; Kuo & Janzen, 2004; Marsack & Swanson, 2009). Another potential reason may be due to taxonomic bias of the studied species within reptiles. Most of the species belong to the suborder saurians (lizards), which have higher mobility compared to the suborder ophidians (snakes) that have been less well studied.

The observed negative effects of habitat fragmentation on the genetic diversity of birds is surprising, given that this group is considered highly vagile and presumably able to cross large areas of unsuitable habitat compared to the other tetrapod groups (Avise, 1996; Busch *et al*., 2000; Crochet, 2000; Ehrich & Stenseth, 2001; Wang & Schreiber, 2001). Most of the studies up to now have been conducted in bird species of the orders Passeriformes and Galliformes. Within Passeriformes group there is high incidence of philopatric bird species with restricted flight capacity and specific habitat requirements (Avise, 1996; Boone & Rhodes, 1996, Kurtis *et al*., 1999). Therefore, for this particular taxonomic group, habitat fragmentation may reduce gene flow between remnant populations increasing genetic drift and genetic erosion (*e.g*., Bates, 2000; Segelbacher & Storch 2002; Brown *et al*., 2004; Mercival *et al*., 2007; Lindsay *et al*., 2008; MacDougall-Shackleton *et al*., 2011).

Like amphibians and birds, mammals had lower genetic diversity in fragmented environments. The majority of species studied are small philopatric mammals that are particularly sensitive to environmental perturbations. Such biological characteristics make them particularly vulnerable because isolated populations of small mammals are less capable to disperse across the inhospitable matrix, restricting gene flow and increasing genetic drift,

thereby losing genetic variability (*e.g*., Telfer *et al*., 2003, White & Searle, 2007; Lada *et al*., 2008; Olivieri *et al*., 2008, Meyer *et al*., 2008; Pacioni *et al*., 2011).

According to our results, the genetic variability of species with large body size within each tetrapod group was more strongly affected by habitat fragmentation. Body size is positively related to the range of distribution, as larger species require more amount of habitat for feeding and breeding. Also, large-sized species usually occur in low densities. Therefore, larger spatial requirements together with lower population densities may make large-sized species particularly susceptible to suffer genetic erosion in fragmented habitats (Bergl *et al*., 2008). In addition, bird and mammal species of large body size in particular have reproductive traits such as low number of offspring per reproductive event and longer time to reach sexual maturity, which can also increase genetic erosion susceptibility (Wooten & Smith, 1985; Caro & Laurenson 1994; Caughley, 1994; Frankham, 1995; Jost & Brandl, 1997; Ewers & Didham, 2006; Prugh *et al*., 2008).

Conservation implications. The controversy about whether ecological and demographic factors are more important than genetic factors for the decline and extinction of populations or even species has been recently evaluated (Frankham *et al.*, 2003, Spielman *et al*. 2004). Most taxa are not driven to extinction before genetic factors have been negatively affected (Spielman *et al.*, 2004). Tetrapod species surviving in fragmented habitats are, overall, likely to suffering genetic erosion, compared to populations living in continuous forests. Therefore, it is crucial to detect susceptible tetrapod groups of species that may experience lower evolutionary potential due to their ecological and life history traits.

Here we observed that habitat fragmentation reduces allelic richness of all tetrapod groups evaluated, and also the genetic diversity expressed as expected heterozygosity of amphibian, bird, and mammal populations. Moreover, large-bodied species living in highly

fragmented systems are particularly prone to suffer strong genetic erosion, regardless of their taxonomic identity. The information gathered in this quantitative review should help to identify and determine the probability of risk of extinction of wild populations to prioritize conservation efforts (Amos & Balmford, 2001; Lowe *et al*., 2005; Aguilar *et al*., 2008).

Despite these unequivocal signs of fragmentation effects on genetic variability, there is a clear gap in the literature of population genetics of tetrapods that prevents additional generalizations. Most data come from adults, and their genetic makeup may differ from that of their progeny that have been subjected to fragmentation conditions. Such is the case with the few studies that looked at the effect of fragmentation on vagile species and the poor studies that examined the progeny established in fragmented habitats (Aguilar *et al*., 2008). We call upon an increase of studies assessing genetic effects on tetrapod progeny, which will allow us to estimate mating and gene flow patterns in fragmented conditions, and assess how changes in mating patterns may affect the genetic diversity of future generations of tetrapod populations.

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Supporting information

Additional Supporting Information can be found in the online version of this article:

Appendix 1. List of publications used in the meta-analysis.

Appendix 2. Phylogenetic tree of tetrapods used to performing correction in phylogenetic in phyloMeta, in format Newik and image.

Figure Legends

Figure 1. Overall weighted mean effect sizes and 95% bias-corrected confidence intervals (CI) of habitat fragmentation on expected heterozygosity (*He*), number of alleles (*A*), and inbreeding coefficient (F_{IS}). Sample sizes for each meta-analysis are shown in parenthesis; dotted line indicates Hedge's d = 0.

Figure 2. Weighted mean effect sizes and 95% bias-corrected CI of habitat fragmentation effects on *He*, *A*, and F_{IS} in different tetrapod groups (Amp = amphibians, Rep = reptiles, Bir = birds, Mam = mammals). Sample sizes for each group are given in parentheses; dotted line Indicates Hedge's d = 0.

Figure 3. Weighted mean effect sizes and 95% bias-corrected CI of habitat fragmentation effects on *He* and *A* of tetrapod groups (Amp = amphibians, Rep = reptiles, Bir = birds, Mam = mammals) with different body size (large and small). Sample sizes for each group are given in parentheses; dotted line Indicates Hedge's d = 0.

Figure 4. Weighted mean effect sizes and 95% bias-corrected CI of habitat fragmentation effects on *He*, *A*, and F_{IS} of tetrapod populations subjected to different extent of habitat fragmentation (extreme and moderate habitat loss). Sample sizes for each group are given in parentheses; dotted line Indicates Hedge's d = 0.

FIGURE 1.

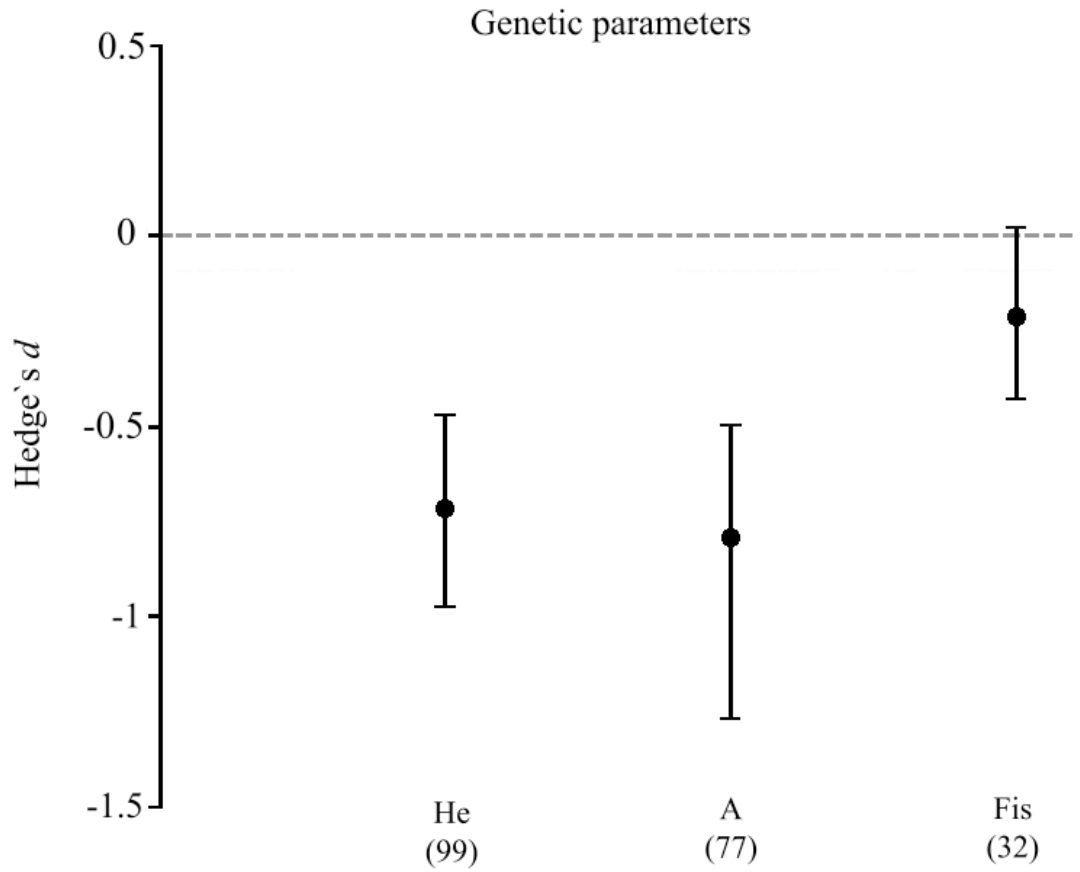


FIGURE 2.

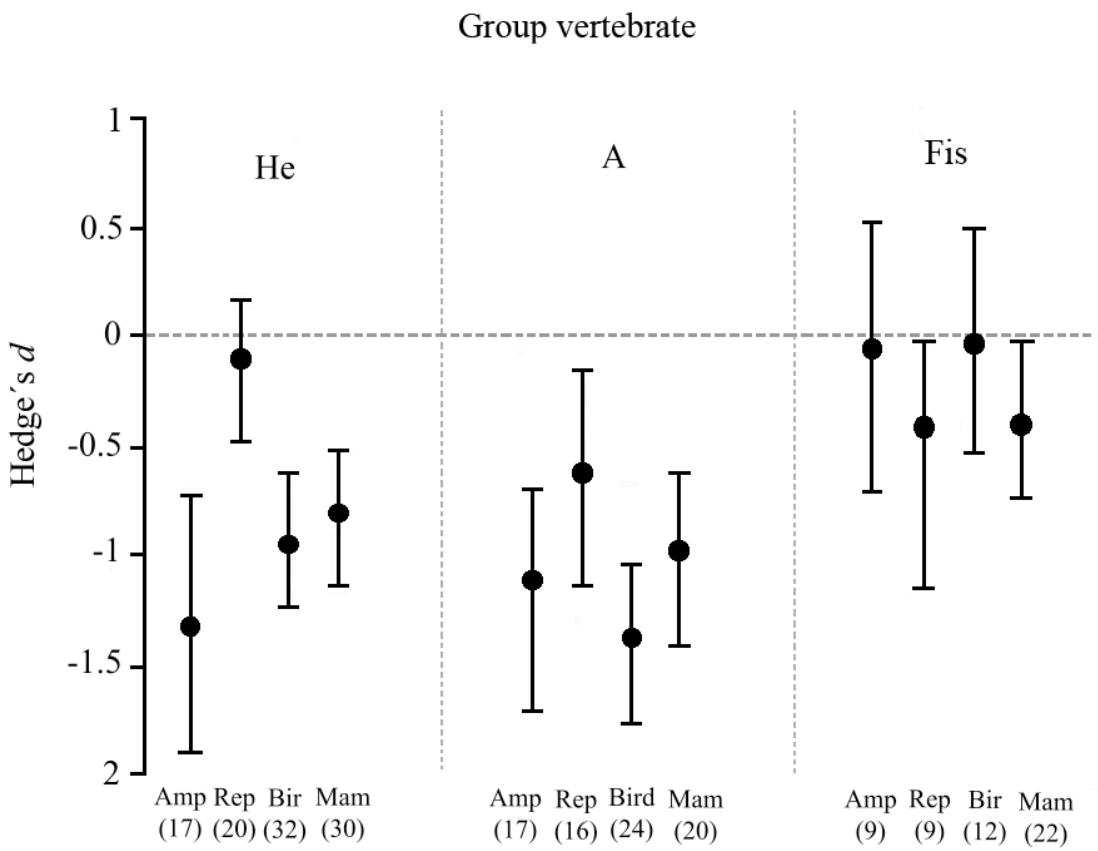

Group vertebrate
He
A
Fis
Hedge´s d
1
0.5
0
-0.5
-1
-1.5
2
Amp (17)
Rep (20)
Bir (32)
Mam (30)
Amp (17)
Rep (16)
Bird (24)
Mam (20)
Amp (9)
Rep (9)
Bir (12)
Mam (22)

FIGURE 3.

