Primates
DOI 10.1007/s10329-014-0415-5

NEWS AND PERSPECTIVES

Mammal assemblages in forest fragments and landscapes occupied by black howler monkeys

Ariadna Rangel-Negrín · Alejandro Coyohua-Fuentes · Domingo Canales-Espinosa · Pedro Américo D. Dias

Received: 27 January 2014 / Accepted: 14 February 2014

Abstract Species assemblages in disturbed habitats vary as a function of the interaction between species requirements and the spatial configuration of the habitat. There are many reports accounting for the presence of howler monkeys in fragments where other mammals are absent, suggesting that they are more resilient. In the present study we explored this idea and predicted that if howler monkeys were more resilient to habitat loss and fragmentation than other mammals, mammal assemblages in fragments occupied by howler monkeys should include fewer species with decreasing amount of habitat (smaller fragment size and less habitat in the landscape) and increasing number of forest fragments. We explored these relationships by additionally considering the feeding and life habits of mammal species, as well as the isolation and proximity of each fragment to human settlements and roads. We sampled the presence of mammals in five fragments occupied by black howler monkeys (*Alouatta pigra*) in the Mexican state of Campeche. Through direct sights performed during 240 h in each fragment, we observed 23 species. At the landscape scale, higher fragmentation was associated with a decrease in herbivores, omnivores and total number of species. At the fragment scale semiarboreal, omnivore, and total number of species increased with increasing fragment size. This study supports the idea that howler monkeys are more resilient to forest loss and fragmentation than other native mammals, and our exploratory analyses suggest that the specific mammal assemblages that are found in fragments are related to both landscape and fragment scale spatial attributes, as well as with species-specific characteristics.

Keywords *Alouatta* · Fragment size · Landscape spatial attributes · Mexico · Trophic level

Introduction

There is abundant evidence that habitat loss and fragmentation result in the extinction of many animal species (Galetti and Dirzo 2013). However, extinction probabilities in disturbed habitats vary among species. Whereas some species are highly sensitive to habitat loss and become extinct in habitats that are too small (Bolger et al. 2000; Lindenmayer et al. 2002), other species survive in small forest fragments (hereafter, fragments) (Didham et al. 1998).

Differences in extinction probabilities between species living in fragmented landscapes have been linked to different characteristics, such as body size (Canale et al. 2012), trophic level (Komonen et al. 2000), and dispersal abilities (Driscoll and Weir 2005). For instance, populations of arboreal mammals (i.e., low dispersal ability) and large carnivores (e.g., jaguars) decrease in fragmented habitats (Crooks and Soulé 1999; Laurance et al. 2008); whereas, terrestrial or semiarboreal (i.e., high dispersal ability) omnivores (e.g., raccoons) tend to increase (Crooks and Soulé 1999; Crooks 2002; McKinney 2002; Daily et al. 2002). These characteristics determine the ability of individuals to use disturbed landscapes (sensu Dunning et al.

A. Rangel-Negrín (✉) · A. Coyohua-Fuentes · D. Canales-Espinosa · P. A. D. Dias
Instituto de Neuroetología, Universidad Veracruzana, Av. Luís Castelazo Ayala s/n Col. Industrial Ánimas, 91190 Xalapa, Veracruz, Mexico
e-mail: ari_rangel@hotmail.com

Published online: 12 March 2014

1992), affect species distribution, and ultimately, determine extinction probabilities. Therefore, although the richness of mammal species may generally decrease in disturbed landscapes, the specific composition of mammal assemblages may vary among landscapes as a function of the interplay between the particular spatial attributes of the habitat (e.g., amount of available habitat, fragment size or isolation) and species biology.

