UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOMÉDICAS
INSTITUTO DE ECOLOGÍA

EFECTOS DE LA FRAGMENTACIÓN EN LA COMUNIDAD DE MAMÍFEROS TERRESTRES Y LA DEPREDACIÓN DE SEMILLAS EN UN BOSQUE TROPICAL HÚMEDO

TESIS
QUE PARA OBTENER EL GRADO ACADÉMICO DE
DOCTOR EN CIENCIAS
PRESENTA:
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México D.F. MARZO – 2010

Gracias:

Instituto de Ecología

Posgrado en Ciencias Biomédicas

Universidad Nacional Autónoma de México

AGRADECIMIENTOS PARA LA FAMILIA Y AMIGOS

Deseo agradecer primero a mi querida Luisa, compañera, bióloga y esposa, además de madre amorosa. Gracias por tu apoyo y sentido común, por convencerme de que no dejara el doctorado a medio camino. Gracias Luisa por tu amor, comprensión, paciencia y sacrificio durante todos estos años.

Gracias mi querido Andrés Eduardo, a mis chiquitas Mónica María y Natalia Isabel, ustedes son mis tres amores, que también me inspiraron a seguir. Espero que perdonen mi ausencia, estar lejos hasta México, durante tantos momentos importantes y situaciones difíciles.

A mis queridos padres, Jafeth y Emma, y mi hermana Gaby, por gran su amor, su emoción y entusiasmo para que yo terminara este posgrado. Muchas gracias por el inmenso esfuerzo que han hecho para ayudarme siempre. La UNAM sigue siendo para mi mamá y papá parte de sus vidas, hace años representó estudio, trabajo, formación, guardería, partidos, días de campo, ahora es donde su hijo mayor realiza un posgrado.

A mis ejemplares tías Sara, Pacha y Martha, y a mis tíos Federico y Claudio, por su enorme y decidido apoyo. Me han ayudado mucho, tanto emocionalmente como económicamente. Les agradezco por estar siempre al pendiente, por animarme a continuar, y por poder contar siempre con ustedes.

A mis suegros, Rolando y Luisa, y a mis hermanos-cuñados Pancho, Marco, Rolando, Gloria y Favis, gracias por su comprensión, cariño y buenos deseos.

A mi jefe de tantas giras de campo, Frank, quien decisivamente me empujó para que siguiera y terminara mi doctorado. Gracias por enseñarme que antes de subir al tren hay que leer con atención a dónde va.

AGRADECIMIENTOS PARA ASESORES Y COLABORADORES

Gracias a mi comité de tesis, mi tutor Dr. Gerardo Ceballos, y mis asesores Dr. Rodolfo Dirzo y Dr. Ignacio Méndez. Muchas gracias por su dedicación y ayuda durante todas las etapas del doctorado. Les agradezco muchísimo por no dejarme botado después de tantos años. Gracias por todas sus enseñanzas.

Un especial agradecimiento para el Dr. César Domínguez por su amistad y ayuda siempre, incluso desde antes de que yo iniciara con el doctorado.

A mis sinodales, Dra. Alma Orozco, Dra. Ana Elena Mendoza, Dr. Víctor Sánchez-Cordero, Dr. Rodrigo Medellín, muchas gracias por revisar y corregir el manuscrito de mi tesis, valoro mucho que, aún con lo ocupados que siempre están, se tomaron el tiempo para esta tarea extra.

Gracias a Luisa Moreno, Zenaida Martínez, Patricia Martínez, Allison Deines, Frank Joyce, Mauricio García, Edgardo Arévalo, Gladys Valencia, Marvin Hidalgo, Yuber Rodríguez, Eladio Cruz, Richard LaVal, Karen Nassi, Gibi Barrantes, William Eberhard, Joaquín Sánchez, Álvaro Miranda, Mariano Arguedas, Eduardo Arguedas, Franklin Arce, Oscar Brenes, Wally VanSikle, Sabrina Amador, Alejandro Farji, Gustavo Vargas, Alfredo Cascante, Barbara Lewis, Johnny Rosales y Giselle Rodríguez, por su ayuda en las distintas etapas de mi proyecto, ya sea durante el trabajo de campo, corrigiendo cosas, discutiendo los detalles, identificando material, otorgando permisos, o ayudando en los interminables trámites, mil gracias.

Gracias a las instituciones que me apoyaron logística y económicamente durante el desarrollo de mi trabajo: Instituto de Ecología de la Universidad Nacional Autónoma de México, Estación Biológica Monteverde, Organización de Estudios Tropicales, Idea Wild, WWF – Centro América y Asociación Conservacionista de Monteverde.

DEDICATORIA

Francisco, Silvia y Teresa

Lamento mucho que partieran tan temprano, sus recuerdos viven en el bosque.

CONTENIDO

RESUMEN GENERAL

El deterioro ambiental es una de las causas más importantes de la desaparición de poblaciones de especies nativas, sin embargo se han estudiado poco los efectos de el deterioro ambiental sobre la estructura, función e interacciones ecológicas en las comunidades afectadas, en particular en comunidades neotropicales. En estos estudios evaluamos el efecto de la fragmentación del bosque tropical húmedo premontano, sobre la depredación de semillas por mamíferos y la vegetación del sotobosque en ausencia de mamíferos herbívoros. Realizamos estos trabajos en Monteverde, Costa Rica, de agosto de 1999 a noviembre de 2005. Evaluamos la composición de especies de mamíferos en bosque continuo (donde se mantiene la fauna histórica original), fragmentos de bosque maduro y pastizal. Evaluamos la depredación de semillas y la riqueza de plantas del sotobosque en parcelas bajo exclusión y abiertas. En los fragmentos encontramos menos especies de mamíferos en relación al bosque continuo, sin embargo casi la mitad de las especies usan, o están presentes en los fragmentos, estos sitios son importantes para la conservación de los mamíferos en la región. Al considerar cuatro especies de semillas de árboles nativos, la depredación de sus semillas por mamíferos no fue estadísticamente diferente entre el bosque continuo y los fragmentos, debido probablemente a la mayor abundancia de depredadores pequeños (roedores) en los fragmentos, que podría compensar a la ausencia de mamíferos depredadores de semillas de especies medianas y grandes, más susceptibles a desaparecer por fragmentación. Posiblemente la saciedad de los depredadores de semillas podría ser lo que determina la remoción de las semillas en los fragmentos. Por otra parte, las parcelas bajo exclusión terminaron con menor la riqueza de plantas, sobretodo en los fragmentos de bosque. Este efecto fue menos evidente en parcelas abiertas donde las especies de mamíferos menos conspicuas, nocturnas o sin valor para los cazadores, podrían estar manteniendo niveles adecuados de herbivoría, manteniendo la riqueza de plantas sin disminuciones drásticas, como ocurre en sitios defaunados.

LISTA DE FIGURAS

LISTA DE CUADROS

INTRODUCCIÓN GENERAL

En Centroamérica la creciente explotación de los ambientes naturales para la producción agrícola y la extracción de madera, han generado una acelerada deforestación de sus bosques tropicales (Wright 2005). Como consecuencia, lo que hasta hace unos años eran áreas extensas cubiertas con bosque natural, se han convertido en paisajes fragmentados, con remanentes boscosos de diferentes formas y tamaños, en su mayoría parches muy pequeños (pocas hectáreas de bosque maduro) inmersos dentro de una matriz de pastizales, carreteras, campos agrícolas y ciudades. Este proceso de fragmentación reduce la riqueza de especies nativas de diferentes grupos taxonómicos (Daily et al. 2003, Didham *et al*. 1998, Lawrence y Bierregaard 1997).

En el caso de los vertebrados, la reducción del tamaño del área boscosa, asociada con los denominados "efectos del borde" (Murcia 1995), así como las distancias hasta los otros parches de bosque, determinan la composición de especies capaces de permanecer en esos fragmentos, disminuyendo, en consecuencia, su riqueza (Lawrence *et al*. 2000, Phillips 1997, Lovejoy *et al*. 1986). Para el caso de los mamíferos, además de ser afectados por la disminución del área y distancias entre fragmentos, también dependen de los elementos del paisaje que existen alrededor del bosque (Chaves-Campos *et al*. 2003, Daily *et al.* 2003, Chiarello 1999, Gascón y Lovejoy 1998, Guindon 1997). En general, todavía conocemos muy poco sobre el potencial de los paisajes fragmentados para mantener especies de vertebrados en el tiempo; sobretodo en bosques montanos y premontanos (elevaciones intermedias), en los que el recambio de especies puede llegar a ser muy significativo a lo largo del gradiente altitudinal, así como entre los picos de montañas (Stiles 1988, Tosi 1969).

Los bosques montanos en Costa Rica, además de proveer uno de los más importantes servicios ambientales al mantener la captación de agua (Zadroga 1981), son sitios particularmente diversos (Nadkarni y Wheelwright 2000). Su diversidad y estructura están muy definidas por interacciones ecológicas, ligadas a factores ambientales abióticos (Timm y LaVal 2000, Nadkarni y Matelson 1992, Nadkarni 1994, Pounds y Crump 1994, Murray 1986), por lo que la fragmentación de estos sistemas es un problema muy relevante. En un futuro cercano, los bosques montanos adquirirán además mayor importancia debido al cambio climático, pues es esperable que servirán de "refugio" para las especies provenientes de zonas bajas (Pounds *et al*. 2006).

Los remanentes de bosque, al disminuir en riqueza de especies, cambian además en las interacciones ecológicas que puedan ocurrir en ellos. Se podría esperar que las interacciones entre animales y plantas como herbivoría, frugivoría, visitación a flores, polinización, dispersión de semillas, depredación de semillas, entre otros (Chinchilla 2009, Dirzo et al. 2007, Kitamura y Yumoto 2002, Rao *et al*. 2001, Roldán y Simonetti 2001, Cascante 1998, Ferreira y Laurance 1997, Phillips 1997, Terborgh y Wright 1994) se encuentren muy modificadas, al dejar de estar presentes las especies que participaban en tales interacciones. En el caso particular de los mamíferos, su ausencia de sitios con bosque debida a (1) el efecto de la reducción del área boscosa por fragmentación del hábitat, (2) su cacería frecuente, y (3) la combinación entre fragmentación del bosque y cacería, afecta y disminuye significativamente a la riqueza de plantas del sotobosque. Para el caso de los mamíferos este fenómeno se ha denominado "defaunación contemporánea" (Mendoza y Dirzo 2007, Dirzo 2000, Dirzo y Miranda 1991).

En sitios defaunados se observa disminución, o ausencia, de la herbivoría sobre las plantas debida a mamíferos, así como también ausencia de pisoteo sobre la vegetación (Dirzo y Miranda 1991). Estas condiciones de menor "presión" sobre la vegetación, benefician a aquellas especies de plantas que puedan "competir" mejor utilizando más rápidamente los recursos, ganando entonces espacio dentro del sotobosque y convirtiéndose con el tiempo en las especies con mayor densidad, o dominancia por unidad de área, lo que se ha llamado "formación de alfombras monoespecíficas" (Dirzo 2000, Dirzo y Miranda 1991), reduciéndose entonces la diversidad florística del sotobosque en un principio, y posiblemente reduciendo también la riqueza de árboles en el futuro, pues dentro del sotobosque están presentes también plántulas de árboles.

La menor riqueza de plantas del sotobosque debida a la ausencia de mamíferos, podría verse compensada por una serie de eventos relacionados con el mismo aumento en la densidad de ciertas especies ahora dominantes. Existen datos experimentales de Dirzo (2000) que indican que las parcelas monoespecíficas, donde fueron añadidas plantas de *Omphalea oleifera* (Euphorbiaceae), presentan mayor incidencia de insectos fitófagos específicos, en este caso larvas de *Urania fulgens* (Lepidoptera), que las parcelas bajo el tratamiento control, parcelas más diversas. La mayor incidencia de *U. fulgens* a su vez produce el ataque de sus parasitoides, que en este caso son dípteros de Tachiinidae. El aumento de larvas de *U. fulgens* por el aumento de la planta de la que se alimentan, representa cambios en un interacción de segundo orden; la mayor incidencia de los dípteros parasitoides representa cambios en una interacción de tercer orden. Esta secuencia de interacciones modificadas, ocurriría porque desaparece la interacción de primer orden, con la ausencia de los mamíferos por defaunación contemporánea. Estos resultados pueden estar indicando la existencia de mecanismos ecológicos no muy bien evaluados, mediante los cuales la riqueza de plantas podría mantenerse en el tiempo, pues las plantas bajo la presión de los insectos herbívoros estarían de nuevo bajo una "perturbación intermedia" en el sentido de Connell (1978), lo que mantendría un estado de mayor riqueza de especies, y cuyos extremos hipotéticos serían, por un lado, la ausencia total de herbivoría y por el otro lado, la herbivoría "excesiva"; en ambos extremos la riqueza específica sería menor.