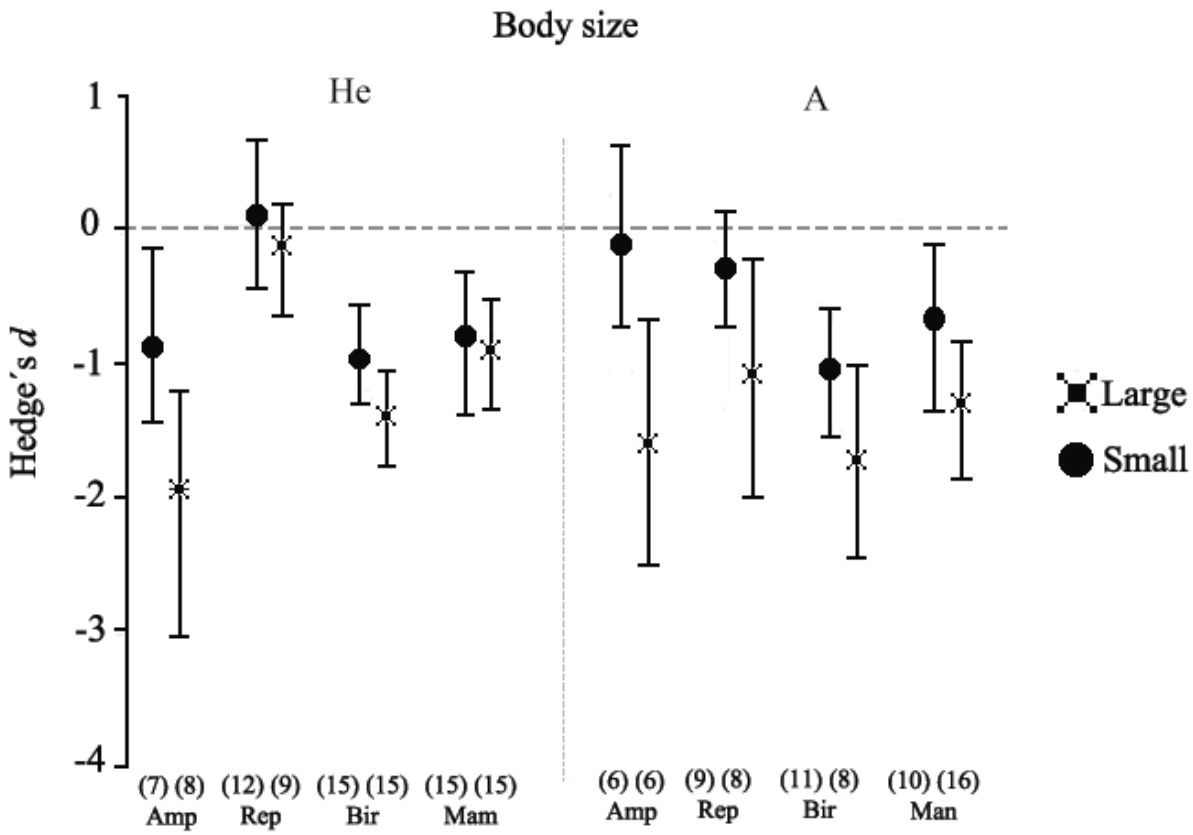
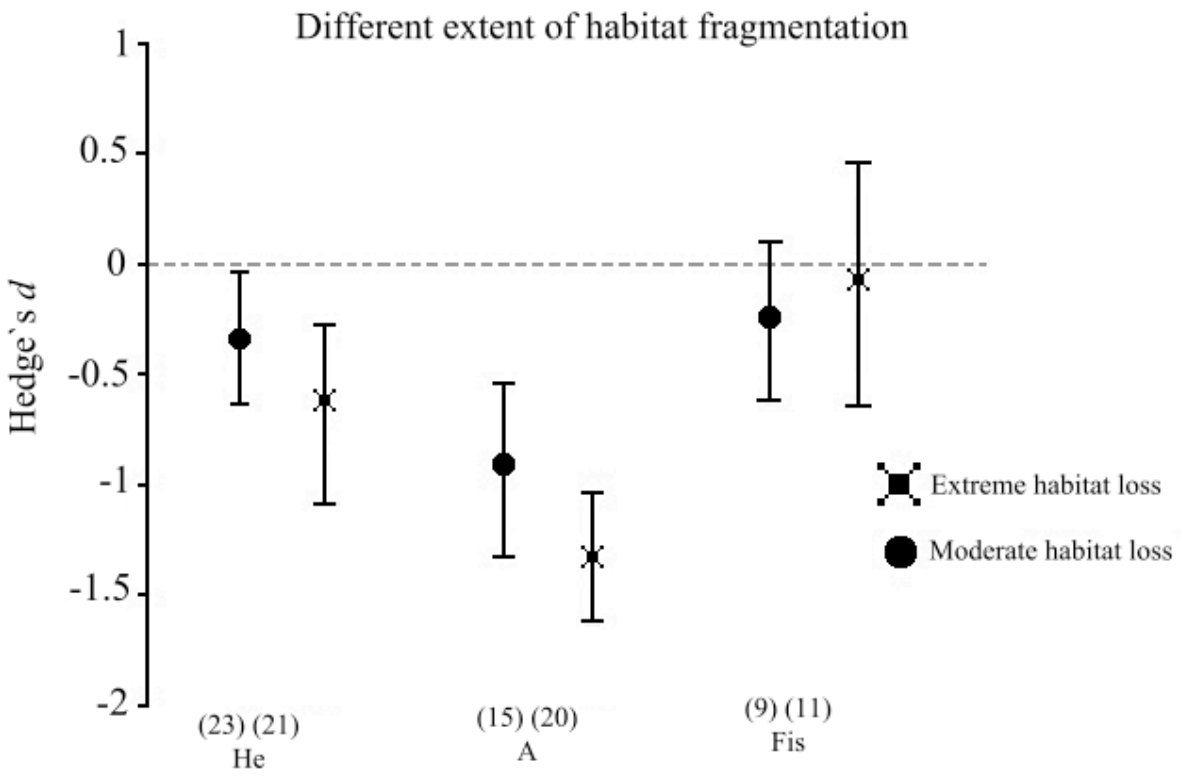

Body size
He
A
1
0
-1
-2
-3
-4
Hedge's d
(7) (8) Amp
(12) (9) Rep
(15) (15) Bir
(15) (15) Mam
(6) (6) Amp
(9) (8) Rep
(11) (8) Bir
(10) (16) Man
Large
Small

FIGURE 4.


Different extent of habitat fragmentation
Hedge`s d
1
0.5
0
-0.5
-1
-1.5
-2
(23) (21)
He
(15) (20)
A
(9) (11)
Fis
Extreme habitat loss
Moderate habitat loss

7.0 Capítulo III

Rivera-Ortíz, F. A., Arizmendi,

M. C., Solórzano, S. and Oyama, K.

Genetic structure of the Military Macaw (*Ara militaris*) in Mexico: implications for conservation

Sera enviado a la revista Conservation Genetic

Conservation genetics of the Military Macaw

Genetic structure of the Military Macaw (*Ara militaris*) in Mexico: implications for conservation.

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Abstract The loss and fragmentation of ecosystems have been identified as the main threats to the survival of wild populations including the Military Macaw. Accordingly, these processes are expected to have influenced the genetic diversity and structure of this species. We used microsatellites as a molecular marker to determine levels of genetic variability and gene flow in seven sites of nesting and feeding Military Macaws in Mexico. The results suggest that, compared with other species of Psitttacidae, the Military Macaw has a intermediate genetic diversity, and that individuals along the Gulf of Mexico are genetically distinct from populations of the Military Macaw on the Pacific slope. This may be due to two barriers: the Central Mexican Plateau and the Trans-Mexican Volcanic Belt. The intermediate genetic diversity detected for the Military Macaw does not seem to represent a threat for survival of this species, while habitat destruction and poaching are factors that adversely affect their wild populations. One important factor that influences the genetic structure of the Military Macaw seems to be the topography, as revealed by the barrier analysis. Given that the genetic structure observed serves to protect different regions in order to maintain genetic diversity in the Military Macaw, we posit that the creation of a system of natural corridors between remnant populations of the species will ensure gene flow between Military Macaw populations and thus, their survival in nature.

Keywords *Aramilitaris*, Genetic structure, Genetic variability, Military Macaw, Macaws, Psittacidae.

Resumen La pérdida y la fragmentación de los ecosistemas han sido identificados como las principales amenazas para la supervivencia de las poblaciones silvestres , incluyendo la Guacamaya Verde. En consecuencia, se espera que estos procesos han influido en la diversidad genética y la estructura de esta ave. Se utilizó microsatélites como marcadores moleculares para determinar los niveles de variabilidad genética y el flujo genético en siete sitios de anidación y alimentación de la Guacamaya Verde en México. Los resultados sugieren que, en comparación con otras especies de psitácidos, la Guacamaya Verde tiene una diversidad genética intermediaa y que los individuos de la vertiente del Golfo de México son genéticamente distintos de las poblaciones de Guacamaya Verde de la vertiente del Pacífico, debido a dos barreras: El Altiplano Mexicano y el Eje Neo-Volcánico Transversal. La diversidad genética moderada detectada en la Guacamaya Verde no parece representar una amenaza para la supervivencia de esta especie, mientras que la destrucción del hábitat y la caza furtiva son los factores que afectan negativamente a sus poblaciones silvestres. Un factor importante que influye en la estructura genética de la Guacamaya Verde parece ser la topografía, según lo revelado por el análisis de barreras. Dado que la estructura genética observada sirve para proteger a las diferentes regiones con el fin de mantener la diversidad genética en la guacamaya verde, postulamos que la creación de un sistema de corredores naturales entre las poblaciones remanentes de la especie para garantizar el flujo genético entre las poblaciones de Guacamaya Verde, y por lo tanto su supervivencia en la naturaleza.

Palabras clave *Ara militaris*, Guacamaya Verde, Guacamaya, Psitácidos, Variabilidad genética, Estructura genética.

Introduction

The loss and fragmentation of ecosystems have been identified as the main threats to the survival of wild populations (Sutherland 2000; Solórzano et al. 2003). Moreover, the ecological effects of these two processes on natural populations have been recognized as devastating for their long-term persistence (Saunders et al. 1991; Fahrig 2003; Alcaide et al. 2009).

In conservation biology, conceptual and methodological contributions have been proposed to standardize criteria focused on searching for patterns and processes at multiple scales to minimize the loss of biodiversity at all levels (Simberloff1988). However, the challenge remains to determine the conservation status of species, including detailed knowledge of their biology, ecology and genetics (Fernández et al. 2003; Solórzano 2003; Zizumbo 2005).

Conservation genetics aims to investigate genetic patterns and the evolutionary processes of natural populations, with particular emphasis on endangered species. An additional objective in conservation genetics is to identify potential and real threats that endanger the survival of such taxa (Frankham2003; Solórzano 2003; Martínez-Cruz 2011), so that appropriate actions and decisions can be taken for their management and protection (Lande1999; Solórzano 2003).

The particular case of the Military Macaw (*Ara militaris*), an emblematic threatened bird species, is a challenge in conservation genetics. This evasive species is widely distributed in fragmented tropical dry forests along Mexico´s slopes, crossing down into Central America and even into parts of South America. Some field studies have concluded that the global population of this bird amounts to no more than 10, 000 individuals, which represents a clear decrease in its population size and distribution (Collar et al. 1992; Snyder et al. 2000; BirdLife International 2013). This species is listed in Appendix I of the Convention on

International Trade in Endangered Species of Fauna and Flora (CITES1998), and at the global level it is considered vulnerable due to habitat destruction and illegal trade (BirdLifeInternational 2013). In Mexico, the Military Macaw is considered an endangered species according to the official standard [Norma Oficial Mexicana (SEMARNAT 2002)].

In Mexico, the Military Macaw has been recorded along the Pacific slope, from the northern state of Sonora through Chihuahua to southern Chiapas (Peterson and Chaliff1989; Howell and Webb1995). In the northeast of Mexico, along the slope of the Gulf of Mexico, it has been reported in the state of Tamaulipas, crossing into the central states of San Luis Potosi and Queretaro. In central-south Mexico, the Military Macaw has been recorded in the semiarid Tehuacán-Cuicatlán valley (Peterson and Chaliff 1989; Howell and Webb; 1995; Iñigo-Elías1999; Arizmendi and Márquez2000; Iñigo-Elias 2001a; 2002b; Rivera-Ortíz 2007).

Currently, the Military Macaw lives in highly fragmented forests, in which few individuals have been recorded (20 to 78 individuals in some sites) (Carreón 1997; Gaucín 2000; Rivera-Ortíz et al. 2008), which suggests that large populations have formed small isolated colonies (Iñigo-Elias 1999) that exhibit an insular distribution pattern. In addition, this bird species is found in most tropical deciduous and semi-deciduous forests, with seasonal movements to Pine-Oak forests.

This habitat fragmentation is of conservation concern because of the potential genetic consequences to the species (Triggs et al. 1989; Cunningham and Moritz 1998; Lindsay et al. 2008; Meyer et al. 2008; Solórzano et al. 2009). Changes in landscape configuration imposed by habitat fragmentation can affect the genetic characteristics of populations by limiting gene flow and dispersion, thus reducing the effective population sizes and increasing the effects of genetic drift in small habitat patches (Reed and Frankham 2003; Caizergues et al. 2003). As a result, the distribution patterns of genetic diversity within and among populations (i.e., genetic

structure) can change drastically. Thus, it is important that conservation programs of vulnerable species include assessment of levels of intra-specific genetic diversity (Haig 1998).

In this context, should be directed conservation efforts to maintain genetically diverse populations, therefore need to know the levels of diversity and gene flow to try to guarantee the long-term survival of this bird. Currently, many contributions have been proposed to distinguish at intraspecific level the namely conservation priorities (Loza 1997; Iñigo-Elias 1999; Gaucín 2000; Rubio et al. 2007; Rivera-Ortiz et al. 2013). Moritz (1994) proposed that genetic differentiation and the maintenance of allelic richness should be the main criteria to identify conservation priorities. In the present study we applied these genetic criteria in order to contribute to the conservation of the Military Macaw. For this, population genetic analyses were carried out across the entire distribution range of this species in Mexico. We expected that the recent habitat loss and fragmentation documented for this species (Iñigo-Elías 1999; 2000; Ríos-Muñoz and Navarro-Sigüenza 2009; Rivera-Ortíz et al. 2013) have led to depleted levels of genetic diversity but high genetic structure among populations.

To date, no information is available on the structure and genetic variation of the Military Macaw, and our work is intended to fill this gap. Recently, habitat loss and fragmentation were identified as the main threats to Military Macaw (Ríos-Muñoz and Navarro-Sigüenza 2009; Rivera-Ortíz et al. 2003). Thus, it is expected that these processes have influenced the genetic diversity and structure of this bird.

This study analyzes the structure and genetic variability of the Military Macaw using microsatellites as molecular markers. To achieve this, we characterized levels of genetic variability at seven locations along the distribution of Military Macaw in Mexico and evaluated the level of genetic structure in these populations.

Material and methods

Area of Study. This study was conducted at seven sites in Mexico that represent the largest populations reported for Military Macaw (Gaucín 2000; Gómez-Garduño 2004; Rubio et al. 2007; Rivera-Ortíz et al. 2008; Jiménez-Arcos et al. 2012). Four of these sites are located in the Pacific slope: La Sierrita, Sonora; Nuestra Señora del Mineral, Sinaloa; El Mirador del Águila, Nayarit; El Tuito, Jalisco. Two other areas are found in the Gulf of Mexico slope: El Cielo, Tamaulipas and Santa María de Cocos, Queretaro. One area is found in central Mexico in Santa María Tecomavaca, Oaxaca (Fig. 1).

The Protected Natural Area of the Sierrita (26 ° 52 '48" N, 108 ° 34' 12" W) is located in Alamos, Sonora, with a maximum number of 38-40 individuals (Ordonez and Flores 1995). The Ecological Conservation Area of the Nuestra Señora del Mineral (24 ° 24 '44 "N, 106 ° 41 '22" W) is located in the municipality of Cosalá, Jalisco, with a number of individuals by census of 25-40 individuals (Rubio et al. 2007). The Mirador del Águila, Nayarit (21 ° 30 '28 "N, 104 ° 55' 47" W) is located in Tepic, and has a maximum number of 50 individuals on average (Rivera-Ortíz et al. 2013). The Tuito is located in Jalisco (20 ° 17 '35 "N, 105 ° 23' 6.4" W), with a number of individuals by census of 14-20 individuals (Palomera-Garcia et al. 1994; Rivera-Ortíz et al. 2013). The Biosphere Reserve El Cielo is located in Tamaulipas (23 ° 04 '22 "N, 99 ° 09 '24" W), with a number of individuals by census of of 35-40 individuals (Arizmendi and Márquez 2000; Rivera-Ortíz et al. 2013). Santa Maria de Cocos is located in the Biosphere Reserve of the Sierra Gorda, Querétaro (21 ° 18 '37 "N, 99 ° 40' 4" W), with a maximum number of 70 individuals (Gaucin 2000). Santa María Tecomavaca is located in the Biosphere Reserve Tehuacán-Cuicatlán, Puebla-Oaxaca (17 ° 51 '43 "N, 97 ° 02 '40" W), with a maximum number of 76 individuals (Rivera-Ortiz et al. 2008) (Fig.1).