Howler monkeys (*Alouatta*) are Neotropical primates that are frequently found in disturbed fragments and landscapes. The persistence of howler monkeys under such conditions has been linked to energy minimizing time budgets (Bicca-Marques 2003) and their high foraging/digestive flexibility, which enable them to feed on abundant foods (e.g., leaves Gaulin et al. 1980; Mittermeier and van Roosmalen 1981), use more plant species as food sources (Bicca-Marques 2003; Cristóbal-Azkarate and Arroyo-Rodríguez 2007), and consume alternative food items (e.g., lianas: Asensio et al. 2007). More recently, it has been suggested that landscape supplementation may also facilitate howler monkey persistence in fragmented landscapes (Asensio et al. 2009; Pozo-Montuy et al. 2013). There are accounts of the presence of howler monkeys in fragments and fragmented landscapes where other mammals are absent, suggesting that when hunting pressures are low (Canale et al. 2012), they may be highly resilient to habitat loss and fragmentation (e.g., Schwarzkopf and Rylands 1989; Van Belle and Estrada 2006; Terborgh et al. 2001). However, the effects of both fragment and landscape scale spatial configuration (sensu Arroyo-Rodríguez et al. 2013) on the mammal assemblages present in fragments occupied by howler monkeys have not been assessed to date. In the present study we explored this gap by comparing mammal assemblages among fragments and landscapes with different spatial attributes but which were all occupied by howler monkeys. If howler monkeys are more resilient to habitat loss and fragmentation than other native mammals, we predicted that mammal assemblages should include fewer species with decreasing amount of habitat (smaller fragment size and less available habitat overall in the landscape) and increasing number of forest fragments. We further explored these relationships by considering the feeding and life habits of each mammal species, as well as the isolation and proximity of each fragment to human settlements and roads.

Methods

This study adhered to the ethical and legal requirements of SEMARNAT (the natural resources agency of Mexico): SGPA/DGVS/01273/06 & 04949/07.

Study sites

The study was conducted in the Mexican state of Campeche (Fig. 1). Campeche has a total area of 57,924 km^2, of which approximately 40 % is protected. The remaining non-urban territory of Campeche consists of highly humanized landscapes, where original habitats have been converted into forest-agricultural mosaics.

In the context of a concurrent project on the responses of black howler monkeys to habitat disturbance, between February 2006 and November 2007 we focused on five groups of black howler monkeys living in different forest fragments: ejido General Ignacio Gutiérrez (18°54′6.58″N, 90°53′37.90″W; hereafter, Chilar); ejido Chicbul (18°46′51.66″N, 90°56′13.45″W; hereafter, Chicbul); Rancho El Álamo (18°48′45.44″N, 90°58′54.61″W; hereafter, Álamo); Laguna de Términos Reserve (18°51′15.38″N, 91°18′41.70″W; hereafter, Calax); Calakmul Biosphere Reserve (18°19′00.28″N, 89°51′28.92″W; hereafter, Calakmul).

Vegetation in all fragments was originally semi-perennial tall rainforest, although habitat disturbance and loss resulted in highly modified plant assemblages in the smaller fragments. Accordingly, vegetation in Chilar and Chicbul was dominated by light demanding tree species typical of secondary forests, such as *Guazuma ulmifolia* Lam., *Lonchocarpus castilloi* Standl. or *Enterolobium cyclocarpum* (Jacq.) Griseb. In contrast, tree species typical of mature forests were dominant in Calakmul and Calax, such as *Brosimum alicastrum* Sw, *Manilkara zapota* (L.) P. Royen or *Nectandra salicifolia* (Kunth) Nees. Finally, in Álamo, dominant tree species included both taxa typical from old-growth forests, such as *Alseis yucatanensis* Standl., and *Metopium brownei* (Jacq.) Urb., and from disturbed forests, such as *Spondias mombin* L.

Fragment and landscape characterization

In order to explore the influence of landscape attributes on mammal assemblages, we characterized the spatial configuration of 1,200 ha landscapes surrounding each fragment (Fig. 1). Each landscape was digitized with ArcGIS 9.3.1 (ESRI Inc., Redlands, CA, USA), using orthophotos (1:10,000, resolution 1 m) taken between 2004 and 2008, where we classified land cover types as: forest; pasture lands or crops; human settlements; roads. For each landscape we calculated: total amount of habitat as the sum of forested areas; number of forest fragments; mean (±SD) fragment size. For each forest fragment where mammal sampling was performed we calculated its size and the distance to the nearest fragment, road and human settlement (Table 1). For these calculations we used Patch Analyst 3.12 for ArcView