Por otra parte, se ha sugerido que la defaunación contemporánea no es un proceso que afecte igualmente a todas las especies de mamíferos, sino que afecta principalmente a especies de tamaño mediano y grande (Mendoza y Dirzo 2007). Los roedores de tamaño corporal pequeño estarían entonces libres de la presión de cacería. Además estos animales pueden permanecer más fácilmente en bosques fragmentados, porque, relativamente a su tamaño, los remanentes de bosque siguen teniendo un área adecuada para ellos. Por otra parte, debido a que las especies de carnívoros grandes y medianos desaparecen de los bosques fragmentados, los roedores pequeños quedan libres también de sus depredadores naturales; típicamente se pueden observar densidades más altas de ratones en fragmentos de bosque que en sitios de área equivalente dentro del bosque continuo (véase Capítulo 1). Por ser los roedores pequeños animales que se alimentan principalmente de semillas, se podría esperar que la depredación de semillas en fragmentos de bosque sea muy alta, sobre todo en el caso de semillas de tamaño pequeño.

Considerando que la fragmentación del bosque es un proceso general en la región tropical, y que además de la disminución en la riqueza de especies podría estar afectando las interacciones ecológicas entre mamíferos y plantas, en esta tesis investigo:

(1) Si fragmentos que ya existen en la región de Monteverde, Costa Rica, tienen algún valor para la conservación de mamíferos nativos no voladores, comparando la riqueza, composición y abundancia de las especies en estos sitios y en un área del bosque continuo. (Capítulo 1: "*Value of premontane moist forest fragments for mammalian conservation in Costa Rica: trash or treasure?*" Enviado al Journal of Mammalogy)

(2) Al determinar si las especies de roedores de tamaño corporal pequeño tienen mayores densidades en los fragmentos de bosque, evaluar si esto conlleva un aumento en la depredación de semillas de especies nativas en los fragmentos, (Capítulo 2: *"Seed predation by mammals in forest fragments in Monteverde, Costa Rica"* Publicado en: Revista de Biología Tropical (ahora Internacional Journal of Tropical Biology) 57 (3): 856 – 877, Septiembre 2009.

(3) Si en estos fragmentos de bosque ocurre defaunación contemporánea, determinar si ocurren y se mantienen "alfombras monoespecíficas" a largo plazo de tiempo, o si por el contrario ocurren mecanismos de compensación que mantengan la riqueza de especies en el tiempo (Capítulo 3: *"Contemporary defaunation reduces plant richness in forest fragments in Monteverde, Costa Rica"* Enviado al Journal of Tropical Ecology)

Capítulo 1:

“Value of premontane moist forest fragments for mammalian conservation in Costa Rica: trash or treasure?”

VALUE OF PREMONTANE MOIST FOREST FRAGMENTS FOR MAMMALIAN CONSERVATION IN COSTA RICA: TRASH OR TREASURE?

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Abstract: Habitat deterioration is one of the leading causes of disappearance of populations and species, but the impacts of habitat fragmentation on the community structure of tropical mammals are poorly studied. We investigated the importance of forest fragments of different size and habitat heterogeneity (i.e. tree diversity) for the conservation of non-flying mammals by comparing continuous forest, fragments, and pasture in premontane moist forest, Monteverde, Costa Rica, from August 1999 to March 2001. Species richness declined significantly from continuous forest to fragments to pasture, and species richness correlated positively with both fragment size and tree species richness. We recorded 33 native species, most of which (88%) were present in continuous forest and 12 were not observed elsewhere; 51% were found in fragments, but most of these (14) were found in continuous forest; and only 3 occurred in both forests and pasture. In addition, one species was restricted to pasture, for a total of 4 (12%) observed there. Despite intensive habitat fragmentation, there have been only two local extinctions, the giant anteater and the white-lipped peccary. Other species, such as the black-handed spider monkey are rare and may become locally extinct in the foreseeable future if habitat deterioration continues. Our study detected that although fragmentation has a negative effect on the mammalian community, forest fragments, especially the larger ones, represent an important habitat to maintain populations and individuals of many (over 50%) of all native terrestrial mammals, including endangered species, while pastures have little value for long-term conservation of native mammals.

Key words: forest fragmentation, mammal diversity, cloud forest, conservation, Costa Rica.

Introduction

The increasing exploitation of natural habitats for agricultural and timber production has produced an accelerated rate of deforestation in neotropical forests (Wright 2005). A concomitant consequence of this is the habitat fragmentation of large continuous tracts of forest into remnants of various sizes and shapes embedded within a human-dominated landscape. Such pattern of land use change is creating fragmented landscapes with an over-representation of small patches of natural vegetation, and just a few, if any, large tracts of more or less continuous forest (e.g. Mendoza et al. 2005). In general, it has been found that fragmentation decreases species richness in a variety of organisms (Laurance and Bierregaard 1997, Daily et al. 2003). For vertebrate fauna, the reductions in size, and increase in distance between forested areas, together with the associated edge effects may produce drastic changes in species diversity and composition (Didham *et al*. 1998, Laurence *et al*. 2000, Lovejoy *et al*. 1986, Murcia 1995, Phillips 1997, Saunders *et al*. 1991).

Some studies have reported that mammalian species diversity is affected by both fragmentation (Chiarello 1999, Laurence 1990, Laurence 1999, Stevens y Husband 1998) and quality of the landscape surrounding fragments (Gascon and Lovejoy 1998; Daily et al., 2003). Therefore the potential to retain mammalian diversity in fragmented landscape has been poorly investigated. Furthermore, most studies of this type have been carried out in lowland tropical rain forests where altitudinal gradients are almost irrelevant. Very few studies have focused on the impacts of fragmentation on the biodiversity of mid-elevation forests, such as the premontane tropical moist forest life zone (Holdridge 1967) of the tropics, where species turnover may be strong in response to elevation.

Premontane forests, also called “cloud forests”, are fundamental in terms of their ecosystem services, particularly watershed maintenance (Zadroga 1981) and their special biodiversity (Nadkarni and Wheelwright 2000). Their diversity and functional structure are strongly defined by the interactions between plants and animals and by the physical and chemical factors associated to abiotic-environment dynamics at mid-elevation (Murray 1986, Pounds and Crump 1994, Nadkarni 1994, Nadkarni y Matelson 1992, Timm and LaVal 2000). In addition, they are crucial conservation targets due to their sensitivity to anthropogenic impacts. For example, deforestation and forest fragmentation in high elevations forests may bring a variety of effects on the communities of the lower elevations, because of the disruption of ecological processes, such as altitudinal animal migrations, that require connected forested areas between high and lower lands (Stiles 1988, Chaves-Campos *et al*. 2003), in addition to preventing deterioration of watersheds and soil erosion (Nadkarni and Wheelwright 2000). Furthermore, their importance is likely to become even greater in the face of climatic change since they may serve as refugia for species inhabiting lowland tropical forests (Pounds et al. 2006).

Given that fragmentation is an omnipresent process in tropical regions of the world it becomes important to examine to what extent biodiversity is affected by fragmentation, and to what extent is biodiversity retained in a human-dominated landscape. Here we investigated the value of forest fragments for the conservation of non-flying mammals in the premontane tropical moist forest in Monteverde, Costa Rica. Our objectives were to (i) compare the species richness, composition, and abundance of the non-flying mammal fauna in the contrasting habitats of a human-dominated landscape, including continuous forest, forest fragments, and pasture lands; (ii) assess the conservation value of forest remnants of different sizes surrounded by pasture in terms of taxonomic diversity they can harbor; and (iii) characterize the faunal change that might have occurred as a result of large-scale deforestation.

Methods

Study area

We evaluated the presence of non-flying mammals between August 1999 and March 2001, in six sites in Monteverde, Puntarenas province, Costa Rica (Figure 1). The study sites all fall within the premontane tropical moist forest life zone of Holdridge's

(1967) classification system. One site, used as a control, was located inside a continuous forest where all but two of the 121 native species of the Monteverde area are extant (57 % of the Costa Rican mammals), the exception being two species that have been locally extirpated, the giant anteater (*Myrmecophaga tridactyla*) and the white-lipped peccary (*Tayassu pecari*) (Hayes and LaVal 1989, Rodríguez and Chinchilla 1996, Timm and LaVal 2000). The next four sites were forest fragments of various sizes (Table 1), and the sixth was a pasture (see also Figure 1).

All six study sites are located on private property. All sites are surrounded by dairy pastures. All fragments were fenced off several years ago to prevent cattle from entering. The fragments are located at similar elevations and all are remnants of the original continuous forest (Table 1). A description of the vegetation of the Monteverde area is given in Haber *et al.* (1996), Hayes *et al.* (1988), and Nadkarni and Wheelwright (2000).

Data collection and analysis

To evaluate the presence and abundance of small mammals, we established a sampling plot with 49 Sherman live traps, disposed on the ground, one trap every ten meters in a grid of 7 by 7 traps, for three consecutive nights per month in each site. Each trap was baited with a mixture of two parts of raw rice with one part of wet oat milk with vanilla. This was repeated once a month, for a total of 16 months (August to December 1999, February to April and July to December 2000, and February to March 2001) systematically on the darkest nights of each month. The sampling effort was 2352 trap nights on each site, for a total of 14,112 trap nights.

To evaluate the presence and abundance of larger mammals, every month we walked two transects on each site during a total of ten months (August to December 1999, February to April, July, and October 2000). These consisted of two hours of slow walk through the forest, one walk during the morning and the other in the early hours after night falls, counting both diurnal and nocturnal species (a total of 240 transect-hours). These transects were carried out on the darkest nights of each month. Along these transects we recorded mammal tracks, sounds and other signs of mammal presence. In all cases we counted only one individual per transect for each of the species recorded.

To analyze the effect of fragment size on species richness we performed regression analyses, with area (transformed to a logarithmic scale) as the independent variable. In addition, for an analysis of covariance, we considered the effect of other independent variables, including (a) site elevation, (b) fragment age (determined by the owner of the property), (c) minimal distance to continuous forest, (d) number of tree species present, (e) percent of canopy cover of each site (arcsine-transformed). To consider the number of tree species, we established three 50 X 2 m transects near the trapping quadrants of all six sites. All trees with diameter at breast height (DBH) $\geq$ 10.0 cm were sampled and later identified at the Department of Natural History of the National Museum of Costa Rica. We made a rough estimate of canopy cover every 5m along the same transects, using an overhead acetate sheet with a grid of 50-1cm^2 squares. We determined percent canopy cover by counting the number of squares filled with and without canopy.

For the functional structure of mammal communities from each site we considered (a) the diet of each species following the classification by Robinson and Redford (1986), and (b) the habit (terrestrial, arboreal, scansorial, or fossorial) of each species. In addition, relative abundance of the species was calculated following Hayes and LaVal (1989) and Timm and LaVal (2000) criteria, considering a given species as "abundant" if it was recorded (observed and/or captured) one or more times in 80% of the visits to a site; as "common" if it was recorded in 40 to 80% of the visits; as "uncommon" if it was recorded on 10 to 40% of visits, and "rare" if it was recorded on less than 10% of visits.

For this article, we use the common and scientific names the first time. Subsequently we use only common names according to Timm and LaVal (2000) for the Monteverde mammals, except for rats and mice, for which we use scientific names always.

Results

Overall species richness and composition

Our sampling was successful, both in terms of recorded species and the number of records (Table 2). We had a total of 400 captures and 228 records of 33 species, which represent around 53% of non-flying species of mammals of Monteverde (Appendix). Six orders were represented but most species belonged to Rodentia (14 species) and Carnivora

(Table 2). Trapping success was relatively homogeneous in forest and some forest fragments, varying from 2.64% in the continuous forest (EBM) to 2.47% in CAT and 2.93% in BTI. Trapping success was higher in the fragments MAR (5.48%) and FAR (3.36%) and was much lower in the pasture (0.13%). Guilds included nine frugivore–omnivore species, 12 frugivore–granivore species, four frugivore–herbivore species, one herbivore–browser species, two insectivore–omnivore species, and five carnivore species (Table 3). In terms of the species habits, we recorded 17 terrestrial species, seven scansorial species, and nine arboreal species (Table 3).