Sample Collection. A total of 86 feather samples were collected at seven sites during the fieldwork carried out during 2010 to 2012, and each sample was considered an individual.

These feathers were collected at the base of the trees in sites of nesting, feeding and resting, and in some cases they were obtained directly from nests (each nest represented an individual). These feathers were considered from different individuals until genotyping confirmed they were from the same individuals.

We collected feathers from five individuals in La Sierrita and 23 individuals at Nuestra Señora del Mineral. Thirty-six feathers were collected in El Mirador del Águila, six in Santa Maria Tecomavaca and El Tuito, while five were taken in Santa Maria de Cocos and El Cielo. The sampled feathers were cleaned with 90% alcohol and maintained at the environmental temperature in paper bags during their transportation to the laboratory.

DNA extraction and Genotyping. The total genomic DNA was extracted using the standard digestion proteinase K/SDS, followed by chloroform:alcohol purification as described by Leeton and Christidis (1993).

In total, nine polymorphic nuclear microsatellite loci were amplified, of these; six were designated for Blue-and-yellow Macaw (*Ara ararauna*) (Caparroz et al. 2003), and three for The Saint Vincent Amazon (*Amazon guildinguii*) (Russello et al. 2001; 2005) (Table 1).

The nine loci assayed were prepared in individual PCR reactions using the QIAGEN Multiplex PCR kit (QIAGEN), with a final volume of 5 µL including master Mix (contains HotStarTaq DNA Polymerase, Multiplex PCR buffer, 3 mM MgCl2, and dNTPs), primers (5 pmol / µL), distilled / deionized water, and template (total genomic DNA, 20-50 ng/µL).

The amplifications were carried out in a GeneAmp PCR System 2720 Thermal Cycler (Applied Biosystems) using multiplex PCR protocol for amplification of microsatellite loci (QIAGEN): 15 min at 95 ° C (initial stage activation), followed by 30 cycles of denaturation at 94 ° C for 30 s, and followed by 90 s of alignment of the primers at specific temperatures (Table 1), followed by an extension of 72 ° C for 30 min, and a final extension of 60 ° C for 30 min. The PCR products were mixed with formamide and Gene Scan LIZ-500 standard size

(Applied Biosystems) and denatured for 5 min at 95 ° C for their analysis by the sequencer ABI PRISM 3100-Avant (Applied Biosystems) for detecting the primer and the internal standard size. The analyses of the produced fragments and their final size were determined using Gene Mapper 4.0 software (Applied Biosystems). We verified and corroborated the assignment of the genotype of the eight loci by testing null alleles, small alleles domain registration and stutters for each population using the software Micro-Checker (Oosterhout et al. 2004).

Genetic diversity. We estimated the total number of alleles (N_T) and effective number of alleles (Nae) for loci, using the software Genalex 6.3 (Peakall and Smouse 2006). For each population we estimated the average number of alleles (A) and private allelic richness (P_A) by rarefaction with ADZE 1.0 software (Szpiech et al. 2008) due to differences in sample size among the seven populations of the Military Macaw studied. Furthermore, we estimated observed heterozygosity (HO), expected heterozygosity (HE), and the inbreeding coefficient (FIS) by locus and for each population. Also, we estimated the probability of significant deviation from the equilibrium under Hardy-Weinberg (Nei, 1978) through the Markov chain method with the following parameters: dememorizations1000, batches 50 and iterationss1000, adjusted to a nominal level of 5% with Bonferroni correction, with GENETIX 4.05 software (Belkhir et al. 2004).

Differentiation and Genetic structure patterns. The genetic differentiation of populations paired was calculated by FST (Weir and Cockerham1984) according to the infinites alleles model (IAM) with 10,000 permutations using the software 4.05 MSA (Microsatellite Analyzer) (Dieringer and Schlötterer2003). The distribution of genetic variation within and among populations was estimated among the predetermined groups of populations (Pacific slope and slope of the Gulf of Mexico) by analysis of molecular variance (AMOVA) in ARLEQUIN 3.0 (Excoffier et al. 2005), and the statistical significance of FST

and RST was tested with 10,000 permutations. The levels of gene flow between populations were assessed using MIGRATE 3.0 (Beerli 2008), under the Brownian model of microsatellite based on maximum likelihood, with variable theta (θ) assuming a constant mutation rate.

To assign genetic structure patterns, we used a Bayesian method available in the software STRUCTURE 2.3.1 (Pritchard et al. 2000; Falush et al. 2003). In this analysis, all individuals are assigned probabilistically to values of predefined K populations, to identify the optimal number of genetic groups (Evanno et al. 2005). The optimal number of genetic groups (K) is determined by varying the value of K from 1 to 10 and of run the analysis 10 times value with of K, with order to determine the maximum value of the a posteriori probability [lnP (D)]. The duration of the burn-in was 500,000 steps, followed by 10^6 interactions under the model admixture with correlated allele frequencies without any prior information. We determined the most probable value of K using the maximum value of ΔK according to Evannoo et al. (2005). To visualize the pattern of K along the Military Macaw distribution, the proportion of admixture by population was plotted on a map.

To determine whether the pattern of admixture is associated with the geographic location of the populations, we constructed a UPGMA tree with FST distance matrix using SplitsTree version 4.11.3 (Huson and Bryant 2006) and edited version Dendroscope 2, 4 (Huson et al. 2007). To test isolation by distance gene flow model, we performed a Mantel-Haenszel test with AIS 1.0 software (Alleles in Space) with 100, 000 replicas (Miller 2005).

Finally, to determine the geographic location of the major genetic discontinuities between populations, we used the maximum difference algorithm of Monmonier, with BARRIER 2.2 software (Manni et al. 2004). This program creates a map of the geographical coordinates of the locations sampled. The barriers are represented on the map by identifying the maximum values in the distance matrix paired population genetics. A genetic distance

matrix based on the proportion of shared allele (Bowcock et al. 1994) values was calculated with software 4.05 MSA (Microsatellite Analyzer) (Dieringer and Schlötterer 2003).

Results

Genetic diversity. According to the Micro-Checker analysis, the probability of the presence of null alleles was significant for locus UnaCT41 in all populations, and inference of null alleles was 85% with the participation of 86 individuals. Therefore, this locus was eliminated from the genetic analyses. The remaining microsatellite loci showed no deviation from Hardy-Weinberg equilibrium ($p > 0.00833$, adjusted nominal level 5% with Bonferroni correction, $p_{BC} = 0.00833$) (Table 1). For all the loci, 151 alleles were recorded; the loci with less variability were UnaCT43, UnaCT74, UnaCT55 and AgGT19, with 12 to14 alleles, and the loci with most variability were UnaCT21, UnaCT32, AgGT17 and AgGT32, with 20 to 29 alleles. All loci varied in size from 78-227 bp, and showed high levels of observed heterozygosity, from 0.63 to 0.75 (Table 1). All populations showed no deviation from Hardy-Weinberg equilibrium, resulting in non-significant f values ($p > 0.00167$, $p_{BC} = 0.0133$), suggesting random mating within populations (Table 2).

The average number of alleles (A) was high for all populations with values of 16.10 (El Cielo) to 19.27 (El Mirador del Águila), while the private alleles (P_A) ranged from 4.85 (Santa María Tecomavaca) to 8.51 (Santa María Tecomavaca). The expected heterozygosis (H_E) ranged from 0.76 (El Mirador del Águila) to 0.54 (Santa Maria de Cocos and El Cielo), and the observed heterozygosis (H_O) ranged from 0.69 (Heaven) to 0.51 (La Sierrita), whereas in the inbreeding coefficient (FIS), the population of El Cielo showed an excess of heterozygosis (-0.16) (Table 2).

Differentiation and Genetic structure patterns. The comparison of paired populations showed little genetic differentiation (FST) among nearby populations (Table 3). The highest differentiation was in populations of Santa María de Cocos and El Cielo with rest of the

populations (FST = 0.12 to 0.25, P <0.05); however, the lowest differentiation was between in the populations of Mirador del Águila, La Sierrita (FST = 0.02, P> 0.05), Nuestra Señora del Mineral (FST = 0.05, P> 0.05), and El Tuito (FST = 0.09, P> 0.05) (Table 3).

The AMOVA indicated that there was variation due to differences between groups (Table 4). For the F_{ST}, 6.6% of the variation was due to genetic differences between groups, and 93.4% to variation within the groups, similar to the R_{ST}, in which 53.9% of the variation was due to genetic differences between groups, and 46% to variation within groups (Table 4). Gene flow levels (M) among the seven populations are shown in Table 5. More gene flow was detected between populations of Nuestra Señora del Mineral and El Mirador del Aguila (1.39), slightly less between Santa Maria Tecomavaca and La Sierrita (1.36), followed by El Tuito and Santa María Tecomavaca (1.22), and finally Santa Maria de Cocos and El Cielo (1.24) (Table 5).

The ΔK statistic revealed K = 2 to be the optimum value for the number of genetic clusters in the data (Fig. 2). The proportion of ancestry of each population and individuals in these two genetic clusters, represented by the green and red colors, is represented in Figure 3. The populations of La Sierrita, Nuestra Señora del Mineral, El Mirador del Águila, El Tuito and Santa Maria Tecomavaca, all from the Pacific slope, have a higher proportion of the green genotype (80%), in contrast to the populations of Santa María de Cocos and El Cielo along the Gulf slope, that have a higher proportion of 99% of the red genotype (Fig. 3).

The analysis of genetic distances between populations confirmed that the ratio of the admixtures are geographically structured (Fig. 4a). We found that 78% of individuals in the populations on the Pacific slope have the green genotype ($q \geq 0.80$); however, 97% of individuals in the populations along the Gulf Mexico have the red genotype ($q \geq 0.90$). The Mantel-Haenszel test highlighted a correlation between genetic distance and geographic distance ($r = 0.1330$, $p = 0.005$), indicating isolation by distance.

The maximum difference algorithm of Monmonier, applied to matrix linearized F_{ST} values, placed six barriers, of which two barriers have major 95 - 100% support, whereas the other four barriers have 10 - 20% support (Fig. 4b). The first barrier is located between the populations of La Sierrita and Nuestra Señora del Mineral (15% support), the second barrier is located between the populations of Nuestra Señora del Mineral and El Mirador del Águila (15% support), and the third barrier is located between the populations of Mirador del Águila and El Tuito with support of 20% (Fig 4). The fourth barrier separates the populations of the Pacific slope from the population of the slope of the Gulf Mexico, with a support of 100% (Fig 4). The fifth barrier is located between the population of Santa María de Cocos and El Cielo (10% support; Fig 4). The sixth barrier separates the population of Santa María Tecomavaca from the population of the slope of the Gulf Mexico, with a support of 95% (Figure 4). This analysis was very consistent with the results obtained from the structure and UPGMA tree based on genetic distances (Fig 5).

Discussion

The levels of heterozygosis we found in the Military Macaw (H_E = 0.63) are relatively moderate compared with other studies of macaws. Historically, the species of macaws that have had low values for heterozygosis are Spix's Macaw (*Cyanopsitta spixii*), Lears Macaw (*Anodorhynchus leari*) and the Hyacinth Macaw (*Anodorhynchus hyacinthinus*) (Faria et al. 2008; Presti et al. 2011; Presti et al. 2013) with H_E values from 0.36 to 0.51. By contrast, the macaw species that have had high levels for heterozygosis are the Scarlet Macaw (*Ara macao*) (Nader et al. 1999; Presti et al. 2011) and Blue-and-Yellow Macaw (*Ara ararauna*) (Caparroz et al. 2003) with H_E levels of 0.86 and 0.80, respectively. Although the Military Macaw is a vulnerable species globally and is considered endangered by Mexican norms, this

species maintains moderate levels of genetic diversity in Mexico, despite anthropogenic pressures on wild populations (Iñigo-Elias 1999; Rivera-Ortiz et al. 2008).

When we compared the values of genetic diversity among populations of the Military Macaw, we observed that populations of the slope of the Gulf of Mexico have a lower genetic diversity (H_E = 0.54). This is likely due to isolation from the rest of the distribution of the Military Macaw, which causes gene flow to be more restricted than in the Pacific slope populations. However, these relatively high levels of heterozygosity may reflect still the diversity contained in ancestral large populations. As the estimators are strongly affected by historical factors they did not detect the effects of population size decreasing and genetic isolation.

We did not find a pattern of genetic differentiation in populations of the Macaw Military due to fragmentation and habitat loss, because the Military Macaw has a long life expectancy (60 years captive individuals) (Iñigo-Elias 1999), and fragmentation in the geographic distribution of this species is a recent event (less than 50 years), considering the life cycle of this species. Possibly, some individuals that are still breeding may be older than the first anthropic disturbances. Thus, the effects of these impacts may have not yet affected the genetic structure and diversity of this species. Furthermore, with a long life expectancy, it is possible that the current population of Military Macaw is composed mainly of old individuals, and when these old individuals die, the populations will suffer a sudden, drastic size reduction, which may cause a reduction in genetic variability (Leite et al. 2008).

An important result is that is found clear genetic differentiation due to the biogeographic regions. In this way we found significant genetic differentiation in populations of the slope of the Gulf of Mexico compared to populations of the Pacific slope. This suggests that the two Military Macaw populations along the Gulf coast of Mexico are closely related, whereas the populations along the Pacific coast of Mexico in La Sierrita, Nuestra Señora del

Mineral, El Mirador del Águila, El Tuito and Santa Maria Tecomavaca show a close relationship among them. Specifically, these results indicate connectivity among these populations of Military Macaws, that are able to fly long distances (Gaucín et al. 2000), and this hypothesis is reinforced by the high values for gene flow between these populations. The dispersion that occurs is not effective, because it is limited by the selective use of the habitat and availability of forest resources, and for this reason the movements are determined by the spatial-time patterns from fruiting (Collar 1997, Rivera-Ortiz et al. 2008; Contreras-González et al. 2009; Rivera -Ortiz et al. 2013). Consequently, habitat fragmentation appears to be an important factor in the distribution and choice of breeding sites of the populations of the Military Macaw (Faria et al. 2008).