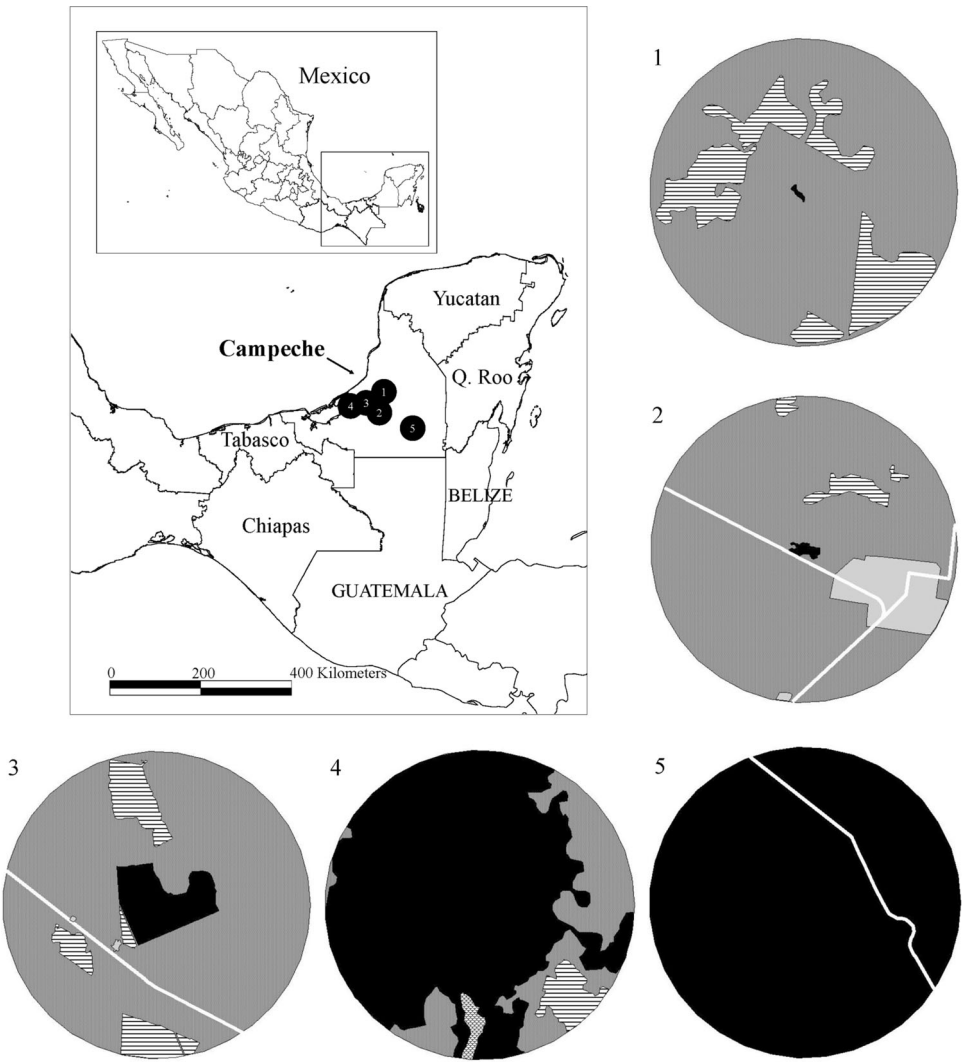


Fig. 1 Location of the study landscapes and fragments in the state of Campeche. *1* Chilar; *2* Chicbul; *3* Álamo; *4* Calax; *5* Calakmul. Land cover types: forests (*black* for fragments where mammals were sampled, and *white* with *black stripes* for remaining fragments in the landscape); pasturelands or crops (*gray with weave*); human settlements (*light gray*); roads (*white lines*); water (*white with waves*)

Table 1 Landscape and fragment attributes recorded in this study

	Chilar	Chicbul	Álamo	Calax	Calakmul
Landscape attributes[a]					
Total amount of habitat (ha)	270.6	33.7	193.1	985.6	1,200
Number of fragments	7	4	6	2	1
Mean fragment size (ha; ± SD)	38.7 ± 31.2	8.4 ± 8.5	32.2 ± 31.1	492.8 ± 636.8	1,200 ± 0
Fragment attributes					
Fragment size (ha)	2.1	5	86	3,000	140,000
Distance to nearest fragment (m)	540	492	14	73	0
Distance to nearest road (m)	>1,997[b]	0	299	>1,997	0
Distance to nearest human settlement (m)	>1,997	320	190	>1,997	>1,997