The role of continuous forest and the importance of fragments

Species composition, richness, and abundance were positively affected by forest area. The highest number of species was found in the continuous forest, followed by forest fragments, and pastures (Figure 2). A total of 29 species were found in the continuous forest (EBM), 47 in all forest fragments, and only 4 species in the pasture. Two additional trends were evident (see table 2). First, there were more species in the larger forest fragments, including 15 in fragment CAT, 13 in BTI, 13 in MAR and 6 in FAR. Second, many more species were present in the fragments than in the pasture (Table 2)

Differences among the continuous forest, forest fragments, and pasture are illustrated by the species restricted to each habitat. There were twelve species occurring exclusively in the continuous forest, so we considered them as forest or habitat specialists. This group includes three small rodents (*Oryzomys albigularis*, *Nyctomys sumichrasti* and *Tylomys watsoni*), paca, black-handed spider monkey, raccoon, puma, jaguarundi, margay, collared peccary (*Pecari tajacu*), brocket deer (*Mazama americana*), and the common opossum (*Didelphis marsupialis*) (Table 2). The continuous forest was unique in that it had the highest species richness, and had a high number of species not represented in forest fragments and pasture. The forest fragments were important in harboring individuals and populations of approximately 50% of the recorded species. Fourteen species were shared between continuous forest and fragmented forest (Figure 2, Table 2). These species and three more occurring only in the forest fragments were considered as forest generalists, and include four small rodents, the two-toed sloth, the white-faced Capuchin, the mantled howler monkey, two species of squirrels (*Sciurus variegatoides* and *S. granatensis*), the agouti, the white-nosed coati, the long-tailed weasel, kinkajou, and ocelot. The three other forest generalists were recorded only in fragments, but very likely also found in the continuous forest, are the woolly opossum, the prehensile-tailed porcupine, and the pygmy rice mouse (Table 2). Three other species are difficult to classify as either forest specialists or generalists, including the Alston´s brown mouse which was present in continuous forest and in the pasture, as well as the gray fox and the nine-banded armadillo, which were present in all the sites (Table 2). One species representing an unusual case is the coyote, found during this study only in the pasture. This species has never been observed in forested areas in Monteverde, and could be considered as a species more typical of edge, agricultural lands, or other open areas.

There was a strong significant positive relationship between species richness and forest log area ($R^2 = 0.94$, $F = 65.72$, $p = 0.001$; Figure 3). These results were consistent when we omitted the zero value of the grassland ($R^2= 0.95$, $F= 91.4$, $p= 0.002$), to account for the fact that the grassland is not a fragment habitat. Interestingly, among the other variables associated to the fragments, the number of tree species also had a significant effect on the richness of mammals ($R^2 = 0.18$, $p = 0.05$). Other factors such as elevation, fragment age, distance to the continuous forest, and canopy cover did not have a statistically significant effect on mammalian species richness. ($p> 0.05$ in all cases). Tree species richness in turn is unrelated to fragment size. The 12 frugivore-granivore species were mainly small rodents, recorded principally in the continuous and fragmented forests. The four frugivore–herbivore species, the herbivore–browser and the five carnivores were present only in forested sites (continuous and fragmented forests). The insectivore-omnivore species were recorded only in the pasture (Tables 2 and 3). Terrestrial and scansorial species were found in all types of habitats (continuous forest, fragments and pasture), but the arboreal species were present only in the forested sites. We did not encounter any of the fossorial species known to be present in the area.

Relative abundance

Those species that occurred in more than one site had distinct relative abundances in each of those sites, except for six species (Table 4). Two of these were the rodents *Peromyscus mexicanus,* which was abundant at all sites in which it occurred, and *Oryzomys* *alfaroi*, which was rare in both continuous forest and fragment sites CAT and MAR. The other four exceptions were the gray fox, which was rare in continuous forest, fragments CAT and MAR and pasture; the long-tailed weasel, which was rare in all forested sites; the kinkajou, also rare in the continuous forest and fragments CAT and BTI; and the ocelot, rare in continuous forest and fragment BTI. Species rare in continuous forest, but also occurring in forest fragments, were found to be rare there also.

In the case of rare species present in more than one site, we found two kinds of abundance patterns. The first was one in which the relative abundance of a species tended to increase or decrease from continuous forest to fragments (according to size) and to pasture. Examples of this are the two-toed sloth, which was common in the continuous forest but rare in the four fragments; and the nine-banded armadillo, which was abundant in continuous forest and the large fragment (BTI), but uncommon in the medium fragment MAR and in the pasture. In general the monkey troops showed the same kind of abundance distribution: white-faced Capuchin was common in continuous forest and uncommon in fragments CAT, BTI, and MAR, and mantled howler monkey was common in continuous forest, but rare in fragments BTI and MAR. The variegated squirrel was abundant in the continuous forest and the larger fragments CAT and BTI, but only common in the smaller fragments MAR and FAR. Also following a linear pattern, but in the other direction (i.e., more abundant in smaller fragments) was the Desmarest´s spiny pocket rat. It was uncommon in the continuous forest, common in the largest fragment CAT, and abundant in the smaller fragments BTI, MAR, FAR.

The second type of abundance pattern includes those species that showed no consistent trends in relative abundance in relation to forest size. Examples were the red squirrel, which was abundant in continuous forest and the large fragment BTI but uncommon in the largest fragment CAT; the agouti, common in continuous forest, uncommon in the largest fragment CAT, abundant in the large fragment BTI, and rare in the medium one MAR. White-nosed coati was uncommon in the continuous forest and the medium fragment MAR, rare in the largest fragment CAT, and common in the large fragment BTI.

Fifteen species were present in only one site. Four of these were the rat *Oryzomys albigularis*, the common opossum and the paca in the continuous forest, and the coyote in the pasture; all of them were uncommon in their respective sites. Ten species were rare, having been recorded one or very few times during the course of the study. Only collared peccaries were common in their respective site, the continuous forest (Table 4).

Long-term faunal change

Our compilation of records of non-flying mammals in Monteverde shows the historical presence of 63 species (Appendix). Our documented history of the area indicates that the forest fragmentation process started more than 40 years ago (Table 1). During that period, at least two species, the giant anteater and the white-lipped peccary, have gone locally extinct. Our observations in the recent years suggest that populations of species such as the jaguar (*Panthera onca*) and the black-handed spider monkey have been diminishing. However, other species like agoutis, nine-banded armadillos and raccoons may have been increasing in the last twenty years in the Monteverde zone (R. LaVal, pers. com.).

Discussion

The fact that more species were found in continuous forest than in forest fragments, particularly smaller ones, is similar to results reported by other authors (Laurence and Bierregaard 1997). However, in our study the number of tree species present at each site was also an important factor influencing the mammal species richness. This suggests an important relationship between the resources represented by trees and mammals as consumers, since the majority of mammals recorded were basically frugivores and granivores such as small rodents, gray foxes, porcupines, coatis, squirrels, and agoutis, among others, or folivores (e.g. monkeys, sloths, squirrels), or wood- and sap-eaters (squirrels and porcupines). Also some species of carnivores, like the margay and ocelot, include fruits in their respective diets (Chinchilla 1997), and depend on trees for hunting and shelter. In Monteverde almost one third of the species recorded were arboreal and seven were scansorial, signifying that the trees represent a directly utilized resource for almost all the mammals in the area.

The number of tree species also depends on the size of the forested area (Lovejoy *et al*. 1986). The reproductive success (pollinization, seed set, and genetic diversity) of tree species is also affected by fragmentation (Aizen and Feisinger 1994; Cascante 1998), and the changing conditions produced by edge effects increase tree mortality, particularly in smaller fragments and near the edges of the forest fragments (Murcia 1995; Ferreira and Laurence 1997; Laurence *et al.* 2000). Considering those circumstances, plus the changes in mammalian fauna, changes in interactions with herbivores, seed eaters, and flower visitors, among others, we could expect a decrease of tree diversity in Monteverde fragments in the near future.

Four species of mammals recorded in the fragments were not present in the continuous forest. The absence in the continuous forest of prehensile-tailed porcupines and woolly opossums could be related to the arboreal habits and nocturnal activity of these two species, making them more difficult to locate and thus perhaps were overlooked by chance. It is known that both are in fact present in the continuous forest of Monteverde (Timm and LaVal 2000, and personal observations). The mouse *O. fulvescens* is a very uncommon species in the area (Hayes and LaVal 1989), and it was present only once in one of the fragments during this study. With the exceptions explained above, our results support Patterson's claim (1987) that the communities of mammals found in forest fragments are subsets of those found in the continuous forest, but unexpectelly diverse, considering the small forested area of these study sites.

The mammalian fauna of Monteverde consists basically of forest-related species. We recorded 12 forest specialists, 14 generalists, and three species recorded only in the fragments but expected in the continuous forest. The absence from the fragments of most of the carnivores, brocket deer, paca, collared peccaries, and black-handed spider monkeys, represents an impoverishment in terms of interactions with other species, and it is known that their absence may produce changes in structure and composition of forest fragment (Dirzo and Miranda 1991, Phillips 1997). This strongly supports the fundamental importance of the continuous forest in the conservation of many of the species we studied.

The fourth species not found in the continuous forest was the coyote, which differs from the three previous species in not being part of the original native fauna of Costa Rica. Instead, it is an invasive species newly arrived to these latitudes (Vaughan 1983). The continental range of coyotes has spread from Mexico to Central America as a result of deforestation. This species actually occurs as far south as the forested zone in the province of Darien, Panama, near the border with Colombia. If it manages to cross this forested natural barrier, it could become a successful species in South America, as it is on the deforested cattle ranches of Central America, where it benefits from its omnivorous diet. The presence of coyotes in Monteverde is a result of the fragmentation in the area. We do not know yet how its presence is now affecting the mammalian community. That should be studied to understand more about the ecological processes in fragmented landscapes, and the value of the forest remainders for conservation.

Although this study makes it evident that, as compared to continuous forest, fragments and the surrounding human-dominated matrix only contain a subset of the native mammlain spacies, it also highlights the importance of the remaining forest fragments in retaining a fraction of such fauna. This underscores the need to develop restoration plans in which fragments can operate as partial reservoirs and corridors to connect the vegetation and faunal remnants of the current tropical landscapes.

Acknowledgments

We are especially grateful to Ignacio Méndez for his guidance in all phases of this study. We thank Luisa Moreno, Allison Deines, Frank Joyce, Mauricio García, Edgardo Arévalo and Yuber Rodríguez for help in the field. Mariano Arguedas, Eduardo Arguedas, Franklin Arce, granted permission to work in their properties. Oscar Brenes, Gladys Valencia, Marvin Hidalgo, Wally VanSikle, Sabrina Amador, Barbara Lewis and Johnny Rosales provided invaluable logistic and moral support. The study was funded by the Institute of Ecology of the National Autonomous University of Mexico (UNAM), Idea Wild, Organization for Tropical Studies (OTS), WWF-Central America, the Mesoamerican Biological Corridor Program (CBM), Monteverde Conservation League (MCL) and the Monteverde Biological Station (EBM). We thank Richard LaVal, Gretchen Daily, Rodrigo Medellín and Karen Nassi for comments and corrections.

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Table 1. Characterization of the six study plots used to assess the non-flying mammal species diversity and composition in Monteverde, Costa Rica.

Site type and local name	**Elevation (m)**	**Approximate size (ha)**	**Time after disturbance (yrs)**
Continuous forest, Monteverde Biological. Station (**EBM)**	1460	≈ 55000	
Largest fragment, Hoge property **(CAT)**	1250	350	≈ 30
Large fragment, Bajo del Tigre, Monteverde Conservation League (**BTI)**	1240	110	≈ 50
Medium fragment, Finca Americas, Los Llanos **(MAR)**	1150	60	≈ 45
Small fragment, Arce property, Los Llanos (**FAR**)	1170	20	≈ 45
Pasture, Monteverde Biol. Station **(PEB)**	1400	0	≈ 20

Table 2. Mammal species found in the six study plots used to assess non-flying mammal diversity in Monteverde, Costa Rica.

Scientific name	**Common name**	**Study site**						**Evidence of presence**
		EBM	CAT	BTI	MAR	FAR	PEB	
ORDER RODENTIA								
Peromyscus mexicanus	Deer mouse	X	X	X	X	X		Traps
Scotinomys teguina	Brown mouse	X					X	Traps
Oryzomys albigularis	Tome´s rice rat	X						Traps
Oryzomys alfaroi (group)*	Alfaro´s rice rat	X	X		X			Traps
Oligoryzomys fulvescens	Pygmy rice rat		X					Traps
Nyctomys sumichrasti	Vesper mouse	X						Traps
Tylomys watsoni	Climbing rat	X						Traps
Heteromys desmarestianus	Spiny pocket rat	X	X	X	X	X		Traps
Reithrodontomys gracilis	Harvest mouse	X	X					Traps
Sciurus variegatoides	Squirrel	X	X	X	X	X		Seen
Sciurus granatensis	Red Squirrel	X	X	X				Seen
Sphiggurus mexicanus	Porcupine		X			X		Seen
Agouti paca	Paca	X						Tracks
Dasyprocta punctata	Agouti	X	X	X	X			Seen
ORDER DIDELPHIMORPHIA								
Didelphis marsupialis	Common opossum	X						Seen/tracks
Caluromys derbianus	Wolly opossum				X			Seen
ORDER PILOSA								
Choloepus hoffmani	Two-toed sloth	X	X	X	X	X		Seen
ORDER XENARTHRA								
Dasypus novemcintus	Armadillo	X		X	X		X	Seen/tracks
ORDER PRIMATES								
Cebus capucinus	White-faced	X	X	X	X			Seen
Ateles geoffroyi	Spider monkey	X						Seen/listened
Alouatta palliata	Howler monkey	X		X	X			Seen
ORDER CARNIVORA								
Canis latrans	Coyote						X	Tracks
Urocyon cinereoargenteus	Gray fox	X	X		X		X	Seen
Nasua narica	Coati	X	X	X	X			Seen
Procyon lotor	Raccoon	X						Tracks
Mustela frenata	Weasel	X	X	X	X	X		Seen/traps
Potos flavus	Kinkajou	X	X	X				Seen/listened
Puma concolor	Puma	X						Tracks
Herpailurus yaguaroundi	Jaguarundi	X						Seen
Leopardus pardales	Ocelot	X		X				Tracks
Leopardus wiedii	Margay	X						Tracks
Pecari tajacu	Collared peccary	X						Seen/tracks
Mazama Americana	Brocket deer	X						Tracks
Total number of species		29	15	13	13	6	4	

* The taxonomy of the *O. alfaroi* group is still debatable.