We predicted a strong genetic structure among the populations of the Pacific slope and the slope on the Gulf of Mexico. This hypothesis is supported by the Bayesian analysis, which shows a major compression of the structure within and between populations (see Figure 3), meaning that the populations of the slope of the Gulf Mexico are different from the populations of the Pacific slope, which is consistent with the geographical region.

This structural pattern of the Military Macaw is similar to the biogeographic patterns found in other species of Mexican birds, such as the Ferruginous Pygmy Owl (*Glaucidium brasilianum*) (Proudfoot et al. 2006) and Wild Turkey (*Melagris gallopavo*) (Mock et al. 2002) where the genetic differences are due to the presence of geographic barriers such as mountain ranges (The Sierra Madre Oriental and The Sierra Madre Occidental) and the Central Mexican Plateau (Mock et al. 2002, Proudfoot et. al. 2006).

The two genetic groups detected in this study have a geographic concordance (see Figure 4), indicating that each slope can be considered a priority conservation unit, namely Management Units (MUs) (Moritz, 1994a, 1994b). MUs are defined as a population or a group of individuals with high allelic differences, regardless of the evolutionary history given

by these alleles; such is the case of the populations of Military Macaw. While it is true that sample size is an important factor in conservation studies, the small sample size in some populations of Military Macaw is not cause to dismiss the results, because endangered species typically have small population sizes (Moritz 1994a, 1994b; Solórzano et al. 2009).

The moderate genetic variation seen in Military Macaws does not appear to pose problems for current conservation efforts; rather, the high degree of specialization in their diet and nesting sites, and low reproductive rates, appear to be the strongest threats arising from human factors (loss of habitat and illegal hunting) (Iñigo-Elias et al. 1999; Rivera-Ortiz et al. 2008; Contreras-González et al. 2009; Ríos-Muñoz and Navarro-Sigüenza 2009; Rivera-Ortiz et al. 2013).

Our results on the genetic structure of Military Macaw populations has implications for conservation, since most of the sites we studied represent breeding populations, and therefore need effective protection actions at the regional level to preserve the habitat of the Military Macaw, and with it the genetic diversity of this bird. The biological conservation criteria within species are not entirely sufficient for the whole taxon (e.g. Moritz 1994a; Young 2001). Therefore, we propose that these two groups (Gulf of Mexico and Pacific slope) be considered a reference for conservation programs of the Military Macaw in Mexico, including maintenance of the genetic connectivity among different groups with its effects on sustaining gene flow, in order to preserve the genetic diversity of the Military Macaw.

In this respect, it has been suggested that the habitats of the Military Macaw continue to be evaluated (Rivera-Ortiz et al. 2013), and that from these data a system of natural corridors be created between remnant populations of the Military Macaw, then incorporated into national systems of protected areas. These measures can help to ensure the maintenance of the species populations in nature.

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Table 1. Genetic diversity estimated by locus over the eight population of Military Macaw. The total number of alleles (N_T), the number effective of alleles (N_{AE}), observed (H_O) and expected (H_E) heterozygosity, the inbreeding coefficient (F_{IS}).

Locus	Sequence (5'-3')	ºT	Allelic size range	Genetic Diversity				
				N_T	N_{AE}	H_O	H_E	F_{IS}
UnaCT21•	CTTTCCCATACTTAGCCATA	58	153-277	29	4	0.48	0.63	0.23*
UnaCT32•	TCTTGCTTATTCTTCCCCAG	56	248-268	27	4	0.78	0.72	-0.09*
UnaCT43•	TCATCCTATCACCAGAAGG	60	184-216	14	3	0.68	0.70	0.01*
UnaCT74•	CTGGACTGCTGCTCTTAAA	58	138-190	15	3	0.57	0.63	0.08*
UnaGT55•	TCTGCCCTCTGTCTTATGCC	58	181-257	13	4	0.76	0.75	-0.01*
AgGT17°	CCTGGATGTGCTCTGTGAG	60	134-242	21	3	0.81	0.65	-0.25*
AgGT19+	CCTGCCTCCCAAAAGAACT	60	167-189	12	2	0.66	0.64	-0.03*
AgGT32+	ACCCAGCTTCAGGTTTGTA	60	78-120	20	4	0.56	0.65	0.12*
Overall				151	28	0.66	0.67	0.005

•Caparroz et al. 2003, °Russello et al. 2001, +Russello et al. 2005

*HWD, Bonferroni correction P > 0.05

Table 2. Estimates of genetic diversity patterns of the Military Macaw.

Populations	N	A	P_A	H_E	H_O	F_{IS}
La Sierrita	5	18.05	4.65	0.60 ± 0.04	0.51 ± 0.12	0.33
Ntra. Sra. Mineral	23	18.67	6.37	0.72 ± 0. 03	0.59 ± 0.08	0.19*
El Mirador del Águila	36	19.27	6.11	0.76 ± 0.02	0.58 ± 0.06	0.25*
El Tuito	6	18.06	4.95	0.60 ± 0.05	0.66 ± 0.08	0.06
Sta. Ma. Tecomavaca	6	17.98	4.85	0.61 ± 0.05	0.61 ± 0.08	0.09
Sta. Ma. Cocos	5	17.55	8.51	0.54 ± 0.07	0.48 ± 0.13	0.31*
El Cielo	5	16.10	5.70	0.54 ± 0.10	0.69 ± 0.14	-0.14
Overall		17.95	5.87	0.62 ± 0.08	0.58 ± 0.07	0.15

The average values are given ± s. e. as the case. N = Sample size, A = allelic richness, P_A = private alleles, H_E = expected heterozygosis, H_O = observed heterozygosis, and F_{IS} = index inbreeding.
*HWD, Bonferroni correction P > 0.05

Table 3. Paired genetic differentiation (F_{ST}) among the seven populations the Military Macaw.

Populations	**Ntra. Sra. Mineral**	**El Mirador del Águila**	**El Tuito**	**Sta. Ma. Tecomavaca**	**Sta. Ma. Cocos**	**El Cielo**
La Sierrita	0.083*****	0.025^{ns}	0.180*****	0.140*****	0.142*****	0.253*****
Ntra. Sra. Mineral		0.056^{ns}	0.094*****	0.075*****	0.166*****	0.167*****
El Mirador del Águila			0.093^{ns}	0.046^{ns}	0.120*****	0.169*****
El Tuito				0.125*****	0.177*****	0.118*****
Sta. Ma. Tecomavaca					0.184*****	0.206*****
Sta. Ma. Cocos						0.075^{ns}

*****P < 0.05, **ns** = non significant P < 0.05

Table 4. Analysis of Molecular Variance (AMOVA), comparing genetic distance between and within of the populations the Military Macaw.

Source of variation	d. f.	Sum of squares	Variance components	Percentage of variation	F-statistic
Among populations	6	38.91	0.19	6.61	F_{ST} = 0.066****
Within populations	165	443.79	2.68	93.39	
Total	171	482.70	2.87		
Among populations	6	144673.37	1142.36	46.10	R_{ST}=0.46*
Within populations	165	220414.19	1335.84	53.90	
Total	171	365087.56	2478.20		
**P*=0.0001					

663 Table 4. Levels of gene flow between the seven populations the Military Macaw.

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Populations	**[+]La Sierrita**	**[+]Ntra. Sra. Mineral**	**[+]El Mirador del Águila**	**[+]El Tuito**	**[+]Sta. Ma. Tecomavaca**	**[+]Sta. Ma. Cocos**	**[+]El Cielo**
La Sierrita	-	1.01	1.11	1.35*****	0.85	1.17	0.85
Ntra. Sra. Mineral	1.12	-	1.39*****	1.07	1.25*****	1.07	1.02
El Mirador del Águila	0.96	1.18	-	0.79******	1.02	0.89	0.77
El Tuito	0.86	0.98	1.14	-	0.65******	0.88	0.74
Sta. Ma. Tecomavaca	1.36*****	0.82	0.71	1.22*****	-	0.89	090
Sta. Ma. Cocos	1.08	0.45******	0.89	1.32*****	0.99	-	1.05
El Cielo	0.77	0.58******	0.93	1.09	0.73	1.24*****	-

[+]Receiving population**, *** Populations with greater gene flow, ****** Populations with lower gene flow

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Figure Legends

Figure 1. Location of populations of the Military Macaw. 1 = La Sierrita, Sonora, 2 = Nuestra Señora del Mineral, Sinaloa, 3 = El Mirador del Águila, Nayarit, 4 = El Tuito, Jalisco, 5= Santa Maria Tecomavaca, Oaxaca, 6 = Santa Maria de Cocos, Queretaro, 7 = El Cielo, Tamaulipas. The gray shading represents the potential historic distribution of the Military Macaw, taken from Rivera-Ortiz et al. 2003.

Figure 2. Estimated genetic groups (K) from the clustering analysis of STRUCTURE. Statistical plot of ΔK with regarding to the genetic clusters K (1 to 10

Figure 3. Graphic of the genetic structure of K = 2. A vertical line represents each individual with colored segments in proportion to their membership of a genetic group. Black lines separate the different populations. 1 = La Sierrita, 2 = Nuestra Señora del Mineral, 3 = El Mirador del Águila, 4 = El Tuito, 5 = Santa Maria Tecomavaca, 6 = Santa Maria de Cocos and 7 = El Cielo.

Figure 4. A) Distribution of the Military Macaw populations in Mexico, indicating the barriers between populations. B) Frequency distribution of genotypes obtained by Bayesian analysis in populations related with barriers. The Roman numerals indicate the number of barriers. 1 = La Sierrita, 2 = Nuestra Señora del Mineral, 3 = El Mirador del Águila, 4 = El Tuito, 5 = Santa Maria Tecomavaca, 6 = Santa Maria de Cocos and 7 =El Cielo.

Figure 5. UPGMA tree obtained with genetic distances between pairs of populations (FST). The ratio of admixture of the group of populations is represented by genotypes green and red color obtained from the results of K = 2 of Bayesian analysis.

FIGURE 1.

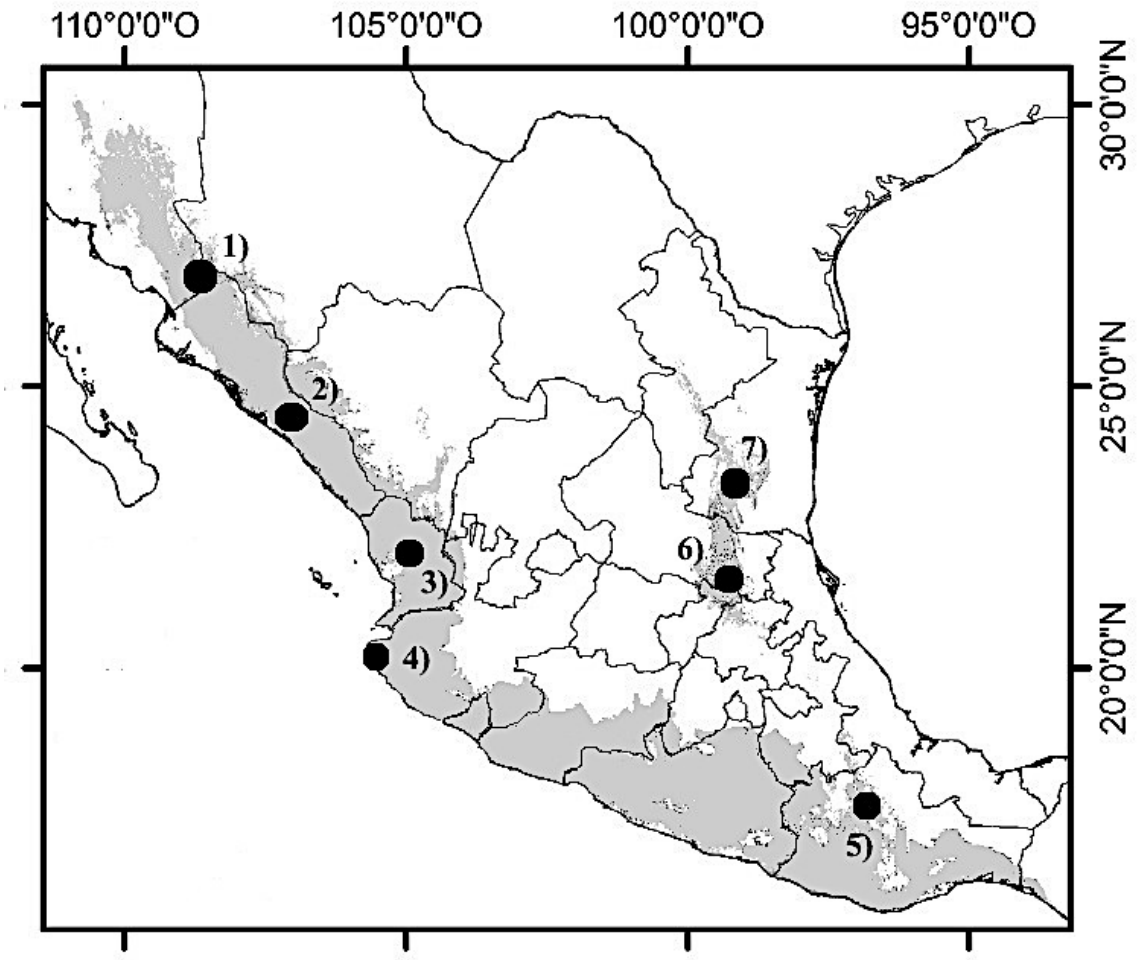

FIGURE 2.

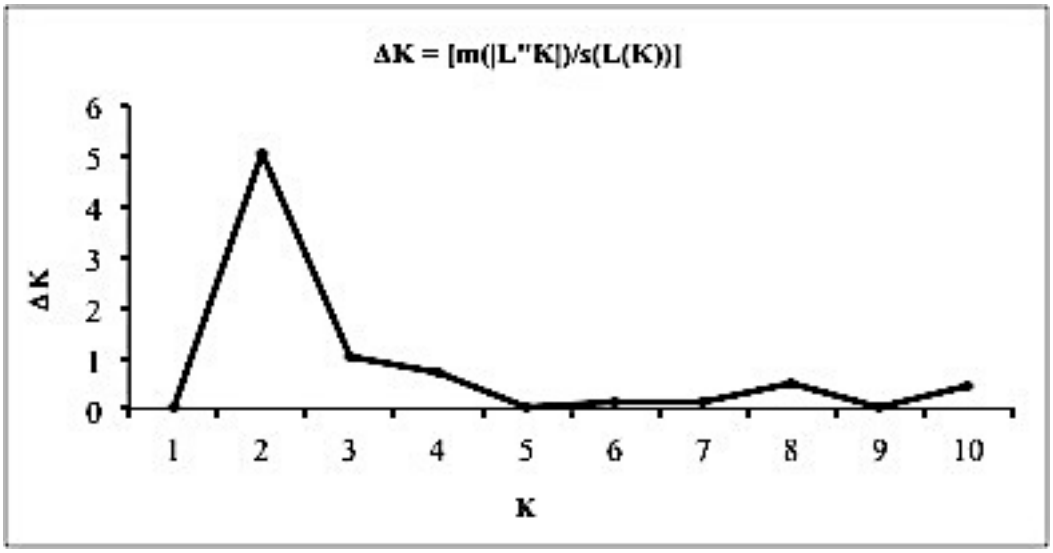

FIGURE 3.