[a] Distances higher than 1,997 m (i.e., the radius of the landscape area) indicate that no road or human settlement was present in the sampled landscape

[b] Corresponds to 1,200 ha landscapes surrounding each fragment sampled for the presence of mammal species

3.2 and Patch Analyst 4.2 for ArcGIS 9.3.1, as well as self-developed geostatistical processes created in ModelBuilder for ArcGIS (ESRI Inc., Redlands, CA, USA).

Mammal samplings

We recorded the presence of large and medium mammals in each fragment through direct sightings during the sampling of black howler monkeys. Sampling effort was 240 h of field presence in each fragment equally divided between the dry (November to May) and the rainy (June to October) seasons. Observations were performed from 6:00 to 18:00 during ca. 30 days per season.

Each recorded mammal was classified according to its life habit (arboreal, semiarboreal, terrestrial or semiaquatic) and feeding habit (carnivore, herbivore, insectivore or omnivore) (Guzmán-Soriano et al. 2013).

Data analyses

We used goodness-of-fit chi-square to test for differences among fragments in the frequencies (total, per life habit and per feeding habit) of observed mammals. We analyzed similarity between fragments in the mammal species that were recorded with the Jaccard's similarity coefficient (Krebs 1998). To explore the effects of both landscape and fragment scale variables on mammal assemblages we used Kendall tau correlations. All tests were two-tailed and significance was set at $p < 0.05$.

Table 2 Mammals recorded in each forest fragment

Scientific name	Common name	Life habit	Feeding habit	Sites
Alouatta pigra	Black howler monkey	Arboreal	Herbivore	All
Ateles geoffoyi	Spider monkey	Arboreal	Herbivore	Calakmul, Calax
Bassariscus sumichrasti	Cacomistle	Arboreal	Omnivore	Calakmul
Conepatus semistriatus	Striped hog-nosed skunk	Terrestrial	Omnivore	Calax
Dasyprocta punctata	Central American agouti	Terrestrial	Herbivore	Álamo
Dasypus novemcinctus	Nine-banded armadillo	Terrestrial	Insectivore	Álamo, Calakmul, Calax
Didelphis marsupialis	Common opossum	Semiarboreal	Omnivore	Calakmul, Calax
Eira barbara	Tayra	Semiarboreal	Carnivore	Calakmul
Galictis vittata	Greater grison	Semiaquatic	Omnivore	Chicbul
Mazama pandora	Yucatan brown brocket	Terrestrial	Herbivore	Calakmul
Nasua narica	White-nosed coati	Semiarboreal	Omnivore	Calax
Odocoileus virginianus	White-tailed deer	Terrestrial	Herbivore	Calakmul
Panthera onca	Jaguar	Terrestrial	Carnivore	Calakmul
Pecari tajacu	Collared peccary	Terrestrial	Omnivore	Álamo, Calakmul, Calax
Potos flavus	Kinkajou	Arboreal	Herbivore	Álamo
Procyon lotor	Raccoon	Semiarboreal	Omnivore	Álamo, Calakmul, Calax, Chicbul
Puma concolor	Puma	Terrestrial	Carnivore	Calakmul
Puma yagouaroundi	Jaguarundi	Terrestrial	Carnivore	Álamo
Sphiggurus mexicanus	Mexican tree porcupine	Arboreal	Herbivore	Álamo, Calax
Sylvilagus sp	Cottontail rabbit	Terrestrial	Herbivore	Chicbul
Tamandua mexicana	Northern tamandua	Arboreal	Insectivore	Chilar
Tapirus bairdii	Baird's tapir	Terrestrial	Herbivore	Calakmul
Urocyon cinereoargenteus	Gray fox	Terrestrial	Omnivore	Calakmul, Chilar

Results

General trends in mammal assemblages

We observed 23 mammal species (Table 2). Sixty-five percent of all observed species were recorded in Calakmul, with seven species exclusively recorded at this site, including all large carnivores. In contrast, only two species were observed at Chilar, the smallest fragment. At Calax we observed nine species, of which six were also present in Calakmul. Spider monkeys were only present in the two largest fragments. Seven species were observed at Álamo, of which three were exclusively observed here (jaguarundi, kinkajou and agouti). At Chicbul we observed only three species, including raccoons, which were also recorded in the three largest fragments. More than half of all observed mammals were terrestrial, and we recorded omnivore species in all fragments. In contrast, carnivores were observed in only two fragments (Álamo and Calakmul) and herbivores were present exclusively in the three largest fragments.