Table 3. Dietary category and habit of the species found in our study in continuous forest, forest fragments and pasture in Monteverde[1].

Species	**Dietary category**	**Habit**
Peromyscus mexicanus	Frugivore – omnivore	Terrestrial
Scotinomys teguina	Insectivore– omnivore	Terrestrial
Oryzomys albigularis	Frugivore – granivore	Terrestrial
Oryzomys alfaroi (group)	Frugivore – granivore	Terrestrial
Oligoryzomys fulvescens	Frugivore – granivore	Terrestrial
Nyctomys sumichrasti	Frugivore – granivore	Scansorial
Tylomys watsoni	Frugivore – granivore	Scansorial
Heteromys desmarestianus	Frugivore – granivore	Terrestrial
Reithrodontomys gracilis	Frugivore – granivore	Scansorial
Sciurus variegatoides	Frugivore – granivore	Arboreal
Sciurus granatensis	Frugivore – granivore	Arboreal
Sphiggurus mexicanus	Frugivore – granivore	Arboreal
Agouti paca	Frugivore – granivore	Terrestrial
Dasyprocta punctata	Frugivore – granivore	Terrestrial
Didelphis marsupialis	Frugivore – omnivore	Scansorial
Caluromys derbianus	Frugivore – omnivore	Arboreal
Choloepus hoffmani	Herbivore – browser	Arboreal
Dasypus novemcintus	Insectivore– omnivore	Terrestrial
Cebus capucinus	Frugivore – omnivore	Arboreal
Ateles geoffroyi	Frugivore – herbivore	Arboreal
Alouatta palliata	Frugivore – herbivore	Arboreal
Canis latrans	Frugivore – omnivore	Terrestrial
Urocyon cinereoargenteus	Frugivore – omnivore	Scansorial
Nasua Larica	Frugivore – omnivore	Scansorial
Procyon lotor	Frugivore – omnivore	Scansorial
Mustela frenata	Carnivore	Terrestrial
Potos flavus	Frugivore – omnivore	Arboreal
Puma concolor	Carnivore	Terrestrial
Herpailurus yaguaroundi	Carnivore	Terrestrial
Leopardus pardales	Carnivore	Terrestrial
Leopardus wiedii	Carnivore	Terrestrial
Pecari tajacu	Frugivore – herbivore	Terrestrial
Mazama americana	Frugivore – herbivore	Terrestrial

[1] Following the classification by Robinson and Redford (1986) and Chiarello (1999).

Table 4. Relative abundance of the species found in our study in continuous forest, forest fragments and pasture in Monteverde [1, 2].

SPECIES	**SITES**					
	EBM	**CAT**	**BTI**	**MAR**	**FAR**	**PEB**
Peromyscus mexicanus	A (T)	A (T)	A (T)	A (T)	A (T)	
Scotinomys teguina	C (T)					U (T)
Oryzomys albigularis	U (T)					
Oryzomys alfaroi (group)	R (T)	R (T)		R (T)		
Oligoryzomys fulvescens		R (T)				
Nyctomys sumichrasti	R (T)					
Tylomys watsoni	R (T)					
Heteromys desmarestianus	U (T)	C (T)	A (T)	A (T)	A (T)	
Reithrodontomys gracilis	C (T)	U (T)				
Didelphis marsupialis	U (N)					
Caluromys derbianus				R (N)		
Choloepus hoffmani	C (D)	R (D)	R (D)	R (D)	R (D)	
Dasypus novemcintus	A (N)		A (N)	U (N)		U (N)
Cebus capucinus [3]	C (D)	U (D)	U (D)	U (D)		
Ateles geoffroyi [3]	R (D)					
Alouatta palliata [3]	C (D)		R (D)	R (D)		
Sciurus variegatoides	A (D)	A (D)	A (D)	C (D)	C (D)	
Sciurus granatensis	A (D)	U (D)	A (D)			
Sphiggurus mexicanus		R (N)			R (D)	
Agouti paca	U (H)					
Dasyprocta punctata	C (D)	U (D)	A (D)	R (D)		
Canis latrans						U (H)
Urocyon cinereoargenteus	R (D)	R (D)		R (D)		R (D)
Nasua Larica	U (D)	R (D)	C (D)	U (D)		
Procyon lotor	R (D)					
Mustela frenata	R (D)	R (D)	R (D)	R (D)	R (T)	
Potos flavus	R (N)	R (N)	R (N)			
Puma concolor	R (H)					
Herpailurus yaguaroundi	R (D)					
Leopardus pardales	R (H)		R (H)			
Leopardus wiedii	R (H)					
Pecari tajacu [3]	C (D)					
Mazama americana	R (H)					
Total number of records	82	33	79	20	9	5

[1] Following Hayes and LaVal (1989): **A = Abundant**: species recorded (observed and/or captured) one or more times on at least 80% of the visits to the site. **C = Common**: recorded on 40 – 80% of visits. **U = Uncommon**: recorded on 10 – 40% of visits. **R = Rare**: recorded on fewer than 10% of visits.

[2] (N) = Nocturnal records, (H) = Recorded by tracks, (T) = Recorded by traps, (D) = Direct observations during the day.

[3] Species seen always in groups.

FIGURES

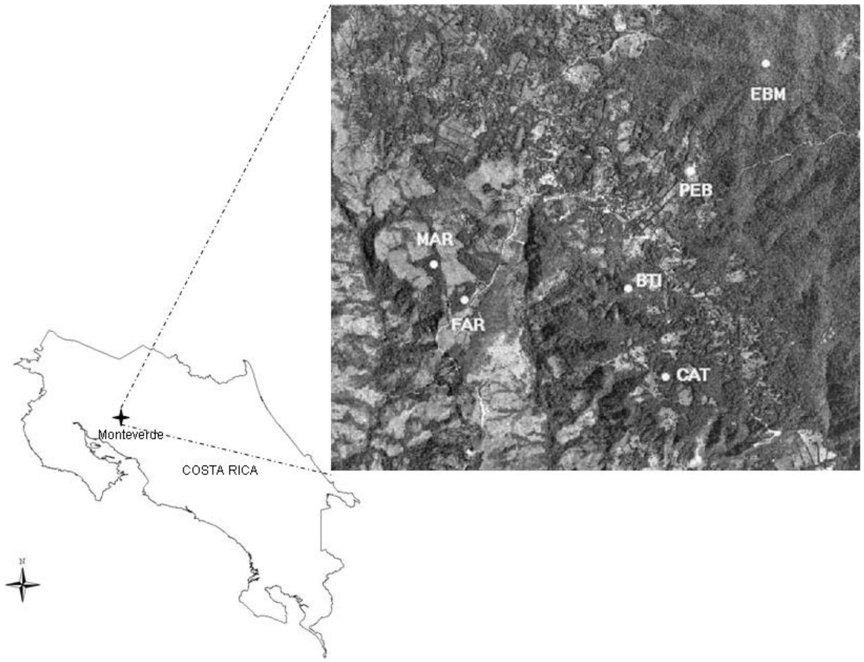

Fig. 1. Study sites in Monteverde, Costa Rica. The photo indicates the location of the six sites: EBM = Continuous forest at the Monteverde Biological Station; CAT = study site at Hoge property, largest fragment about 350 Ha; BTI = study site at Bajo Tigre, Children Eternal Rainforest, large fragment about 110 Ha; MAR = medium fragment about 60 Ha, at Finca Las Americas, Los Llanos; FAR = small fragment about 20 Ha, at Arce property, Los Llanos; PEB = Pasture site at Monteverde Biological Station.

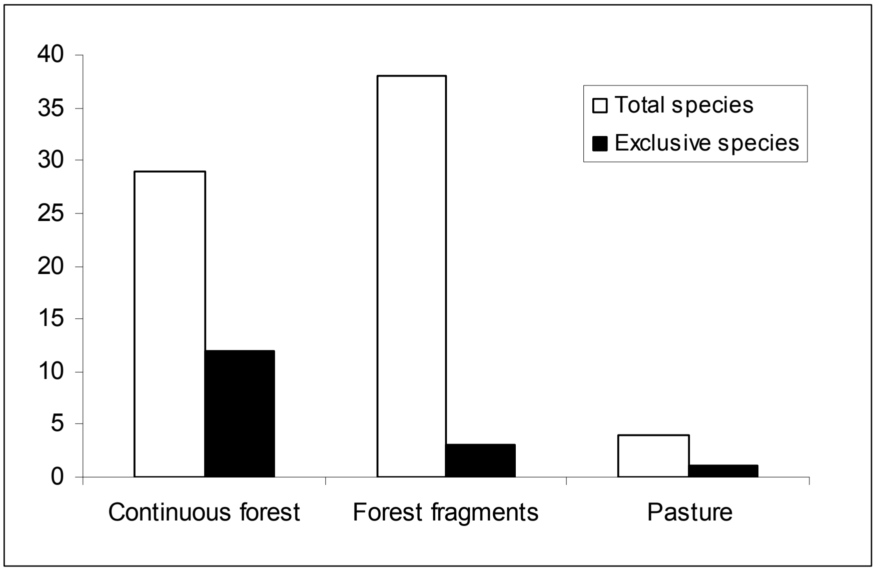

Figure 2. Number of species of mammals found in continuous forest, four forest fragments, and one pasture. Exclusive species are those only found in that type of place.

Appendix. Documented non-flying mammal species of Monteverde, Puntarenas Costa Rica. Modified from Timm and LaVal (2000), Hayes and LaVal (1989) and Rodríguez and Chinchilla (1996).

SCIENTIFIC NAME	ENGLISH NAME	RECORDED IN THIS STUDY	LOCALLY EXTIRPATED
DIDELPHIMORPHIA	Marsupials		
Didelphidae	American opossums		
Caluromys derbianus	Woolly Opossum	X	
Chironectes minimus	Water Opossum		
Didelphis marsupialis	Common Opossum	X	
Marmosa mexicana	Mexican Mouse Opossum		
Micoreus alstoni	Alston´s Opossum		
Philander opossum	Gray Four-eyed Opossum		
INSECTIVORA	Shrews		
Soricidae	Shrews		
Cryptotis nigrescens	Blackish Small-eared Shrew		
Cryptotis (new sp.)	Small-eared Shrew		
Cryptotis (new sp.)	Small-eared Shrew		
PRIMATES	Primates		
Cebidae	New World monkeys		
Alouatta palliata	Mantled Howler Monkey	X	
Ateles geoffroyi	Black-handed Spider Monkey	X	
Cebus capucinus	White-face Capuchin	X	
XENARTHRA	Edentates		
Megalonychidae	Two-toed sloths		
Choloepus hoffmanni	Hoffmann Two-toed Sloth	X	
Dasypodidae	Armadillos		
Cabassous centralis	Northern Naked-tailed Armadillo		
Dasypus novemcinctus	Nine-banded Armadillo	X	
Myrmecophagidae	Anteaters		
Myrmecophaga tridactyla	Giant Anteater		X
Tamandua mexicana	Northern Tamandua		
LAGOMORPHA	Rabbits		
Leporidae	Rabbits and hares		
Sylvilagus brasiliensis	Forest Rabbit		
Sylvilagus floridianus	Cottontail Rabbit		
RODENTIA	Rodents		
Geomyidae	Pocket Gophers		