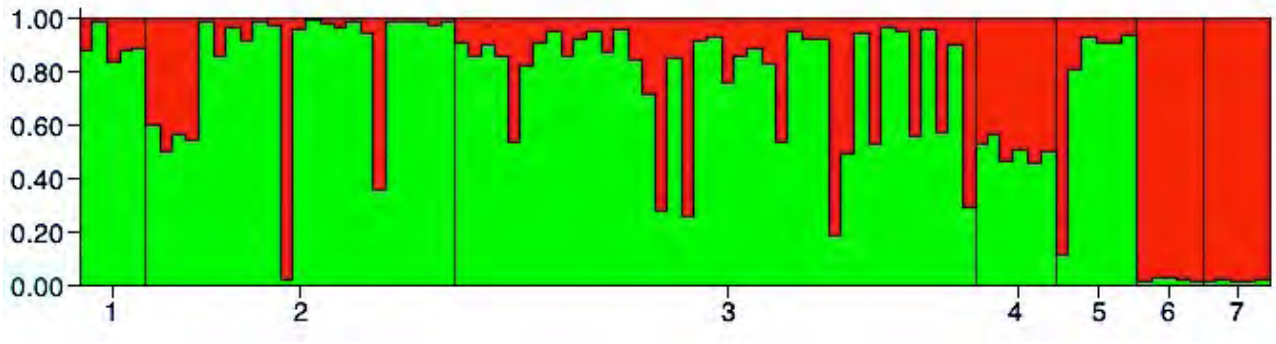

FIGURE 4.

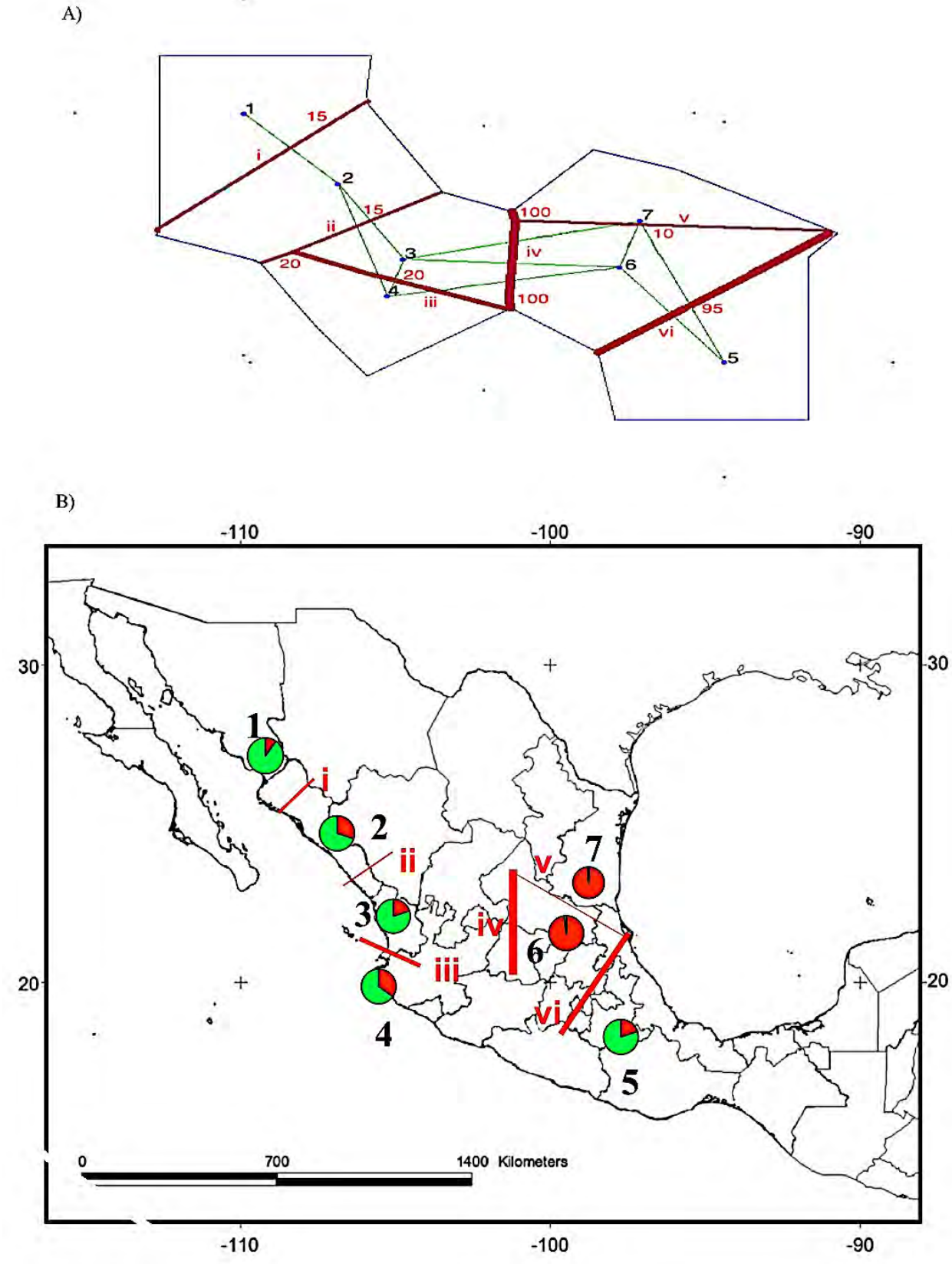
A)
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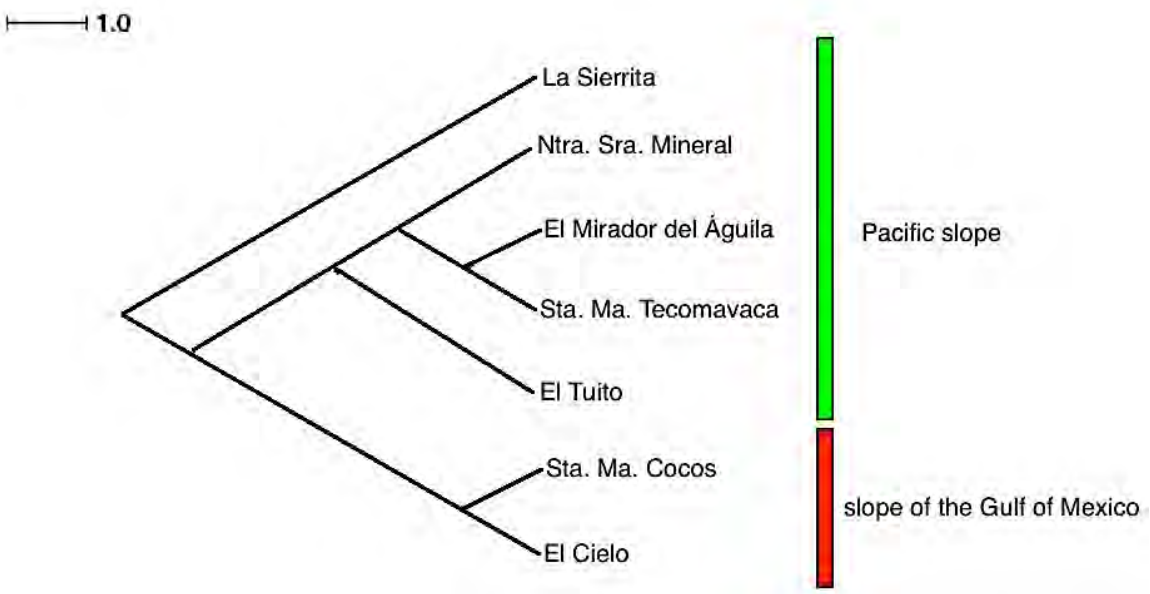
FIGURE 5.


1.0
La Sierrita
Ntra. Sra. Mineral
El Mirador del Águila
Sta. Ma. Tecomavaca
El Tuito
Sta. Ma. Cocos
El Cielo
Pacific slope
slope of the Gulf of Mexico

8.0 Discusión general

Cada uno de los tres capítulos de la tesis nos permitió contestar preguntas especificas a diferentes niveles (ecología y genética) y que refieren al campo de la biología de la conservación. Este campo ha contribuido con propuestas conceptuales y metodológicas para minimizar la pérdida de la diversidad biológica que nos permita conocer el estatus de conservación en cada especie (Simberlloff, 1988). En la biología de la conservación se reconoce a los procesos de fragmentación y de pérdida de hábitat como las principales amenazas que han causado un declive poblacional y ha colocado en riesgo de extinción a varios taxa (Brower et al., 1990; Solórzano, 2003).

En el Capítulo I mostramos la idoneidad de los hábitats para la Guacamaya Verde y cómo se ha perdido dicho hábitat por la fragmentación y pérdida del hábitat.

Las variables estructurales del hábitat de esta especie indicaron que el tipo de vegetación influye en la selección del hábitat. La Guacamaya Verde se considera una especie de dosel (Iñigo-Elías, 1996; Loza, 1997; Gómez, 2004), ya que requiere árboles de gran tamaño con un dosel grande en bosques tropicales caudifolios y subcaducifolios para alimentación, reproducción y nidificación, así como la protección contra los depredadores (Forshaw, 1989; Collar y Juniper, 1992; Collar, 1997; Loza, 1997; Iñigo-Elías, 1999; Salazar, 2001; Peterson et al., 2004; Rivera - Ortiz et al, 2008; Contreras -González et al., 2009).

La idoneidad de los hábitats de esta especie requiere la presencia de especies de ciertos géneros de árboles, como *Brosimum*, *Cyrtocarpa*, *Celtis*, *Hura*, *Quercus*, *Bunchonsia*, *Lysiloma* y *Bursera*, las cuales son importantes tanto para anidar o como suministro de alimentos (Carreón, 1997; Loza, 1997; . Gaucín, 2000 y Contreras-González et al., 2009). En las poblaciones de Colombia y Perú también se

reportan especies de *Hura* y *Bursera* como árboles importantes para la alimentación (Flores y Sierra, 2004). Estas plantas tienen gran cantidad de nutrientes, tales como lípidos, carbohidratos y proteínas que son importantes para la puesta de huevos y el desarrollo de los pollos (Contreras-González et al., 2009).

Estos resultados fueron respaldados al comparar la estructura de la vegetación y composición florística en sitios con y sin presencia de la Guacamaya Verde, donde se encontraron diferencias significativas en la composición florística pero similitudes estructurales. Las especies florales con las que se observa una gran relación son: *Brosimum alicastrum*, *Bursera simaruba*, *Ceiba aescutifolia*, *Ceiba pentandra*, *Cyrtocarpa procera*, *Guaiacum coulteri, Guazuma ulmifolia*, *Hura polyandra*, *Haematoxylon brassileto*, *Ipomea arborences*, *Lysiloma divaricata*, *Lysiloma microphylla, Plumeria rubra* and *Taxodium mucronatum*.

Estos hallazgos indican que la dependencia de la Guacamaya Verde en la composición florística específica, patrones que se encuentran comúnmente en las especies de aves especialistas debido a la estrecha relación entre la disponibilidad de recursos alimenticios y la actividad reproductiva (Saunders, 1977; Saunders, 1990; Collar y Juniper, 1992). Ello tiene implicaciones importantes para la conservación de esta especie (Ruth et al., 2003).

Al realizar los modelos de cambio de cobertura vegetal sobre los modelos de distribución potencial de la Guacamaya Verde se observó que la Guacamaya Verde y las 14 especies de plantas arbóreas asociadas se encuentran en áreas con características similares, por lo menos en un espacio ambiental ordinario; esto se ve reforzado por las alta superposición ambiental encontrados en el análisis discriminante. En el presente estudio identificamos una reducción del 32% de la distribución potencial de la Guacamaya Verde comparando cuatro escenarios de

cambio de uso del suelo desde 1976 al 2010. Estos cambios fueron especialmente dramáticos en zonas donde se presenta la Guacamaya Verde asociada a seis especies de plantas (*Lysiloma microphylla*, *Lysiloma divaricata*, *Hura polyandra*, *Ceiba aescutifolia*, *Guaiacum coulteri*, *Ipomea arborences*).

Estos hallazgos indican los posibles efectos negativos sobre la supervivencia de la especie si se continúan produciendo reducciones de hábitat disponibles en el futuro (Peterson et al., 2006; Ríos-Muñoz y Navarro-Sigüenza, 2009; Contreras-Medina et al., 2010). Lo anterior concuerda con lo reportado en otros estudios, por ejemplo Ríos-Muñoz y Navarro-Sigüenza (2009) reportaron una reducción del 28,5 % en el hábitat disponible de la guacamaya verde en el año 2000. Marin-Togo et al. (2011) y Monterrubio-Rico et al. (2010) declararon localmente extinta a la Guacamaya Verde en la costa del Pacífico mexicano (Michoacán, Guerrero y Oaxaca) y en las zonas costeras de más de 400 m de altitud, con una disminución del 16 % de la distribución hasta el año 2000.

En este capitulo presentamos información sobre el tipo de vegetación y la composición de especies que es fundamental para la conservación de la Guacamaya Verde. Nuestros resultados sugieren la importancia de conocer la composición florística del hábitat de especies en peligro de extinción y el impacto del cambio de uso de suelo y su variación a través del tiempo para los esfuerzos de conservación directas. Vale la pena señalar que el uso de modelos de nicho ecológico y datos geográficos del cambio de uso del suelo son herramientas fundamentales a tener en cuenta en los esfuerzos de conservación de la esta especie.

En este sentido observamos que la fragmentación y perdida del hábitat de especies vulnerables aparte de tener consecuencias ecológicas, podría tener

consecuencias directas sobre la variabilidad genética debido al aislamiento geográfico que se genera entre las poblaciones.