Similarity between sites in mammal assemblages was on average low (mean $\pm$ SD $= 0.199 \pm 0.1$), with the highest similarity found between Calax and Álamo ($J = 0.42$) and the lowest between Álamo and Chilar ($J = 0.1$) (Fig. 2). There were significant differences among fragments in total mammal species ($\chi^2_4 = 11.64$, $p = 0.020$) and in the number of terrestrial species ($\chi^2_4 = 9.7$, $p = 0.045$). Calakmul contributed the majority of non-randomness in both results, with more observed mammal species than expected.

Impact of landscape and fragment spatial attributes on mammal assemblages

At the landscape scale, we found negative associations between the number of fragments and the total number of mammal species ($\tau = -0.80$, $n = 5$, $p < 0.05$; Fig. 3a), the number of herbivores ($\tau = -0.95$, $n = 5$, $p < 0.05$; Fig. 3b) and the number of omnivores ($\tau = -0.80$, $n = 5$, $p < 0.89$; Fig. 3c). At the fragment scale, fragment size was positively associated with total number of mammals ($\tau = 0.99$, $n = 5$, $p < 0.05$; Fig. 3d), the number of semiarboreal species ($\tau = 0.95$, $n = 5$, $p < 0.05$; Fig. 3e) and the number of omnivores ($\tau = 0.89$, $n = 5$, $p < 0.05$; Fig. 3f). Fragments that were less isolated had more mammal species ($\tau = 0.80$, $n = 5$, $p < 0.05$; Fig. 3g); and those that were closer to human settlements had more insectivores ($\tau = 0.84$, $n = 5$, $p < 0.05$; Fig. 3h).

Discussion

As predicted, mammal assemblages varied significantly among forest fragments occupied by black howler monkeys, both in terms of size and species composition. At the landscape scale, higher fragmentation was associated with a decrease in the total number of mammal species, herbivores and omnivores. In the case of herbivores and omnivores, this relationship was independent from the amount of available habitat, as represented by the contrast between Chicbul and Calax landscapes, which had a ca. 30-fold difference in amount of habitat but had the same number of species with those feeding habits. At the fragment scale, fragment size was the variable most related to variation in mammal assemblages, as semiarboreal, omnivore and total number of species increased with increasing fragment size. Furthermore, the number of species decreased with fragment isolation but insectivores increased with increasing distance to human settlements. Therefore, this study supports the idea that howler monkeys are more resilient to forest loss and fragmentation than other native mammals, and our exploratory analyses suggest that the specific mammal assemblages that are found in fragments are related to both landscape and fragment scale spatial attributes, as well as with species-specific characteristics.

Changes in mammal assemblages in disturbed habitats depend on both species characteristics and species interactions. In addition to being preferred game species (Peres and Palacios 2007), large-bodied animals tend to have large home ranges, reproduce at a higher age and have low fecundity, traits that increase their vulnerability to habitat