Orthogeomys cherriei	Cherrie´s Pocket Gopher	
Sciuridae	Squirrels	
Microsciurus alfari	Alfaro´s Pygmy Squirrel	
Sciurus granatensis	Neotropical Red Squirrel	X
Sciurus variegatoides	Variegated Squirrel	X
Heteromyidae	Pocket Mice	
Heteromys desmarestianus	Desmarest Spiny Pocket Rat	X
Muridae	Long-tailed rats and mice	
Nyctomys sumichrasti	Vesper Rat	X
Oligoryzomys fulvescens	Pygmy Rice Mouse	X
Oligoryzomys vegetus	Pygmy Rice Mouse	
Oryzomys albigularis	Tome´s Rice Rat	X
Oryzomys alfaroi	Alfaro´s Rice Rat	X
Ototylomys phyllotis	Long-whiskered Rice Rat	
Peromyscus mexicanus	Naked-footed Mouse	X
Reithrodontomys creper	Chiriqui Harvest Mouse	
Reithrodontomys gracilis	Slender Harvest Mouse	X
Reithrodontomys (new sp.)	Harvest Mouse	
Rheomys raptor	Goldman´s Water Mouse	
Scotinomys teguina	Alston´s Brown Mouse	X
Sigmodon hispidus	Hispid Cotton Rat	
Tylomys watsoni	Watson´s Climbing Rat	X
Erethizontidae	Porcupines	
Coendou mexicanus	Prehensile-tailed Porcupine	X
Agoutidae	Pacas	
Agouti paca	Paca	X
Dasyproctidae	Agoutis	
Dasyprocta punctata	Agouti	X
CARNIVORA	Carnivores	
Canidae	Coyotes, foxes, and dogs	
Canis latrans	Coyote	X
Urocyon cinereoargenteus	Gray Fox	X
Mustelidae	Skunks, weasels, and otters	
Conepatus semistriatus	Striped Hog-nosed Skunk	
Eira barbara	Tayra	
Galictis vittata	Grison	
Lutra longicaudis	Southern River Otter	
Mustela frenata	Long-tailed Weasel	X
Procyonidae	Raccoons	
Bassaricyon gabbii	Olingo	
Nasua narica	White-nosed Coati	X
Potos flavus	Kinkajou	X
Procyon lotor	Raccoon	X
Felidae	Cats	
Herpailurus yaguarondi	Jaguarundi	X

Felis (Leopardus) pardalis	Ocelot	X	
Felis (Leopardus) wiedii	Margay	X	
Felis (Leopardus) tigrina	Little Spotted Cat		
Felis (Puma) concolor	Puma	X	
Panthera onca	Jaguar		
ARTIODACTYLA	Deer and peccaries		
Tayassuidae	Peccaries		
Tayassu pecari	White-lipped Peccary		X
Pecari tajacu	Collared Peccary	X	
Cervidae	Deer		
Mazama americana	Brocket Deer	X	
Odocoileus virginianus	White-tailed Deer		
PERISSODACTYLA	Tapirs and horses		
Tapiridae	Tapirs		
Tapirus bairdii	Baird´s Tapir		

Capítulo 2: “Seed predation by mammals in forest fragments in Monteverde, Costa Rica” Internacional Journal of Tropical Biology (antes Rev. Biol. Trop.) 57 (3): 856 – 877, Septiembre 2009.

Seed predation by mammals in forest fragments in Monteverde, Costa Rica

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Abstract: Few studies have evaluated seed predation in fragmented landscapes, in which lower species diversity is expected to modifying ecological interactions. I investigated the rates of seed removal by mammals in continuous forest and two fragmented patches of Premontane Tropical Moist Forest, in Monteverde, Costa Rica. I recorded the composition of mammalian seed-predators in each site during 16 months and studied the removal of four native tree species of experimental seeds: *Ocotea valeriana* and *Ocotea whitei* (Lauraceae), *Panopsis costaricensis* (Proteaceae) and *Billia colombiana* (Hippocastanaceae) in forest understories, during two annual fruiting seasons for each species. Results indicated similar species composition of seed-predators between continuous forest and the large fragment (350 hectares). However the smaller fragment (20 hectares), had fewer seed predators. In this fragment, the specialized seed predator *Heteromys desmarestianus* (Rodentia) was more abundant. Unexpectedly, seed-predation in the two forest fragments and the continuous forest did not differ statistically for any of the seed species. Apparently, the higher abundance of small seed-predators in the fragments was compensated by the absence of medium and large seed-predators, like *Agouti paca*, *Dasyprocta punctata* (both Rodentia) and *Pecari tajacu* (Artiodactyla) recorded in continuous forest. Removal of experimentally – placed seeds was higher when the number of naturally occurring seeds in the sites was lower. This result could best be attributed to differential satiation of seed predators rather than differences in richness or abundance of seed predators.

Key words: seed removal, seed predators, forest fragmentation, predator satiation.

Tropical communities are among the most diverse and less - studied biological systems that currently are being modified and cleared (Wright 2005), causing forest fragmentation, environmental changes, and generalized species loss (Saunders *et al*. 1991, Murcia 1995, Laurance and Bierregaard 1997, Didham *et al*. 1998, Chiarello 1999, Ruiz 2003). But forest fragmentation also means changes in animal–plant interactions, such as herbivory, frugivory, pollination, seed dispersal, trampling of seedlings and seed predation, among many others (Dirzo and Miranda 1991, Terborgh and Wright 1994, Ferreira and Laurance 1997, Phillips 1997, Cascante 1998, Rao *et al*. 2001, Roldán and Simonetti 2001, Kitamura and Yumoto 2002, Dirzo et al. 2007). These interactions can be expected to be changing because lower species richness in fragmented landscapes may modify more than just forest structure and species diversity.

In Costa Rica, Premontane Tropical Moist Forest life zone is considered an endangered life zone, because only 12.8 % of its total area is protected in reserves (Nadkarni and Wheelwright 2000, Sánchez-Azofeifa *et al*. 2003). Outside reserves and national parks, this life zone is present in fragmented landscapes, which increases the conservation value of the remnants (Guindon 1997). Although the patterns of species richness and diversity are well documented in forest fragments, the effects of fragmentation on ecological interactions are poorly understood (Wright 2003, Fleury and Galetti 2006, Dirzo and Mendoza 2007, Wright *et al*. 2007). In this study I evaluated how is the mammalian seed removal in fragmented and continuous forests in this life zone.

MATERIALS AND METHODS

Study site: I did this study in Monteverde (10° 18' N, 84° 48' W), in the Cordillera de Tilarán, Costa Rica. I worked in three different forested sites: one continuous forest area at the Monteverde Biological Station (EBM, at 1460 m of elevation) directly connected to an intact expanse of 55,000 forested hectares, and two forest fragments, with 350 and 20 hectares, hereafter referred to as CAT (elevation 1250 m) and FAR (elevation 1400 m) respectively. These three sites belong to Premontane Tropical Moist Forest life zone (Tosi 1969).

All these study sites are private properties. The two forest fragments are surrounded by dairy pastures, and were fenced off more than ten years ago to prevent cattle from entering. These fragments were created 40 to 55 years ago according to the respective owners, when the environs were transformed to cattle pastures. The forests within these fragments are older and mature.

Presence and relative abundance of mammalian seed predators: I assessed the presence and relative abundance of mammalian seed-predator in the three sites from August 1999 to March 2001. To determine which small species were present, in each site I established one 70 x 70 m (0.49 Ha) trapping grid, containing 49 Sherman live traps, placed on the ground, one trap every 10 m in the grid. I baited each trap with a mixture of raw rice, oats and vanilla. I trapped once a month, three nights per site, for 16 months, during the darkest nights of each month. The sampling effort in each site was 2352 traps-night.

To evaluated the presence of larger species (more than 300g), I surveyed sites by walking two transects per month in each site, for ten months total. This consisted of walking through the forest along trails, during the morning and during early hours after dusk. I observed and recorded diurnal and nocturnal species, for a total sampling effort of 120 transect-hours. These transects were also performed on the darkest nights of each month. While walking transects I also recorded mammals tracks and identified them according to Aranda (1981) and Reid (1999).

To evaluate the relative abundance of mammalian seed predators I followed the criteria of Hayes and LaVal (1989) and Timm and LaVal (2000). I considered a given species “abundant” if it were recorded (observed and/or captured) one or more times in 80% of the visits to the site, as “common” if it were recorded in 40 to 80% of the visits, as “uncommon” if it were recorded in 10 to 40% of visits, and “rare” if it were recorded on fewer than 10% of visits. Visits includes both, trapping and walking transects.

Selection of seeds: I chose fresh seeds of four species of native trees in the Monteverde area: (1) *Ocotea valeriana* (Standley) W. Burger, its seeds are 65 mm long; (2) *O. whitei* Woodson, its seeds are 40 mm long (both species in Lauraceae); (3) *Panopsis costaricensis* Stand. (Proteaceae), its seeds are 50 mm long; and (4) *Billia colombiana* (Hippocastanaceae), its seeds are 60 mm long, length measurements from Castro (1998) and Haber *et al*. (1996). I selected these seeds species after observed them in the field with rodent teeth marks.

To test that these seeds were consumed by at least some native mammals, I offered fruits and clean seeds, according to their different fruit production periods, to different individuals of Desmarest ´s spiny pocket mouse (*Heteromys desmarestianus*), naked-footed mouse (*Peromyscus mexicanus*) and slender harvest mouse (*Reithrodontomys gracilis*) previously trapped. All mice were kept in captivity for no more than five hours, or until I observed them feeding. Water was supplied *ad libitum*. I released each rodent at the same point where it was trapped. I also observed these seeds being consumed by agoutis (*Dasyprocta puncata*), Neotropical red squirrels (*Sciurus granatensis*) and collared peccaries (*Pecari tajacu*) in the field during the study.

Seeds predation experiments: I considered all of the removed seeds as seeds that had been preyed upon. To assess differences in seed predation rates in each forest, I set up 12 plots; six plots from which mammals were excluded and six plots in which mammals had free access. Plots were arranged in a paired design, there were six paired plots in each site. Each enclosure consisted of a rectangular cage of galvanized wire mesh of 2 m x 1 m and 0.9 m in height. The squares of the mesh measured 12.7 mm x 12.7 mm and excluded all mammalian seed predators (modified from Terborgh and Wrigth 1994, and Roldán and Simonetti 2001). I also established adjacent control plots 2 m from the enclosure, placing only PVC tubes at the corners of each 1 m x 2 m rectangle. Each pair of plots (enclosure and control) were placed on relative level ground to minimize the probability that seeds would move by rolling downslope. Plots were scattered haphazardly in about 20 hectares at each site. In the forest fragments plots were located at least 50 m away from edges. At

EBM, plots were located near the Jilguero trail and the Cariblancos trail, from 30 m to 200 m away from trails. The distance between plots ranged from 200 m to 300 m.

During two annual fruiting periods, I collected ripe fruits with no visible evidence of damage from the ground and from trees, of each of the four selected species. I took fruits from nearby forest sites rather than the study sites. In the laboratory I removed fruit pulp from each seed, except for *P. costaricensis*. Seeds removed from whole fruits are common in nature, for example *Ocotea spp* cleaned seeds occur in the ground dispersed by resplendent quetzals, three-wattled bellbirds, bare-necked umbrellabirds or black guans. To avoid invertebrates – infested seeds, all the seeds were briefly placed in water container, and I discarded those seeds that floated. I then placed undamaged seeds in a line, with an individual label with numbers from 1 to 350. I then selected the seeds to placed in the field using a random numbers table. Depending on the seeds availability, I included seven or nine seeds per plot, in both enclosure and control plots. I marked experimental seeds with a vertical, semi-buried, labeled wooden spoon. I observed the seeds in each plot and counted them every other day over four weeks, or until all the seeds disappeared from their original location. I repeated this experiment for each species of seed twice, using seeds of *O. valeriana* in April and May of 2000 and April of 2001; seeds of *O. whitei* in July of 2000 and June - July of 2001; seeds of *P. costarricensis* in September 2001 and September 2002, and seeds of *B. colombiana* in October 2000 and October 2001.

Data analysis: I analyzed the effect of treatment (enclosure or free acces plots at each site) on the remainder mean number of seeds per site with analysis of variance tests, using Statgraphics 2.1 (Serrano and Vargas 1995). The proportion of seeds removed was transformed using Box-Cox better transformation (Sokal and Rohlf 2003) to fit assumptions of parametric statistics.

RESULTS

Mammalian seed predators: Altogether, I recorded 15 species of mammals considered as seed-predators (Table 1). Most species (13) were found in the continuous forest, followed by the large fragment (9 species), and the small fragment (4 species). All but one species (the collared peccary) were Rodentia. A list of all the species of mammals found, including the non seed-predators, is reported in Appendix 1. Six species, including the collared peccary, were found exclusively in the continuous forest. Only two species, the pygmy rice mouse (*Oligoryzomys fulvescens*) and the prehensile-tailed porcupine (*Coendou mexicanus*), were not recorded in continuous forest (Table 1).

Species found in two or three sites, had different relative abundances in each site. For example, Desmarest ´s spiny pocket mouse (*H. desmarestianus*) a specialized seed predator, was uncommon in the continuous forest, but was common in the large fragment, and abundant in the small fragment. In contrast, the collared peccary was common in the continuous forest, but absent in both forest fragments. The two species of mice *P. mexicanus* and *Oryzomys alfaroi*, were abundant and rare respectively where they were present (Table 1).

Fragmentation effects on seed-predation: Unexpectedly, overall seed-predation in the two forest fragments and continuous forests did not differ statistically when considering all seeds. However, there was a trend of higher seed-predation in continuous forest (F= 2.73, d.f. = 2, 42, p= 0.077; Fig. 1). Comparing both forest fragments, seed-predation was not statistically different. As expected, more seeds in control plots were preyed upon than seeds in enclosed plots. This applied to all seeds combined as well as individual species (F= 61.19, d.f. = 1, 42, p< 0.001).