La diversidad genética es crucial para determinar el potencial de las poblaciones de animales de adaptarse y evolucionar en entornos cambiantes. Por lo tanto, es importante evaluar los efectos de la fragmentación del hábitat sobre la diversidad genética con el fin de contribuir al desarrollo de herramientas y estrategias para la conservación de las poblaciones silvestres (Ouborg et al., 2006; Pertoldi et al., 2007), por lo que en el Capitulo II se realizó una revisión sobre el efecto de la fragmentación sobre la variabilidad genética (A = riqueza alélica, H_E = heterocigosis esperada y F_{IS} = índice de endogamia) en tetrápodos (anfibios, reptiles, aves y mamíferos).

Encontramos que la fragmentación del hábitat reduce la diversidad genética global de las poblaciones de tetrápodos. Los cuatro grupos de tetrápodos mostraron efectos de la fragmentación negativos similares en la riqueza alélica (A). La disminución en A es probable que sea el resultado inmediato de la repentina reducción poblacional debido a la pérdida y fragmentación del hábitat, generando cuellos de botella genéticos. El impacto de los cuellos de botella en la variación genética depende principalmente de dos factores: el tamaño efectivo de la población y el tiempo durante el cual la población se mantiene pequeña. Una drástica reducción en el tamaño efectivo de las poblaciones causada por la fragmentación del hábitat reduce la variación genética de las poblaciones restantes y también afectará a la variación genética de las siguientes generaciones que permanecen en los fragmentos debido a la interrupción del flujo de genes (Hoelzel ,1999).

También en esta tesis observamos efectos negativos de la fragmentación del hábitat sobre la heterocigosis esperada (H_E) en tres grupos de tetrápodos (anfibios,

aves y mamíferos); esta reducción en poblaciones fragmentadas pueden ser el resultado de deriva genética. Cuando las poblaciones siguen siendo pequeñas y aisladas por generaciones, la reducción de la variabilidad genética se producen por la eliminación al azar de los genotipos heterocigóticos, afectando el número y las frecuencias de los alelos (Reed y Frankham, 2003; Caizergues et al., 2003).

En contraste con los parámetros de diversidad genética, no observamos cambios significativos en el índice de consanguinidad (F_{IS}) en hábitats fragmentados. La gran mayoría de los estudios que evalúan F_{IS} son con individuos adultos, por lo tanto , la ausencia de cambios en el F_{IS} está reflejando por los patrones de apareamiento de los individuos adultos de vida larga, que pueden preceder a los eventos de fragmentación. Sería muy interesante determinar F_{IS} en la progenie generada en nuevos hábitats fragmentados y como las configuraciones nuevas de hábitats pueden ser la causa de los cambios en los patrones de apareamiento hacia una mayor endogamia biparental (Aguilar et al., 2008).

En este capitulo también se mostró que la variabilidad genética de especies con un tamaño corporal grande dentro de cada grupo de tetrápodos fue más fuertemente afectado por la fragmentación del hábitat. El tamaño del cuerpo se relaciona positivamente con el rango de distribución, es decir las especies más grandes requieren más cantidad de hábitat para la alimentación y reproducción. Además, las especies de gran tamaño suelen ocurrir en bajas densidades. Los requerimientos espaciales más grandes, junto con bajas densidades poblacionales pueden hacer que las especies de gran tamaño sean especialmente susceptibles de sufrir erosión genética en hábitats fragmentados (Bergl et al., 2008).

Otro hallazgo es que el tiempo transcurrido en condiciones de fragmentación es crucial para determinar la reducción de la diversidad genética en las poblaciones

de los tetrápodos. Se observaron efectos negativos más fuertes sobre la diversidad genética (H_E) en los estudios realizados en los sistemas que han sido fragmentados por más de 100 años. Estos resultados están de acuerdo con las expectativas teóricas, que predice la erosión genética más fuerte en las poblaciones sometidas a períodos más largos de tiempo en condiciones fragmentadas y aisladas. La deriva genética tendrá efectos más fuertes a medida que más generaciones pasan por tales condiciones, la fijación de alelos homocigotos a través de generaciones y la disminución de la variabilidad genética general (Lande, 1993; Foose, 1993; Mech y Hallett, 2001).

A pesar de estas señales de los efectos de la fragmentación sobre la variabilidad genética, hay una clara diferencia en la literatura de la genética de poblaciones de tetrápodos que evita generalizaciones adicionales. La mayoría de los datos provienen de adultos, y su composición genética puede diferir de la de su progenie que se han sometido a las condiciones de fragmentación. Tal es el caso de los pocos estudios que examinaron el efecto de la fragmentación sobre las especies vágiles y los estudios escasos que examinaron la progenie establecida en hábitats fragmentados (Aguilar et al., 2008). Por lo tanto, hacemos un llamado a un incremento de los estudios que evalúan los efectos genéticos sobre la progenie de tetrápodos, lo que nos permitirá estimar el apareamiento y los patrones de flujo de genes en condiciones fragmentadas y evaluar cómo los cambios en los patrones de apareamiento pueden afectar la diversidad genética de las generaciones futuras de las poblaciones de tetrápodos.

En el Capítulo III unimos los dos primeros capítulos para determinar si la diversidad y estructura genética de las poblaciones de la Guacamaya Verde en México son afectadas por la fragmentación y pérdida del hábitat. Uno de los

resultados es que no se encontró un patrón de diferenciación genética de las poblaciones de la Guacamaya Verde por la fragmentación y pérdida de hábitat, sin embargó se mostró diferenciación genética encontrada entre las poblaciones de la vertiente del Golfo de México y la del Pacífico asociada a las regiones biogeográficas (Figura 5). Se observó una fuerte separación de la vertiente del Pacífico respecto al Golfo de México, barrera que coincidió con el Altiplano mexicano, más específica,mente a la Meseta de Anáhuac, que tiene mayor a 2900 msnm y se extiende al sur colindando con el Eje Neo-Volcánico (Flores, 2005).

Otra división que se observó es la que separa a las poblaciones en el Golfo de México con las poblaciones más meridionales de la vertiente del Pacífico (Santa María Tecomavaca), esta barrera coincide con el Eje Neo-Volcánico que alcanza alturas de más de 4000 msnm (Flores, 2005) . Estas barreras probablemente actúan como barreras físicas para el movimiento y la dispersión de la Guacamaya Verde.

A diferencia de las poblaciones de la vertiente del Pacífico, que forma un grupo, en este caso la distribución de los bosques tropicales caducifolios y subcaducifolios podrían ser un corredor natural entre las poblaciones de la Guacamaya Verde. Este modelo de estructura de la población es muy similar a los patrones biogeográficos encontrados en otras especies de aves mexicanas con marcadores de ADN mitocondrial, como es el caso del búho pigmeo (*Glaucidium brasilianum*) (Proudfoot et al., 2006) y del pavo silvestre (*Melagris gallopavo*) (Mock et al., 2002), donde las diferencias genéticas se deben a la presencia de barreras geográficas como la Sierra Madre Oriental, la Sierra Madre Occidental y el Altiplano Mexicano (Mock et al., 2002 , Proudfoot et al., 2006).

Los dos grupos genéticos detectados en este estudio tienen una concordancia geográfica (véase la Figura 4), lo que indica que se podría considerar

como unidades prioritarias para la conservación, más específicamente como unidades de manejo (MU´s). Sin embargo, el tamaño pequeño de la muestra en algunas poblaciones debe tomarse en cuenta, ya que el tamaño de la muestra es un factor clave en la estudios de conservación, aunque las especies en peligro de extinción tienen pequeños tamaños poblacionales (Moritz, 1994_1, 1994_2; Solórzano et al., 2009). Por otra parte, los niveles de heterocigosis de la Guacamaya Verde (SE = 0.63) son relativamente moderados en comparación con otros estudios de guacamayos (e. g. Nader et al., 1999; Caparroz et al., 2003; Faria et al., 2008; Presti et al., 2011; Presti et al., 2013). Aunque la Guacamaya Verde es una especie vulnerable en todo el mundo y se considera en peligro de extinción por las Normas Mexicanas aun mantiene niveles moderados de diversidad genética a pesar de intensas presiones antropogénicas sobre los recursos naturales y la caza ilegal (Iñigo-Elías, 1999; Rivera-Ortiz et al., 2008).

La variación genética moderada no parece plantear problemas actuales para la conservación de la Guacamaya Verde, por otra parte el alto grado de especialización en su dieta, en los sitios de anidación y tasas de reproducción bajas, parecen ser las amenazas más fuertes relacionados con los factores humanos (pérdida de hábitat y la caza ilegal) (Iñigo -Elías et al., 1999; Rivera-Ortiz et al., 2008, Contreras-González et al., 2009, Ríos- Muñoz y Navarro-Sigüenza, 2009; Rivera-Ortíz et al., en prensa). Los resultados sobre la estructura genética de las poblaciones de esta especie tiene implicaciones para la conservación ya que la mayoría de los sitios presentan poblaciones reproductoras, por lo tanto necesitan una protección eficaz en las regiones que habita, con el fin de preservar los niveles de diversidad genética a lo largo de su distribución. Los criterios biológicos de conservación dentro de las especies no son del todo satisfactorios para todos los

taxones (e.g. Moritz, 1994$_1$; Young, 2001). En este sentido, proponemos que estos dos grupos deben ser considerados como Mu´s y una referencia para los programas de conservación de la Guacamaya Verde en México, por lo tanto, los programas de conservación deben incluir el mantenimiento de la conectividad entre las diferentes poblaciones con la capacidad de mantener el flujo de genes, con el fin de preservar la diversidad genética de la Guacamaya Verde (Solórzano et al., 2009). Estas medidas pueden ayudar a garantizar el mantenimiento de las poblaciones de la especie en la naturaleza.

8.1 Recomendaciones de conservación para la Guacamaya Verde

1.- Protección de los hábitats adecuados y la realización de actividades sostenibles para la conservación de la Guacamaya Verde.

2.- Sugerimos que al menos el 30% de los bosques de la distribución potencial de la Guacamaya Verde debe ser protegido para garantizar áreas específicas de anidación y alimentación, por lo tanto se debe aumentar el tamaño y el número de áreas naturales protegidas en México.

3.- La estructura genética encontrada en las poblaciones de la Guacamaya Verde nos demuestra dos grupos (vertiente del Pacífico y vertiente del Golfo de México) que pueden ser considerados como unidades prioritarias para la conservación independientes por lo que se sugiere programas nacionales de protección y monitoreo específicos para cada grupo.

5.- Dentro de cada vertiente no se observo una diferenciación entre sus poblaciones lo que sugiere que las poblaciones de cada una de las vertientes existe flujo génico reciente, por lo que se recomienda proteger los bosques tropicales caducifolios y subcaducifolios para garantizar el flujo génico entre poblaciones.

6.- Se sugiere realizar el estudio de los patrones filogeográficos de las poblaciones de las Guacamaya Verde con el fin de localizar y enfatizar las unidades prioritarias de conservación.

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10.0 APÉNDICES

10.1 Apéndice 1. Floristic composition and importance value (IVI), of the eight sites studied (A = La Sierrita, B = Nuestra Señora del Mineral, C = Mirador del Águila, D= El Tuito, E = Papalutla, F = Santa María Tecomavaca, G = El Cielo and H = Santa María Tecomavaca).

Family	Plants species	Localites							
		A	B	C	D	E	F	G	H
Anacardiaceae	*Rhus pachyrrhachis*	-	-	-	-	-	-	-	0.155
	Mangifera indica	-	-	-	-	-	-	0.226	-
	Cyrtocarpa procera	-	-	-	-	0.228	0.407	-	-
	Spondias purpurea	-	-	-	0.133	0.028	-	-	-
	Spondias mombin	-	-	-	-	0.037	-	-	-
	Pseudosmodingium perniciosum	-	-	-	-	0.142	-	-	-
Annonaceae	*Annona cherimola*	-	0.037	-	0.215	-	-	-	-
	Annona globiflora	-	0.005	-	-	-	-	-	0.021
	Annona longiflora	-	-	0.009	-	-	-	-	-
Apocynaceae	*Rauvolfia nitida*	0.028	-	-	-	-	-	-	-
	Vallesia laciniata	0.165	-	-	-	-	-	-	-
	Stemmadenia palmeri	-	0.176	-	-	-	-	-	-
	Plumeria acutifolia	-	-	-	-	-	-	0.023	-
	Plumeria rubra	-	-	-	-	0.021	0.123	-	-
Araliaceae	*Dendropanax arboreus*	-	-	-	-	-	-	0.011	-
	Callistephus chinensis	-	-	-	-	-	-	0.006	-
	Montanoa xanthifolia	-	-	-	-	-	-	-	0.068
	Pseudosmodingium multifolium	-	-	-	-	-	0.014	-	-
Begoniaceae	*Begonia angustifolia*	-	0.006	-	-	-	-	-	-
	Begonia monophylla	-	-	-	-	0.016	-	-	-
	Begonia palmeri	-	-	-	-	0.039	-	-	-
Bixaceae	*Cochlospermum vitifolium*	-	0.007	-	-	-	-	-	-
Bombacaceae	*Ceiba acuminata*	0.066	0.05	-	-	0.106	-	-	-
	Ceiba parviflora	-	-	-	-	-	-	-	-
	Pseudobombax ellipticum	-	-	-	-	0.039	-	-	-
	Ceiba pentandra	0.483	-	-	0.018	-	0.054	-	-
	Ceiba aesculifolia	-	-	-	-	-	0.286	-	-