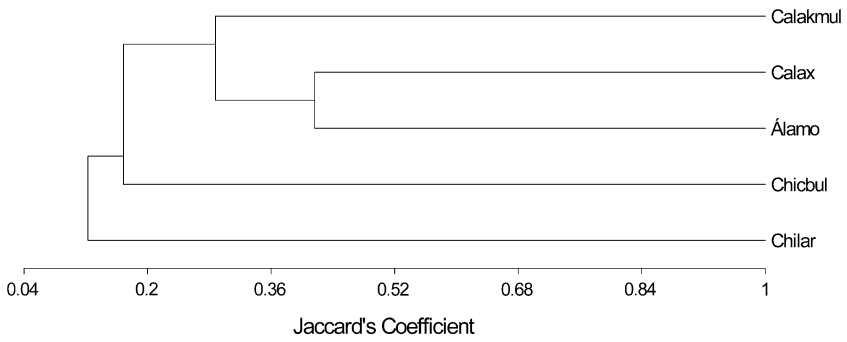
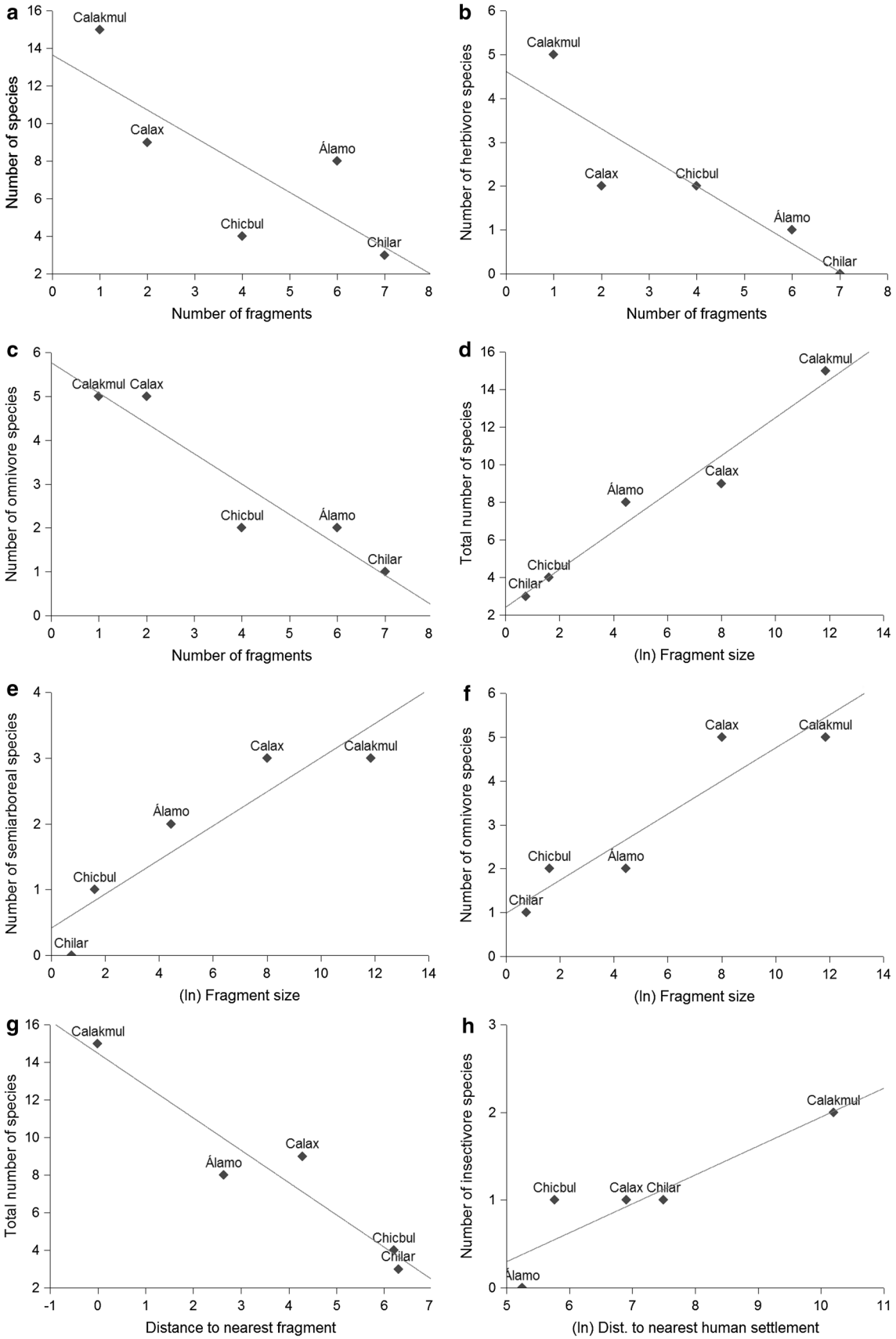