Considering each seed species, trends of seed-predation in both the continuous forest and the large fragment were similar in most of the experimental periods (Fig. 2 to 5). However, seed-predation was higher in the continuous forest when compared to the small fragment in only four of the eight experimental periods. Predation of *O. valeriana* seeds was higher in the continuous forest than the small fragment only in the first fruiting season (F= 8.66 d.f. = 2, 30, p= 0.001, Fig. 2), seeds of *O. whitei* during its first studied fruiting season (F= 7.94, d.f. = 2, 30, p= 0.02, Fig. 3) and seeds of *P. costaricensis* during both studied fruiting seasons of this species (F= 16.54, d.f. = 2, 30, p< 0.001 and F= 24.13, d.f. = 2, 30, p< 0.001,

Fig. 4). Seed-predation of *P. costaricensis* was similar in the continuous forest and the large fragment.

Seed-predation of *B. colombiana* was lower in the large fragment compared to the small fragment during the two studied seasons (F= 10.99, d.f. = 2, 30, p< 0.001, and F= 16.02, d.f. = 2, 30, p< 0.001, Fig. 5).

Temporal variation of seed predation at species level: Two of the four species of seeds, *O. valeriana* and *O. whitei*, were consumed more during their respective second experimental periods (Fig. 2 and 3). However, *P. costaricensis* and *B. colombiana* seeds were consumed similarly during their respective first and second experimental periods. The seed-predation intensity was lower in the small fragment than in the other two sites in the case of *P. costaricensis*, and was higher in the small fragment than in the other two sites in the case of *B. colombiana* (Fig. 4 and 5).

DISCUSSION

This study is the first to evaluate seed-predation by mammals among fragmented and continuous Premontane Tropical Moist forests, and one of the few studies that considers a very small size (20 Ha) fragment (Galetti *et al*. 2003, Fleury and Galetti 2004). In addition to studying small size fragments, my results have shown that continuous forest and a relative large fragment (350 Ha) of forest have similar numbers of mammalian seed predators. This finding helps explain similar levels of seed-predation in both sites. Although two mammal species, the pygmy rice mouse (*O. fulvescens*) and the prehensile-tailed porcupine (*C. mexicanus*), were not recorded in the continuous forest, but were present in fragments, both have been recorded in the continuous site (Hayes and LaVal 1989, Timm and LaVal 2000). This supports the prediction that continuous forest and larger fragmented sites will have similar species composition of seed predators.

Most of the seed-predator mammals that I found were small size species (mice). Their size apears to make them more tolerant to diminished forested area (Didham et al. 1998, Chiarello 1999, Fleury and Galetti 2006). Following this perspective, the mammals not present in fragments are mainly arboreal, and/or bigger species, like pacas (*Agouti paca*) or collared peccaries (*P. tajacu*) (more examples in Appendix). With respect to seed-predation, the absence of large mammals in small fragments can be off – set by the relative higher abundance of specialized small seed predators. For example Desmarest ´s spiny pocket mouse (*H. desmarestianus*), is a specialized seed-predator: its higher abundance in Monteverde fragments likely implies higher rates of seed predation, as other studies have found in temperate ecosystems in which a specialized seed predator is present (Donoso et al. 2003) as well as in tropical rain forest (Fleury and Galetti 20006).

The higher abundance of *H. desmarestianus* in forest fragments could be caused by two phenomena. First, one is its fidelity to forested areas, not been able to use pastures or nearby houses, as the abundant rodent *P. mexicanus* does. Specially young individuals of *H. desmarestianus* may fail to disperse because they are surrounded by inimical habitats. Second, survivorship of mice may be relatively high because of the absence, or scarcity, of carnivores. As a result, small mammals such as *H. desmarestianus* suffer an effect of overcrowding without opportunities to disperse to other forest patches. This high density exacerbates their effect as seed-predators in small forest fragments (Fleury and Galetti 2006, Dirzo *et al*. 2007).

The lower abundance in the forest fragments of bigger sized rodents (*D. punctata* and *S. granatensis*) and other larger – sized mammalian predators (*P. tajacu*), seems to be strongly related with the consistent pattern of higher predation on *P. costaricensis* seeds in the continuous forest. The *P. costaricensis* seeds are large enough and may escape from predation by smaller rodents (Dirzo *et al*. 2007) more abundant in fragments. These seeds are difficult to break and mostly *D. punctata* is the able to gnaw through their hard outer ring to eat them. On the other hand, *Ocotea spp* seedshave relative soft endocarp, experienced higher predation in the fragments than *P. costaricensis* seeds.

The pattern of predation observed in *B. colombiana* seeds in the smaller fragment, contrasts strongly with the other species of seeds: predation on *B. colombiana* seeds was much higher. This result can perhaps be explained by the complete absence of adult trees of *B. colombiana* in that particular fragment. Experimental seeds of this species comprised a different and attractive food. For the other species of seed studied, experimental seeds encountered on the ground were just more of the same type of food produced by trees in each site. Seed-predators did not eat them apparently because they were already satiated by the naturally occurring seeds in that site. But the *B. colombiana* seeds in the small fragment were a novel type of food, that was attractive to at least some of the small mammals present (Janzen 1971, Wright 2003, Xiao *et al*. 2004).

Among the natural factors affecting the production and fate of seeds are climate, flower composition and behavior of visitors to flowers, herbivory, and seed dispersers (Jara 1996, Xiao *et al*. 2004). If all of these factors are changing with the time in fragmented forests, as well as the intensity of seed-predation, recruitment and reproduction of plants in these forest fragments will be difficult to predict. Long term studies information are needed to understand the fate of some plant populations in altered landscapes.

ACKNOWLEDGMENTS

I thank Luisa Moreno, Frank Joyce, Gerardo Ceballos, Rodolfo Dirzo and Ignacio Méndez for their guidance and logistical support. Two anonymous reviewers helped to improved this paper. Frank Joyce edited the English and corrected several details of the first submission. Allison Deines, Mauricio García, Edgardo Arévalo, Yuber Rodríguez Eladio Cruz and Gladys Valencia provided valuable help during the fieldwork. Thank to Marvin Hidalgo, Mariano Arguedas, Eduardo Arguedas and Franklin Arce for permissions to work in their properties. Thank to Oscar Brenes, Marvin Hidalgo, Wally VanSikle, Barbara Lewis and Johnny Rosales for financial support. The Institute of Ecology of the National Autonomous University of Mexico (UNAM), Idea Wild, Monteverde Biological Station (EBM), Organization for Tropical Studies (OTS), WWF-Central America through the Mesoamerican Biological Corridor Program (CBM), and Monteverde Conservation League (MCL) provided financial and logistical support.

Resumen: Pocos estudios han evaluado la depredación de semillas en ambientes fragmentados, en éstos la menor diversidad de especies debe estar modificando las interacciones ecológicas. Investigué la remoción de semillas por mamíferos en bosque continuo y dos fragmentos en Monteverde, Costa Rica. Registré la composición de mamíferos en cada sitio durante 16 meses y observé remoción de semillas experimentales del suelo del bosque. Utilicé semillas de cuatro especies de árboles: *Ocotea valeriana*, *Ocotea whitei*, *Panopsis costaricensis* y *Billia colombiana*, durante dos periodos anuales de fructificación cada una. Mis resultados indican una composición de depredadores de semillas similar entre el bosque continuo y el fragmento de 350 hectáreas, más diversos que el fragmento de 20 hectáreas, en el cual el especialista en semillas *Heteromys desmarestianus* fue más abundante. La depredación de semillas entre el bosque continuo y los fragmentos no fue estadísticamente diferente al considerar todas las especies de semillas, debido a la mayor abundancia de depredadores pequeños, que pudo compensar la ausencia de depredadores de talla mediana y grande que sí están presentes en bosque continuo. La depredación sobre semillas fue mayor cuando la oferta de semillas no experimentales fue menor, indicando que la saciedad de los depredadores puede estar determinando la remoción de semillas en fragmentos, más que la riqueza o abundancia de especies depredadoras.

Palabras clave: remoción de semillas, depredadores de semillas, fragmentación, saciedad de depredadores.

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TABLE 1

Seed predators abundance[1] found at each study site in Monteverde, Costa Rica.

Species	Continuous Forest	Fragment CAT	Fragment FAR	Presence evidence
Peromyscus mexicanus	A	A	A	Traps
Scotinomys teguina	C			Traps
Oryzomys albigularis	U			Traps
Oryzomys alfaroi (group)	R	R		Traps
Oligoryzomys fulvescens		R		Traps
Nyctomys sumichrasti	R			Traps
Tylomys watsoni	R			Traps
Heteromys desmarestianus	U	C	A	Traps
Reithrodontomys gracilis	C	U		Traps
Sciurus variegatoides	A	A	C	Seen
Sciurus granatensis	A	U		Seen
Coendou mexicanus		R	R	Seen
Agouti paca	U			Tracks
Dasyprocta punctata	C	U		Seen
Pecari tajacu	C			Seen/tracks

[1] Abundance: **A** = Abundant species recorded (observed and/or captured) one or more times on at least 80% of the visits to the site. **C** = Common species recorded on 40 to 80% of visits. **U** = Uncommon species recorded on 10 to 40% of visits. **R** = Rare species recorded on fewer than 10% of visits.

FIGURE LEGENDS

Fig. 1. Mean number of surviving seeds considering the four species in each study site and condition (24 plots per condition, between 6 to 9 seeds in each one). Vertical lines are standard deviations.

Fig. 2. **A)** Mean number of surviving *Ocotea valeriana* seeds in enclosures and open plots. Continuous forest (EBM) and forests fragments (CAT and FAR) in Monteverde, in April – May 2000. **B)** During April 2001. Vertical lines are standard deviations.

Fig. 3. **A)** Mean number of surviving *Ocotea whitei* seeds in enclosures and open plots. Continuous forest (EBM) and forests fragments (CAT and FAR) in Monteverde, in July 2000. **B)** During June - July 2001. Vertical lines are standard deviations.

Fig. 4. **A)** Mean number of surviving *Panopsis costaricensis* seeds in enclosures and open plots. Continuous forest (EBM) and forests fragments (CAT and FAR) in Monteverde, in September 2001. **B)** During September 2002. Vertical lines are standard deviations.

Fig. 5. **A)** Mean number of surviving *Billia colombiana* seeds in enclosures and open plots. Continuous forest (EBM) and forests fragments (CAT and FAR) in Monteverde, in October 2000. **B)** During October 2001. Vertical lines are standard deviations.