	Ceiba grandiflora	-	-	-	0.013	-	-	-	-
	Croton sp.	-	-	-	0.018	-	-	-	-
Boraginaceae	*Cordia parviflora*	0.011		-	-	-	-	-	-
	Tabebuia palmeri	0.251	0.053	0.062	0.095	-	-	-	-
	Tabebuia rosea	-	-	-	0.09	-	-	0.012	-
	Tabebuia chrysantha	-	0.083	0.004	0.102	-	-	-	-
	Cordia alliodora	-	0.057	-	-	-	-	-	-
	Cordia sonorae	-	0.005	-	-	-	-	-	-
	Cordia morelosana	-	-	-	-	0.023	-	-	-
	Cordia boissieri	-	-	-	-	-	-	-	0.051
Buddlejaceae	*Buddleja scordioides*	-	-	-	-	-	-	-	0.008
Burseraceae	*Bursea aloxylon*	-	-	-	-	0.053	0.089	-	-
	Bursera aptera	-	-	-	-	-	0.18	-	-
	Bursera arborea	-	-	-	0.082	-	-	-	-
	Bursera ariensis	-	-	-	-	0.12	-	-	-
	Bursera bicolor	-	-	-	-	0.039	-	-	-
	Bursera excelsa	-	0.171	0.079	-	-	-	-	-
	Bursera grandifolia	0.011	-	-	-	-	-	-	-
	Bursera innopinata	0.068	0.016	-	-	-	-	-	-
	Bursera laxiflora	0.008	-	-	-	0.014	-	-	-
	Bursera microphylla	0.265	0.008	-	0.006	-	-	-	-
	Bursera morelensis	-	-	-	-	0.014	0.145	-	-
	Bursera multifolia	-	-	-	-	0.015	-	-	-
	Bursera schlechtendali	-	-	-	-	-	0.152	-	-
	Bursera simaruba	-	0.091	-	0.078	-	-	0.261	0.219
	Bursera xochipalensis	-	-	-	-	0.036	-	-	-
Cactaceae	*Pachycereus pectenaboriginum*	0.008	-	-	-	-	-	-	-
	Myrtillocactus geometrizans	-	-	-	-	-	0.009	-	-
	Neobuxbaumia tetezo	-	-	-	-	-	0.016	-	-
	Opuntia depressa	-	-	-	-	-	0.029	-	-
	Paquicerius hollianus	-	-	-	-	-	0.019	-	-
Cappareaceae	*Capparis sp*	-	0.036	-	-	-	-	-	-
	Capparis angustifolia	-	-	-	-	0.048	-	-	-
	Capparis incana	-	-	-	-	-	0.094	-	0.146
Celastraceae	*Wimmeria concolor*	-	-	-	-	-	-	0.087	-
Clusiaceae	*Calophyllum brasiliense*	-	-	0.097	-	-	-	-	-
Compositaceae	*Senecio praecox*	-	-	-	-	0.017	-	-	-
Convolvulaceae	*Ipomea arborescens*	0.122	0.158	-	0.091	0.065	0.089	-	-
	Ipomea conzantii	-	-	-	-	-	0.008	-	-

	Ipomea sp.	-	-	-	0.013	-	-	-	-
	Ipomea carnea	-	-	-	-	0.023	-	-	-
	Cuscuta sp.	-	-	-	-	0.03	-	-	-
Euphorbiaceae	*Celaenodendron mexicanum*	-	-	-	0.009	-	-	-	-
	Cnidoscolus multilobus	-	-	-	-	-	-	0.007	-
	Croton adspersus	-	-	-	-	-	-	0.009	-
	Croton flavescens	-	-	-	-	0.018	-	-	-
	Croton fragilis	-	0.05	-	-	-	-	-	-
	Croton niveus	-	-	-	-	-	-	0.098	-
	Croton sp.	-	0.059	-	-	-	-	-	-
	Croton sp.	-	-	-	-	-	-	-	0.008
	Croton sp.	-	-	-	0.006	-	-	-	-
	Euforbia pringlei	-	-	-	-	-	0.028	-	-
	Euforbia schlechtendali	-	-	-	-	-	0.091	-	-
	Euphorbia antisyphilitica	-	-	-	-	-	0.038	-	-
	Euphorbia colorata	-	-	-	-	0.013	-	-	-
	Euphorbia francoana	-	-	-	-	0.06	-	-	-
	Euphorbia graminea	-	-	-	0.013	-	-	-	-
	Euphorbia misera	0.116	-	-	-	-	-	-	-
	Euphorbia rossiana	-	-	-	-	0.018	-	-	-
	Hevea brasiliensis	-	-	-	0.019	-	-	-	-
	Hura polyandra	-	0.106	0.573	0.357	-	-	-	-
	Jatrofa elbae	-	-	-	-	0.026	-	-	-
	Jatropha cunneata	0.184	-	-	-	-	-	-	-
	Jatropha dioica	-	0.015	-	-	-	-	-	-
	Jatropha neopaucifolia	-	-	-	-	-	0.126	-	-
	Jatropha rzedowskii	-	-	-	-	-	0.01	-	-
	Jatropha sp.	-	-		0.015	-	-	-	-
	Sapium pedicellatum	-	-	0.017	-	-	-	-	-
	Sebastiana bilocularis	0.122	-	-	-	-	-	-	-
	Sebastiana pavoniana	-	-	-	-	-	0.056	-	-
Fabaceae	*Haematoxylon brassileto*	0.021	0.223	-	-	-	-	-	-
	Senna wislizeni	-	-	-	-	-		-	0.028
	Senna obtusifolia	-	-	-	-	-	0.191	-	-
	Quercus tuitensis	-	-	-	0.315	-	-	-	-
	Quercus sp	-	-	-	0.102	-	-	-	-
	Quercus conspersa	-	-	-	-	0.012	-	-	-
	Quercus castanea	-	-	-	-	0.074	-	-	-
	Quercus sacame	-	-	-	-	-	-	-	0.008

	Pithecellobium dulce	-	-	-	0.035	-	-	-	-
	Parkinsonia preacox	-	-	-	-	-	0.28	-	-
	Mimosa priga	-	-	0.004	-	-	-	-	-
	Mimosa laxiflora	-	-	0.002	-	-	-	-	-
	Erythrina herbacea	-		-	-	-	-	-	0.028
	Desmodium asperum	-	0.005	-	-	-	-	-	-
	Conzattia sericea	-	0.027	-	-	-	-	-	-
	Caesalpinia cacalaco	-	-	-	0.007	-	-	-	-
Flacourtiaceae	*Casearia dolichopylla*	-	-	0.023	-	-	-	-	-
Fouquieriaceae	*Foquieria leonilae*	-	-	-	-	0.039	-	-	-
	Fouquieria formosa	0.048	-	-	-	-	0.035	-	-
Hidrophylaceae	*Nama demiscum*	-	-	-	-	-	-	-	-
	Wigondia urens	-	-	-	0.005	-	-	-	-
Julianaceae	*Amphiterygium adstringens*	-	-	-	0.009	0.027	0.011	-	-
Lamiaceae	*Mentha piperita*	-	-	-	0.01	-	-	-	-
Lauraceae	*Nectandra sanguinea*	-	-	-	-	-	-	0.03	-
	Nectandra salicifolia	-	-	0.009	-	-	-	-	-
Malpighiaceae	*Bunchonsia sp.*	-	-	-	0.127	-	-	-	-
	Bunchonsia canences	-	-	-	-	0.094	-	-	-
	Lasiocarpus salicifolius	-	-	-	-	0.054	-	0.026	-
Malvaceae	*Malviscus arboreus*	-	0.007	-	-	-	-	-	-
	Gaudichaudia mucronata	-	-	-	-	-	-	-	0.007
Meliaceae	*Melia azadarach*	0.047	-	-	-	-	-		-
	Cedrela mexicana	-	-	0.016	-	-	-	0.017	-
	Cedrela occidentalis	-	-	0.012	-	-	-	-	-
	Cedrela odorata	-	-	-	-	-	-	0.292	-
	Swietenia humilis	-	0.018	-	-	-	-	-	-
	Swietenia macrophyla	-	-	0.029	0.025	-	-	-	-
	Trichilia havanensis	-	-	-	-	-	-	0.006	-
Mimosaceae	*Platymiscium lasiocarpum*	-	-	0.034	-	-	-	-	-
	Pithecellobium mangense	-	0.022	-	-	-	-	-	-
	Pitecellubium dulce	-	0.041	-	-	-	-	-	-
	Pitecellobium mexicanun	-	-	0.031	-	-	-	-	-
	Piscidia piscipula	-	-	-	-	-	-	0.01	-
	Piscidia mollis	-	-	-	0.011	-	-	-	-
	Olneya tesota	0.047	-	-	-	-	-	-	-

	Mimosa polyantha	-	-	-	-	0.15	-	-	-
	Mimosa mollis	-	-	-	-	0.127	-	-	-
	Mimosa luisiana	-	-	-	-	-	0.183	-	-
	Lysiloma watsoni	0.056	-	-	-	-	-	-	-
	Lysiloma tergemina	-	-	-	-	0.027	-	-	-
	Lysiloma microphylla	-	-	-	0.008	-	-	-	0.123
	Lysiloma divaricata	0.278	0.433	0.068	0.009	0.083	0.009	0.02	-
	Lysiloma acapulquensis	-	-	-	0.008	0.02	-	0.016	-
	Leucaena leucocephala	-	-	-	-	0.048	-	-	-
	Esenbeckia marginata	-	-	-	-	-	-	0.009	-
	Erythrina occidentalis	-	0.011	-	-	-	-	-	-
	Enterolobium cyclocarpum	-	-	0.074	-	-	-	0.066	-
	Conzattia multiflora	-	-	-	-	0.012	-	-	-
	Chamaecrista flexuosa	-	-	-	-	0.044	-	-	-
	Cercidium preacox	-	-	-	-	0.032	-	-	-
	Cassia emarginata	-	-	-	0.038	-	-	-	-
	Calliandra grandiflora	-	-	-	-	0.036	-	-	-
	Caesalpinia platyloba	0.02	-	-	0.056	-	-	-	-
	Caesalpina emarginata	0.031	-	-	-	-	-	-	-
	Caesalpina celadenia	0.01	-	-	-	-	-	-	-
	Caesalpina pumila	0.092	-	-	-	-	-	-	-
	Acacia pennatula	-	0.023	-	-	0.026	-	-	0.063
	Acacia oligoacantha	0.008	-	-	-	-	-	-	-
	Acacia micrantha	-	-	-	-	-	-	-	0.149
	Acacia cymbispina	0.017	-	0.015	-	-	-	-	-
	Acacia coulteri	-	0.019	-	-	-	-	-	-
	Acacia cornigera	-	0.033	0.004	0.008	-	-	-	-
	Acacia cochiliacantha	-	0.066	-	-	-	0.016	-	-
	Acacia angustissima	-	-	-	-	-	-	0.008	-
	Acacia acatlensis	-	-	-	-	0.017	-	-	-
Moraceae	*Ficus goldmanii*	0.181	-	-	-	-	-	-	-
	Brosimum alicastrum	0.009	0.248	1.209	0.108	-	-	0.609	-
	Chlorophora tinctoria	-	0.018	-	-	-	-	-	-
	Ficus benjamina	-	-	-	-	0.03	-	-	-
	Ficus cotinifolia	-	-	-	-	-	-	0.303	-
	Ficus mexicana	-	0.031	-	-	-	-	-	-

	Ficus microchlamys	-	-	-	0.018	-	-	-	-
	Ficus sp	-	-	0.055	-	-	-	-	-
	Ficus sp	-	-	-	0.061	-	-	0.012	-
Myrtaceae	*Eugenia capuli*	-	-	-	-	-	-	-	-
Nyctaginaceae	*Pisonia aculeata*	-	-	0.004	-	-	-	-	-
Oxalidaceae	*Oxalis angustifolia*	-	-	-	-	0.07	-	-	-
	Oxalis latifolia	-	-	-	-	0.035	-	-	-
Piperaceae	*Pipper arboreum*	-	-	-	0.005	-	-	-	-
	Pipper rosei	-	-	-	0.005	-	-	-	-
Poaceae	*Guadua amplexifolia*	-	-	-	0.018	-	-	-	-
Rhamnaceae	*Karwinskia humboldtiana*	0.048	-	-		-	-	-	-
	Zizyphus amole	-	0.039	-	0.005	-	0.018	-	0.011
	Karwiskia parafolia	-	0.01	-	-	-	-	-	-
	Ziziphus mexicana	-	-	0.019	-	-	-	-	-
Rosaceas	*Licanea arborea*	-	-	0.014	-	-	-	-	-
Rubiaceae	*Randia echinocarpa*	0.156	-	0.077	0.1	0.084	-	-	-
	Borreria verticillata	-	-	-	-	0.056	-	-	-
	Coutarea pterosperma	-	-	0.005	-	-	-	-	-
	Diodia teres	-	-	0.063	-	-	-	-	-
	Krugiodendron ferrum	-	-	-	-	-	-	0.193	0.009
	Randia aculeata	-	-	-	-	-	-	0.007	-
Ruscaceae	*Dracaena marginata*	-	-	-	-	-	-	0.031	-
Rutaceae	*Casimiroa pringlei*	-	-	-	-	-	-	0.022	-
	Esenbeckia berlandieri	-	-	-	-	-	-	0.155	0.082
	Zanthoxylum pringlei	-	-	-	-	-	-	0.107	-
	Zanythoxylum arborescens	-	-	0.003	-	-	-	-	-
Salicaceae	*Salix bonplandiana*	-	-	0.156	-	-	-	-	-
Sapindaceae	*Sapindus lateriflorum*	-	0.039	-	-	-	-	-	-
	Thouinidium decamdrum	-	0.201	-	-	-	-	-	-
	Sapindus saponaria	-	-	-	-	-	-	0.025	-
	Thouinidium decamdrum	-	-	-	0.027	-	-	-	-
Sapotaceae	*Sideroxylon capiri*	0.031	-	-	-	-	-	-	-
Simaroubaceae	*Castela erecta*	-	-	-	-	-	0.038	-	-
Smilacaceae	*Smilax aspera*	0.008	-	-	-	-	-	-	-
Solanaceae	*Solanum americanum*	-	-	0.002	-	-	-	-	-
	Solanum rostratum	-	-	-	-	-	0.02	-	-
	Solanum sp.	-	-	-	0.01	-	-	-	-
	Solanum	-	-	-	0.005	-	-	-	-

	americanum								
	Capsicum annum	-	-	-	0.007	-	-	-	-
Sterculiacea	*Guazuma ulmifolia*	0.013	0.038	0.064	0.067	-	-	0.133	0.279
	Melochia nodiflora	-	-	-	0.02	-	-	-	-
Taxodiaceae	*Taxodium mucronatum*	-	-	0.111	0.123	-	-	-	-
Theophrastaceae	*Jacquinia pungens*	0.048	-	-	0.025	-	-	-	-
Tiliaceae	*Luehea candida*	0.096	0.036	0.029	-	-	-	-	-
Turneraceae	*Turnera ulmifolia*	-	-	-	-	0.029	0.052	-	-
Ulmaceae	*Celtis pallida*	0.171	-	-	-		-	-	-
	Celtis caudata	-	-	-	0.005	0.183	-	-	0.014
	Celtis iguanaea	-	-	-	-	0.052	-	-	-
	Mirandaceltis monoica	-	-	-	-	-	-	0.179	-
Urticaceae	*Parietaria debilis*	-	0.007	-	-	-	-	-	-
	Urera baccifera	-	0.016	0.015	-	-	-	0.007	-
	Urera coracasona	-	-	-		-	-	-	-
Verbenaceae	*Lantana camara*	-	-	-	0.007	-	-	-	-
	Lippia pringlei	0.062	-	-	-	-	-	-	-
	Vitex mollis	-	-	0.027	-	-	-	-	-
	Verbena sp.	-	0.089	-	-	-	-	-	-
	Verbena sp.	-	-	-	0.012	-	-	-	-
	lippia graveolens	-	-	-	-	-	0.017	-	-
Vitaceae	*Cissus sp.*	-	-	-	0.007	-	-	-	-
Zygophyllacae	*Guaiacum coulteri*	0.241	0.008	-	-	-	-	-	-