Fig. 2 Similarity (Jaccard's coefficient) between fragments in mammal species assemblages


a
Number of species
Number of fragments
Calakmul
Calax
Álamo
Chicbul
Chilar
b
Number of herbivore species
Number of fragments
Calakmul
Calax
Chicbul
Álamo
Chilar
c
Number of omnivore species
Number of fragments
Calakmul
Calax
Chicbul
Álamo
Chilar
d
Total number of species
(ln) Fragment size
Calakmul
Calax
Álamo
Chicbul
Chilar
e
Number of semiarboreal species
(ln) Fragment size
Calax
Calakmul
Álamo
Chicbul
Chilar
f
Number of omnivore species
(ln) Fragment size
Calax
Calakmul
Chicbul
Álamo
Chilar
g
Total number of species
Distance to nearest fragment
Calakmul
Calax
Álamo
Chicbul
Chilar
h
Number of insectivore species
(ln) Dist. to nearest human settlement
Calakmul
Chicbul
Calax
Chilar
Álamo

◀**Fig. 3** Relationships (Kendall correlations) between mammal species assemblages and both landscape (**a**–**c**) and fragment (**d**–**h**) scale attributes

loss and fragmentation (Cardillo et al. 2005). In the Neotropics these mammals are best represented by jaguars, tapirs, peccaries and ateline primates (Jorge et al. 2013), which in our study, with the exception of Álamo (where peccaries were also observed), were exclusively present in larger fragments and landscapes with a larger amount of habitat. As large-bodied mammals disappear, populations of medium-bodied species tend to increase due to reductions in competition and predation pressures (Wright 2003). In disturbed habitats, omnivores and carnivores benefit from proximity to human settlements and croplands, where the abundance of prey (rodents) is higher and there are abundant scavenging opportunities (Crooks 2002; Olson et al. 2012). Thus, mammal assemblages in fragmented landscapes tend to be dominated by highly abundant generalist species, particularly generalist mesopredators (Swihart et al. 2003). Our results support this evidence, as gray foxes, grisons and raccoons were present in the smallest fragments and highly fragmented landscapes, but also in larger fragments in conserved landscapes.

It is possible that our sampling method underestimated mammal assemblages in small fragments and more disturbed landscapes, as some species may be more fearful of human presence under these conditions (e.g., Frair et al. 2005). Track, fur or dung identification, and camera traps are indirect sampling methods that minimize the impact of human presence on wildlife studies (e.g., Engeman et al. 2013; Hamel et al. 2013), and it is possible that the use of these methods would render different results. However, it is noteworthy that at Álamo, which was the closest fragment to a human settlement, the number of species that we observed was higher than at the two smallest fragments, suggesting that our results were more related to the effects of forest loss than to the sampling method that was used. Nevertheless, future studies aimed at specifically understanding differences among species in responses to forest loss and fragmentation should more thoroughly describe and quantitatively measure mammal communities with more sophisticated tools (Galetti and Dirzo 2013).

In conclusion, this study corroborates previous accounts of the presence of howler monkeys in forest fragments and fragmented landscapes where other native mammal species do not survive. Specifically, other mammals tended to disappear in more fragmented landscapes and smaller fragments, although these trends were associated with species-specific characteristics, such as feeding and life habits.

Acknowledgments We thank all the students and volunteers that helped during fieldwork. The following people and institutions granted permission to work in their properties and facilitated our fieldwork: Comisarios Ejidales de Abelardo Domínguez, Calax, Conhuas, Plan de Ayala, and Carmén Gómez; Ayuntamiento de Calakmul; Lic. C. Vidal and Lic. L. Álvarez, INAH Campeche; Biól. F. Durand Siller, Reserva de la Biósfera Calakmul, CONANP; Ing. V. Olvera, El Álamo. This study was supported by CFE (RGCPTTP-UV-001/04), Universidad Veracruzana, Conacyt (Grant Number: 235839; i010/458/2013 C-703/2013) and Idea Wild. Some of the ideas included in this paper were presented at the "II Congresso Latino Americano & XV Congresso Brasileiro de Primatologia" (Recife, Brasil, August 2013). We thank conference participants for stimulating discussions, and L.K. Marsh for very constructive comments on a previous version of the manuscript. A. Rangel-Negrín and P.A.D. Dias thank Mariana for support during the writing of this paper.

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