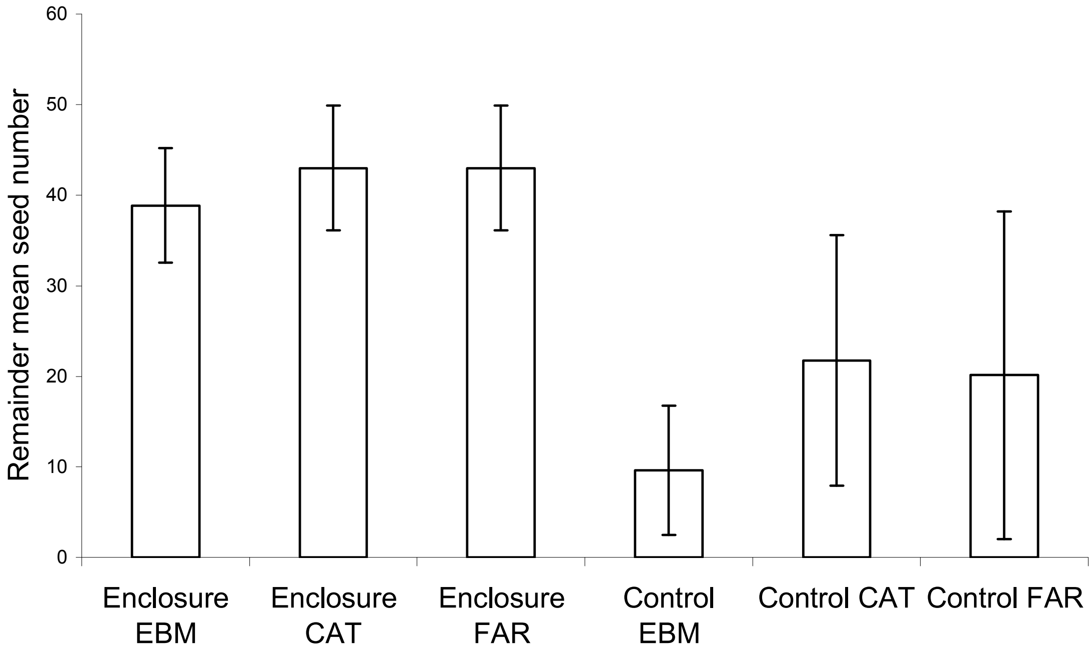
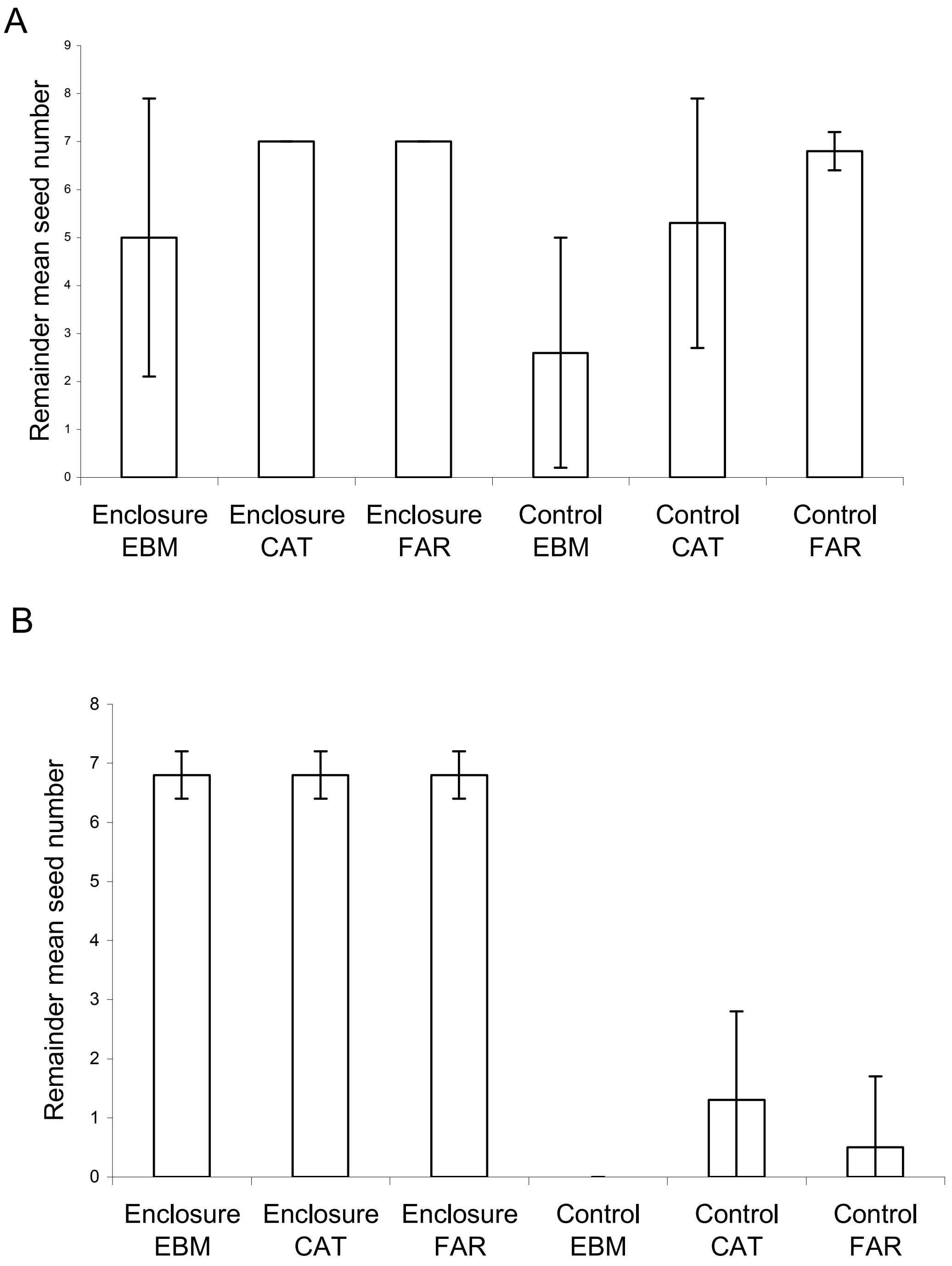


Fig 1


A
Remainder mean seed number
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1
2
3
4
5
6
7
8
9
Enclosure EBM
Enclosure CAT
Enclosure FAR
Control EBM
Control CAT
Control FAR
B
Remainder mean seed number
0
1
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6
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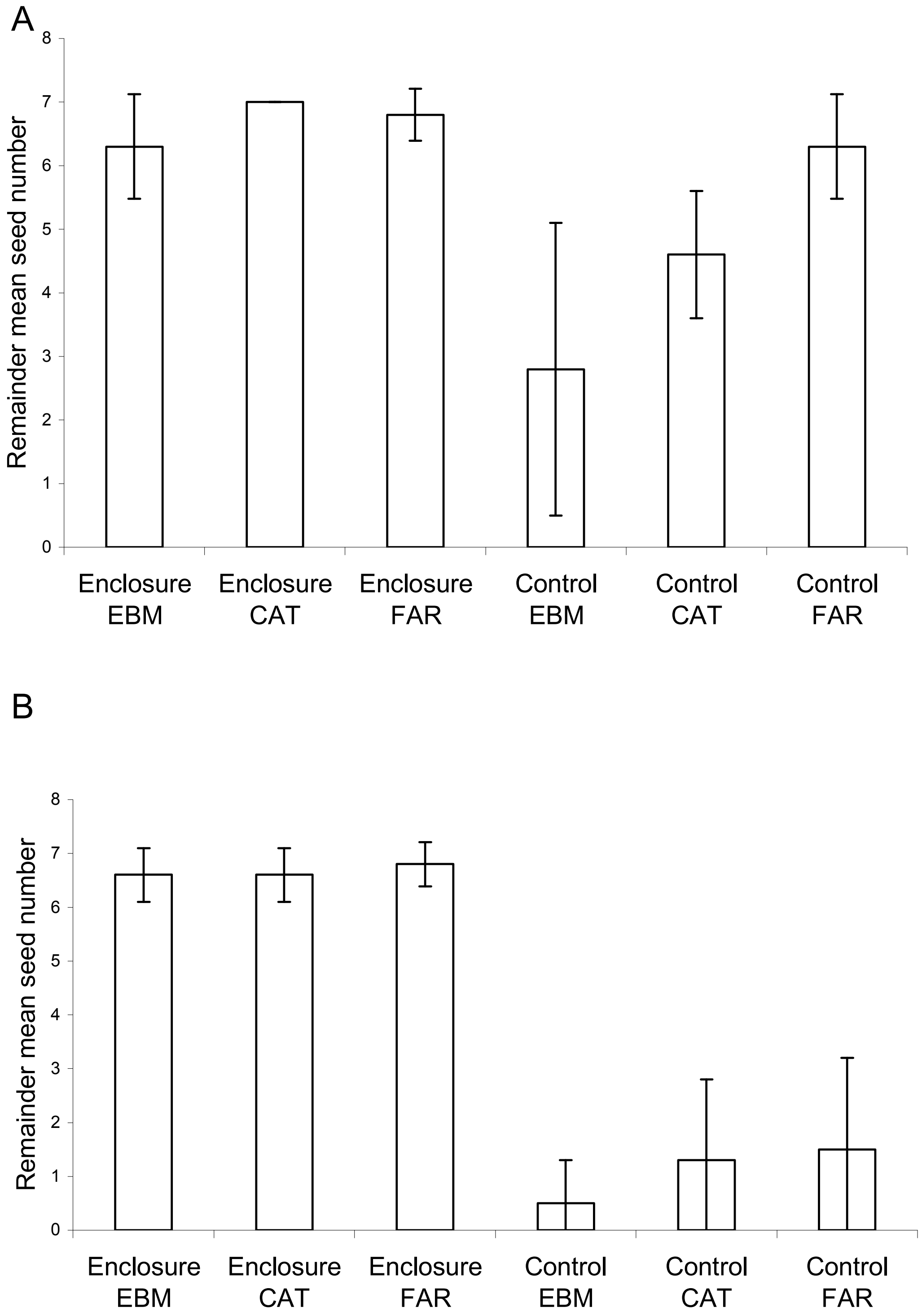
8
Enclosure EBM
Enclosure CAT
Enclosure FAR
Control EBM
Control CAT
Control FAR

Fig 2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8
Enclosure EBM
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Enclosure FAR
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Control FAR
B
Remainder mean seed number
0
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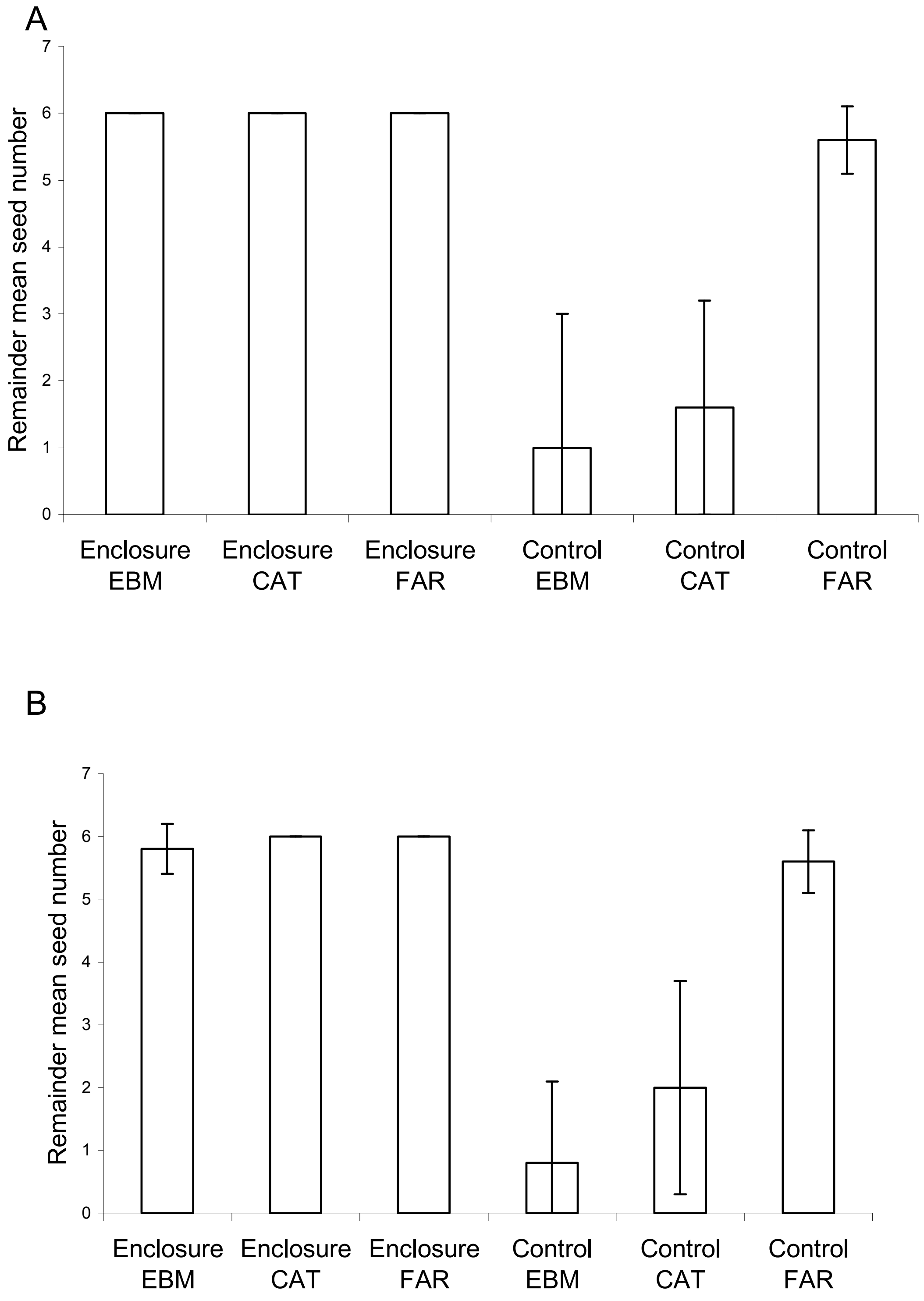
Control FAR