10.2 Apéndice 2. List of publications used for the realization of the meta-analysis.

Publication	Class	Gender	Species
Kraaijeveld-Smit *et al*., 2005	Amphibians	*Alytes*	*Alytes muletensis*
Spear & Storfer, 2010	Amphibians	*Ascaphus*	*Ascaphus montanus*
Wahbe *et al*., 2005	Amphibians	*Ascaphus*	*Ascaphus truei*
Hitchings & Beebee, 1998	Amphibians	*Bufo*	*Bufo bufo*
Dubey *et al*., 2008	Amphibians	*Hyla*	*Hyla arborea*
Luquet *et al*., 2011	Amphibians	*Hyla*	*Hyla arborea*
Gibbs, 1998	Amphibians	*Plethodon*	*Plethodon cinereus*
Jordan *et al*., 2009	Amphibians	*Plethodon*	*Plethodon cinereus*
Noe ̈l *et al*., 2007	Amphibians	*Plethodon*	*Plethodon cinereus*
Noël *et al*., 2010	Amphibians	*Plethodon*	*Plethodon cinereus*
Arens *et al*., 2007	Amphibians	*Rana*	*Rana arvalis*
Lesbarréres *et al*., 2006	Amphibians	*Rana*	*Rana dalmatina*
Wilson *et al*., 2008	Amphibians	*Rana*	*Rana pipiens*
Hitchings *et al*., 1997	Amphibians	*Rana*	*Rana temporaria*
Johansson *et al*., 2005	Amphibians	*Rana*	*Rana temporaria*
Measey *et al*., 2007	Amphibians	*Schoutedenella*	*Schoutedenella xenodactyloides*
Björklund *et al*., 2010	Birds	*Parus*	*Parus major*
Leite *et al*., 2008	Birds	*Amazona*	*Amazona aestiva*
Albertani *et al*., 2000	Birds	*Amazona*	*Amazona Ochrocephala*
Bush *et al*., 2011	Birds	*Centrocercus*	*Centrocercus urophasianus*
Delaney *et al*., 2010	Birds	*Chamaea*	*Chamaea fasciata*
Mercival *et al*., 2007	Birds	*Chiroxiphia*	*Chiroxiphia caudata*
Croteau *et al*., 2007	Birds	*Chiroxiphia*	*Chiroxiphia caudata*
Barnett *et al*., 2008	Birds	*Corapipo*	*Corapipo altera/Manacus candei*
Lindsay *et al*., 2008	Birds	*Dendroica*	*Dendroica chrysoparia*
Meyer *et al*., 2009	Birds	*Emberiza*	*Emberiza schoeniclus*
Brown *et al*., 2004	Birds	*Eucometis*	*Eucometis penicillata*
Bates, 2000	Birds	*Glyphorynchus*	*Glyphorynchus spirurus*
Brown *et al*., 2004	Birds	*Gymnopithys*	*Gymnopithys leucaspis*
Brown *et al*., 2004	Birds	*Henicorhina*	*Henicorhina leucosticta*
Bates, 2000	Birds	*Hylophylax*	*Hylophylax poecilonota*
Bates, 2000	Birds	*Hypocnemis*	*Hypocnemis cantator*
Bech *et al*., 2009	Birds	*Lagopus*	*Lagopus muta pyrenaica*
Bates, 2000	Birds	*Leptopogon*	*Leptopogon amaurocephalus*
Leberg, 1991	Birds	*Meleagris*	*Meleagris gallopavo*
MacDougall-Shackleton *et al*., 2011	Birds	*Melospiza*	*Melospiza melodia*
Roques & Negro 2005	Birds	*Milvus*	*Milvus milvus*
Bates, 2000	Birds	*Myrmeciza*	*Myrmeciza hemimelaena*
Zhan *et al*., 2007	Birds	*Nipponia*	*Nipponia nippon*
Miño & Lama, 2007	Birds	*Platalea*	*Platalea ajaja*

Galbusera *et al*., 2004	Birds	*Pogonocichla*	*Pogonocichla stellata*
Triggs *et al*., 1989	Birds	*Strigops*	*Strigops habroptilus*
Ping-Ping *et al*., 2004	Birds	*Syrmaticus*	*Syrmaticus ellioti*
Caizergues *et al*., 2003	Birds	*Tetrao*	*Tetrao tetrix*
Höglund *et al*., 2007	Birds	*Tetrao*	*Tetrao tetrix*
Segelbacher *et al*., 2003	Birds	*Tetrao*	*Tetrao urogallus*
Bellinger *et al*., 2003	Birds	*Tympanuchus*	*Tympanuchus cupido*
Bouzat *et al*., 1998	Birds	*Tympanuchus*	*Tympanuchus cupido*
Lucid & Cook, 2004	Mammals	*Peromyscus*	*Peromyscus keeni*
He *et al*., 2007	Mammals	*Ailuropoda*	*Ailuropoda melanoleuca*
García del Valle *et al*., 2005	Mammals	*Alouatta*	*Alouatta pigra*
Lada *et al*., 2008	Mammals	*Antechinus*	*Antechinus flavipes*
Telfer *et al*., 2003	Mammals	*Arvicola*	*Arvicola terrestris*
Pacioni *et al*., 2011	Mammals	*Bettongia*	*Bettongia penicillata ogilbyi*
Estes-Zumpf et al., 2010	Mammals	*Brachylagus*	*Brachylagus idahoensis*
Meyer et al., 2009	Mammals	*Carillia*	*Carollia perspicillata*
Tallmon *et al*., 2002	Mammals	*Clethrionomys*	*Clethrionomys californicus*
Redeker *et al*., 2005	Mammals	*Cletherionomys*	*Clethrionomys glareolus*
Banassezek *et al*., 2010	Mammals	*Cricetus*	*Cricetus cricetus*
Magle *et al*., 2010	Mammals	*Cynomys*	*Cynomys ludovicianus*
Aranguren-Méndez *et al*., 2001	Mammals	*Equus*	*Equus asinus*
Bergl *et al*., 2008	Mammals	*Gorilla*	*Gorilla gorilla*
Small *et al*., 2003	Mammals	*Martes*	*Martes americana*
Olivieri *et al*., 2008	Mammals	*Microcebus*	*Microcebus bongolBirdsnsis*
Olivieri *et al*., 2008	Mammals	*Microcebus*	*Microcebus danfossi*
Olivieri *et al*., 2008	Mammals	*Microcebus*	*Microcebus ravelobensis*
Campbell *et al*., 2009	Mammals	*Myotis*	*Myotis macropus*
Haag *et al*., 2010	Mammals	*Panthera*	*Panthera onca*
Taylor *et a*l., 2007	Mammals	*Petauroides*	*Petauroides volans/Pseudocheirus peregrinus*
Banks *et al*., 2005	Mammals	*Antechinus*	*Antechinus agilis*
Goossens *et al*., 2005	Mammals	*Pongo*	*Pongo pygmaeus*
Macqueen *et al*., 2008	Mammals	*Rattus*	*Rattus fuscipes*
White & Searle, 2007	Mammals	*Sorex*	*Sorex araneus*
Biedrzychka & Konopinski, 2008	Mammals	*Spermophilus*	*Spermophilus suslicus*
Heller *et al*., 2010	Mammals	*Syncerus*	*Syncerus caffer*
Meyer *et al*., 2009	Mammals	*Uroderma*	*Uroderma bilobatum*
Proctor *et al*., 2005	Mammals	*Ursus*	*Ursus arctos*
Ohnishi *et al*., 2007	Mammals	*Ursus*	*Ursus thibetanus*
Rodriguez-Robles *et al*., 2008	Reptiles	*Anolis*	*Anolis cooki*
Dutra *et al*., 2008	Reptiles	*Bothrops*	*Bothrops moojeni*
Tzika *et al*., 2008	Reptiles	*Conolophus*	*Conolophus pallidus*
Tzika *et al*., 2008	Reptiles	*Conolophus*	*Conolophus subscrita*
Stow *et al*., 2001	Reptiles	*Egernia*	*Egernia cunninghami*

HOEHN *et al*., 2007	Reptiles	*Gehyra*	*Gehyra variegata*
Cunningham & Moritz, 1998	Reptiles	*Gnypetoscincus*	*Gnypetoscincus queenslandiae*
SUMNER *et al*., 2001	Reptiles	*Gnypetoscincus*	*Gnypetoscincus queenslandiae*
Ennen *et al*., 2010	Reptiles	*Gopherus*	*Gopherus Polyphemus*
Bennett *et al*., 2010	Reptiles	*Graptemys*	*Graptemys geographica*
Marshall Jr *et al*., 2009	Reptiles	*Nerodia*	*Nerodia erythrogaster*
Hoehn *et al*., 2007	Reptiles	*Oedura*	*Oedura reticulata*
Berry *et al*., 2004	Reptiles	*Oligosoma*	*Oligosoma grande*
Berry & Gleeson, 2005	Reptiles	*Oligosoma*	*Oligosoma grande*
Delaney *et al*., 2010	Reptiles	*Plestiodon*	*Plestiodon skiltonianus*
Cunningham *et al*., 2002	Reptiles	*Psammobates*	*Psammobates geometricus*
Delaney *et al*., 2010	Reptiles	*Sceloporus*	*Sceloporus occidentalis*
Moore *et al*., 2008	Reptiles	*Sphenodon*	*Sphenodon punctatus*
Chih-Horng & Janzen, 2004	Reptiles	*Terrapene*	*Terrapene ornata*
Munguia-Vega *et al*., 2009.	Reptiles	*Urosaurus*	*Urosaurus nigricaudus*
Delaney *et al*., 2010	Reptiles	*Uta*	*Uta stansburiana*

Apendice 3. Phylogenetic tree the tetrapods used to performing correction in phylogenetic in phyloMeta, in format Newik and image.

(((((((Schoutedenella_xenodactyloides:4.0,Hyla_arborea:4.0):1.0,Bufo_bufo:5.0):1.0,(Ascaphus_truei:1.0,Ascaphus_montanus:1.0):5.0):1.0,(Rana_arvalis:1.0,Rana_dalmatina:1.0,Rana_pipiens:1.0,Rana_temporaria:1.0):6.0):3.0,Alytes_muletensis:10.0):1.0,(Plethodon_cinereusa:9.0,Plethodon_cinereusb:9.0,Plethodon_cinereusc:9.0,Plethodon_cinereusd:9.0):2.0):10.0,(((((((Platalea_ajaja:2.0,Nipponia_nippon:2.0):1.0,Milvus_milvus:3.0):12.0,(((Amazona_aestiva:1.0,Amazona_ochrocephala:1.0):4.0,(Hylophylax_poecilonota:3.0,((Gymnopithus_leucaspis:1.0,Hypocnemis_cantator:1.0):1.0,Myrmecima_hemimelaena:2.0):1.0):2.0):8.0,(Strigops_habroptilus:12.0,((Leptopogon_amauroce:2.0,Pogonocichla_stellata:2.0,Glyphorynchus_spirurus:2.0):9.0,(((Eucometis_penicilata:4.0,(Henicornia_leucosticta:2.0,(Chiroxiphia_caudata.1:1.0,Chiroxiphia_caudata.2:1.0):1.0,Dendroica_chrysoparia:2.0,Corapipo_altera:2.0):2.0,(Emberiza_schoeniclus:1.0,Melospiza_melodia:1.0):3.0):3.0,Chamaea_fasciata:7.0):1.0,Parus_major:8.0):3.0):1.0):1.0):2.0):1.0,(((Tetrao_urogallus:2.0,(Tetrao_tetrix.1:1.0,Tetrao_tetrix.2:1.0):1.0):1.0,Centrocercus_urophasianus:3.0,Syrmaticus_ellioti:3.0):2.0,(((Tympanuchus_cupido.1:1.0,Tympanuchus_cupido.2:1.0):2.0,Lagopus_muta:3.0):1.0,Meleagris_gallopavo:4.0):1.0):11.0):1.0,Bothrops_moojeni:17.0):1.0,(Psammobates_geometricus:4.0,(Terrapene_ornata:1.0,Gopherus_polyphemus:1.0):3.0,Graptemys_geographica:4.0):14.0):1.0,(Nerodia_erythrogaster:9.0,((((Sceloporus_occidentalis:1.0,Urosaurus_nigricaudus:1.0):1.0,Uta_stansburiana:2.0):1.0,Anolis_cooki:3.0):2.0,(((Sphenodon_punctatus:2.0,(Oligosoma_grande.1:1.0,Oligosoma_grande.2:1.0,Egernia_cunninghami:1.0):1.0,(Gnypetoscincus_queenslandiae:1.0,Plestiodon_skiltonianus:1.0):1.0):1.0,(Gehyra_variegata:1.0,Oedura_reticulata:1.0):2.0):1.0,(Conolophus_pallidus:1.0,Conolophus_subscrita:1.0):3.0):1.0):4.0):10.0):1.0,(((((Gorilla_gorilla:3.0,Pongo_pygmaeus_abelii:3.0):3.0,Alouatta_pigra:6.0):1.0,(Microcebus_bongolavensis:1.0,Microcebus_danfossi:1.0):6.0):2.0,((Bettongia_penicillata:1.0,Antechinus_flavipes.1:1.0,Antechinus_flavipes.2:1.0):7.0,(((((Cletherionomys_glareolus:1.0,Cletherionomys_californicus:1.0):1.0,Peromyscus_keeni:2.0,(Petauroides_volans:1.0,Cricetus_cricetus:1.0):1.0,Arvicola_terrestris:2.0):1.0,Rattus_fuscipes:3.0):3.0,Cynomys_ludovicianus:6.0):1.0,Brachylagus_idahoensi:7.0,(Spermophilus_suslicus.1:1.0,Spermophilus_suslicus.2:1.0):6.0):1.0):1.0):7.0,((((Equus_asinus:10.0,(Panthera_onca:8.0,((Ailuropoda_mel

anoleuca:2.0,(Ursus_thibetanus:1.0,Ursus_arctos:1.0):1.0):4.0,Martes_americana:6.0):2.0):2.0):1.0,Syncerus_caffer:11.0):1.0,((Carollia_perspicillata:2.0,Uroderma_bilobatum:2.0):4.0,Myotis_macropus:6.0):6.0):1.0,Sorex_araneus:13.0):3.0):4.0):1.0);