Fig 3



A
Remainder mean seed number
0
1
2
3
4
5
6
7
Enclosure EBM
Enclosure CAT
Enclosure FAR
Control EBM
Control CAT
Control FAR
B
Remainder mean seed number
0
1
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7
Enclosure EBM
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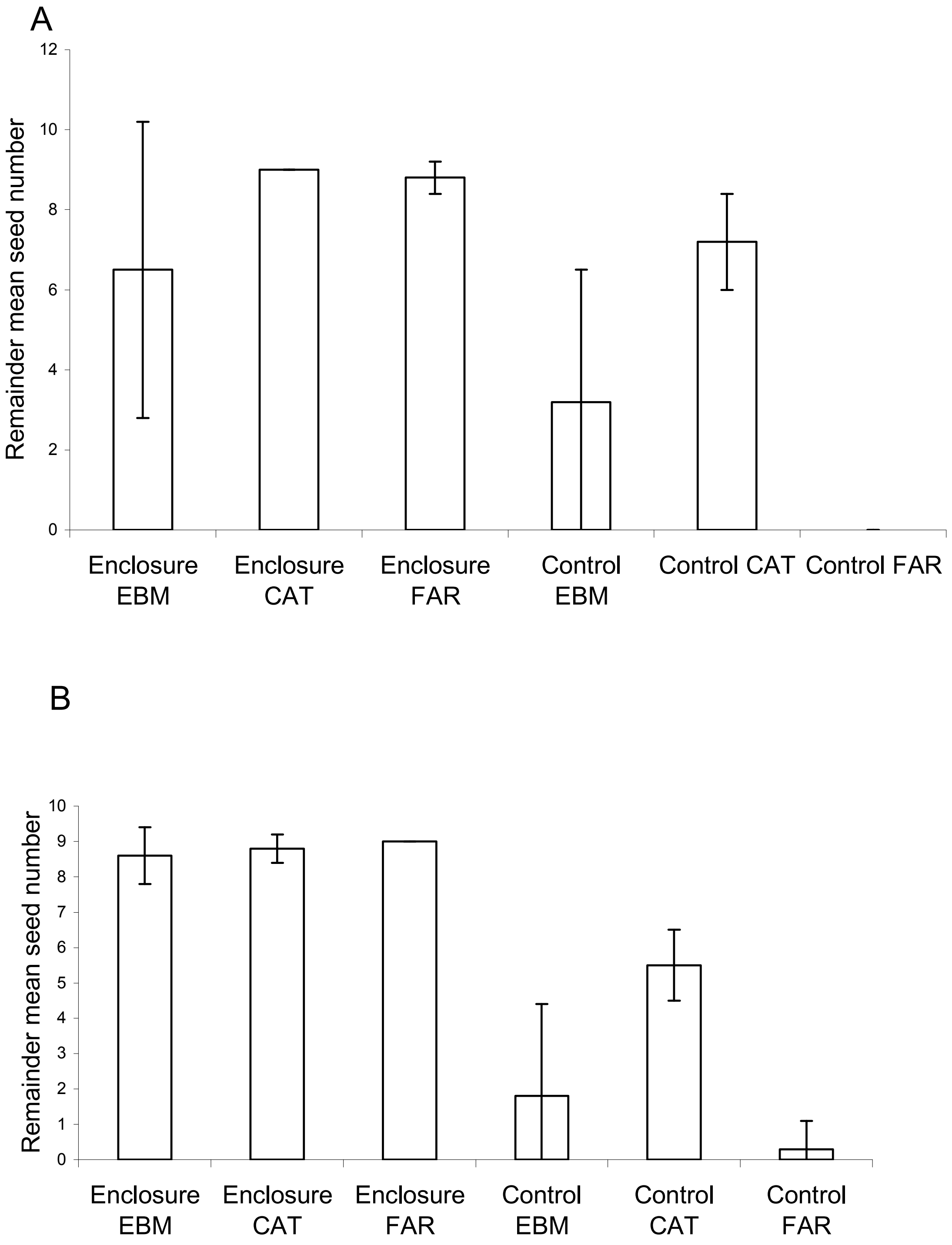
Control EBM
Control CAT
Control FAR

Fig 4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Remainder mean seed number
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2
4
6
8
10
12
Enclosure EBM
Enclosure CAT
Enclosure FAR
Control EBM
Control CAT
Control FAR
B
Remainder mean seed number
0
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2
3
4
5
6
7
8
9
10
Enclosure EBM
Enclosure CAT
Enclosure FAR
Control EBM
Control CAT
Control FAR

Fig 5

APPENDIX 1

Mammal species found in the three study sites in Monteverde, Costa Rica.

Species	Continuous forest	Large fragment CAT	Small fragment FAR	Presence evidence
Peromyscus mexicanus	x	x	x	Traps
Scotinomys teguina	x			Traps
Oryzomys albigularis	x			Traps
Oryzomys alfaroi (group)	x	x		Traps
Oligoryzomys fulvescens		x		Traps
Nyctomys sumichrasti	x			Traps
Tylomys watsoni	x			Traps
Heteromys desmarestianus	x	x	x	Traps
Reithrodontomys gracilis	x	x		Traps
Sciurus variegatoides	x	x	x	Seen
Sciurus granatensis	x	x		Seen
Coendou mexicanus		x	x	Seen
Agouti paca	x			Tracks
Dasyprocta punctata	x	x		Seen
Didelphis marsupialis	x			Seen/tracks
Choloepus hoffmani	x	x	x	Seen
Dasypus novemcintus	x			Seen/tracks
Cebus capucinus	x	x		Seen
Ateles geoffroyi	x			Seen/listened
Alouatta palliata	x			Seen
Urocyon cinereoargenteus	x	x		Seen
Nasua narica	x	x		Seen
Procyon lotor	x			Tracks
Mustela frenata	x	x	x	Seen/traps
Potos flavus	x	x		Seen/listened
Puma concolor	x			Tracks
Herpailurus yaguaroundi	x			Seen
Leopardus pardalis	x			Tracks
Leopardus wieddii	x			Tracks
Pecari tajacu	x			Seen/tracks
Mazama americana	x			Tracks

Capítulo 3:

"Contemporary defaunation reduces plant richness in forest fragments in Monteverde, Costa Rica"

Contemporary defaunation reduces plant richness in forest fragments in Monteverde, Costa Rica

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Abstract: It has been suggested that the loss of herbivorous mammals by direct human exploitation decreases the diversity of the tropical understory plants, leading to "mono-dominated seedlings carpets". The higher densities of plants might also trigger changes in other levels of the trophic structure, increasing insect herbivory, that may compensate the absence of mammalian herbivores. Here I studied if the effects of the loss of mammals (defaunation) correlates with a reduction in understory plant richness. I evaluated plant richness in continuous and fragmented mature forests. Tree species richness was similar among continuous and fragmented forests. However, understory plant richness was lower in the fragments. I also evaluated the changes in plant richness in the natural understory, using enclosed plots (defaunated conditions) and free-access plots during six years. None of the free-access plots were dominated by one species, neither in continuous forest, or in the fragments; species richness did not differ from the richness found six years earlier. However, in the continuous forest four enclosures plots were dominated by *Piper corrugatum* (Piperaceae); in the large fragment (350 hectares) only four enclosures plots were dominated by saplings of *Inga* sp. (Fabaceae); and in the small forest fragment (20 hectares) all the enclosures plots had a dominant species, *Psychotria quinquerradiata* (Rubiaceae) in four plots, *Conostegia oerstediana* (Melastomataceae) in one plot, and *Sorocea trophoides* (Moraceae) in one plot. In six years, the lack of interactions with mammals decreases understory plant diversity and this effect is exacerbated in forest fragments than in continuous forest. Apparently, higher-order interactions do not compensate for the mammalian defaunation effects on the understory plant community.

Keywords: Diversity, fragments, mammals, herbivory, Central America.

Tropical forests are among the most diverse and less studied systems (Wright 2005). These diverse areas are currently being cleared and fragmented, missing in this process their former species richness, and therefore changing also their ecological interactions, such as herbivory, frugivory, pollination, seed dispersal and seed predation among others (Terborgh and Wright 1994, Ferreira and Laurence 1997, Phillips 1997, Cascante 1998, Roldán and Simonetti 2001, Kitamura and Yumoto 2002, Galetti *et al*. 2003, Dirzo *et al*. 2007, Chinchilla 2009). Associated with smaller forested areas, it is easier for local poachers to have access to the native fauna, in particular bigger size mammals (Chiarello 1999), increasing the animal exploitation in the forests remnants (Dirzo 2000). It has been studied that one direct effect of the mammalian disappearance in the forest is the impoverishment of the understory plant richness, an idea known as the contemporary defaunation hypothesis (Dirzo and Miranda 1991, Mendoza and Dirzo 2007), according to which defaunated understories are less diverse, with higher densities of plants (Dirzo and Miranda 1991). There is experimental data suggesting a possible mechanism that might compensate the absence of mammalian herbivory: Changes in defaunated understory richness may be reverted once more to diverse conditions, by the action of higher-order interactions, unleashed by the higher densities of few species in the understory vegetation (Dirzo 2000): the "first-order" interactions between mammalian herbivores and plants, stops by the absence of the mammals (defaunation by poachers, or/and smaller forested area in fragments); then, higher densities of plants increases the plant-eating insect abundances, leading to a "second-order" of interactions between the lately higher amounts of insect herbivores and their momentary more abundant plant resources. As a result of this compensatory process, we could expect lower plant densities, and richer understories that should appear over again. But these changes in the species richness might require time. Furthermore, if secondary – orders of interactions are really mechanisms through which species richness might be restored or maintained, had not been tested in natural understory conditions for long periods of time.

In fragmented landscapes, the forest remnants can be considered defaunated sites, in which ecological interactions have been modified (Wright 2003, Wright 2005, Wright *et al*. 2007, Chinchilla 2009). Forest remnants provide interesting scenarios to test the effects of the absence of mammalian interactions in forest fragments. In this study, followed the initial propositions of Dirzo (2000), I evaluated the consequences of the contemporary defaunation on the understory plant richness in fragmented and continuous forest, asking: do the “mono-dominated seedling carpets” found in other studies occur and prevail after long periods of time? and Are there mechanisms that might compensate the lack of mammalian herbivores in the understory diversity?

MATERIALS AND METHODS

Study site: I conducted this study in Monteverde, located on the Cordillera de Tilarán in Costa Rica (10° 18' N, 84° 48' W), from August 1999 to November 2005. Haber et al. (1996) provides complete information about vegetation types in Monteverde area. I worked in five forested sites, all of them between 1150 and 1460 m elevation above the sea level: one continuous forest site at the Monteverde Biological Station (EBM, at 1460 m of elevation) directly connected to an intact area of 55,000 forested hectares, and four forest fragments, with 350, 90, 60 and 20 hectares (elevations are 1250 m, 1240 m, 1150 m, and 1400 m, respectively). The study sites belong to the Premontane Tropical Moist Forest life zone (Tosi 1969), and they are private properties. The forests within each of these sites are older and mature.

Species composition and abundance of mammals: To assess the presence and abundance of mammals in the continuous forest and in two of the forest fragments (350 hectares and 20 hectares) I established a sampling area with 49 Sherman live traps, disposed on the ground, one trap every ten meters in a grid of 7 by 7 traps, for three consecutive nights per month in each site. I baited each trap with a mixture of two parts of raw rice with one part of wet oat milk with vanilla. This was repeated once a month, for a total of 16 months, systematically on the darkest nights of each month. The sampling effort was 2352 trap nights on each site, for a total of 14,112 trap nights.

To evaluate the presence and abundance of larger mammals, every month I walked two transects on each site during a total of ten months. These consisted of two hours of slow walk through the forest, one walk during the morning and the other in the early hours after night falls, counting both diurnal and nocturnal species (a total of 240 transect-hours). These transects were carried out on the darkest nights of each month. Along these transects I recorded mammal tracks, sounds and other signs of mammal presence (Aranda 1981). In all cases, I counted only one individual per transect for each of the species recorded.

To evaluate the relative abundance of the mammalian species, I followed the criteria of Hayes and LaVal (1989) and Timm and LaVal (2000). For this study, a given species was considered "abundant" if it was recorded (captured or/and observed) one or more times in 80% of the visits to the site, as "common" if it was recorded in 40 to 80% of the visits, as "uncommon" if it was recorded in 10 to 40% of the visits, and "rare" if it was recorded on fewer than 10% of visits. Visits included both, trapping and walking transects.

Number of species of trees and understory plants: To measure the number of species of trees and understory plants, I established three 50 m x 2 m linear transects in each of the five study sites. I sampled all the trees with diameter at breast height ≥ 10.0 cm. I counted all the understory plant species in 1 m^2 plots, one plot every 10 m along the same three linear transects.

Understory plants experimental plots: To assess differences in understory plant composition under defaunated conditions, in the continuous forest and in two of the forest fragments (350 hectares and 20 hectares), I set up 12 plots at each site. Six plots from which mammals were excluded and six plots in which mammals had free access. Plots were arranged in pairs, one enclosed plot and one free-access plot. Enclosures consisted of a rectangular cage of galvanized wire mesh of 2 m x 1 m x 0.9 m in height; the squares of the mesh measured 12.7 mm x 12.7 mm (modified from Roldan and Simonetti 2001). The free – access plots were located at 2 m from each enclosed plot, placing only PVC tubes at the corners of each 1 m x 2 m rectangle. Plots were scattered haphazardly in about 20 hectares at each site. In the forest fragments, plots were located at least 50 m away from the edges. In the continuous forest, at EBM plots were located by the Jilguero and Cariblancos trails, 30 m to 200 m away from the trails. The distance among plots was at least 200 m. During six years I visited all the plots regularly (every month or every other month), to maintain them free of falling down branches, or fix them if necessary. I counted understory plant species two times, in August 1999 and six years later in November 2005, in each plot.

RESULTS

Mammalian composition: Altogether 31 species of mammals were recorded (Table 1). More species (29) were found in the continuous forest, than in the large (350 hectares) fragment with 15 species, and the small (20 hectares) fragment with six species (X^2= 16.18; d.f.= 2; p= 0.0003) . Only two species, the pygmy rice mouse (*Oligoryzomys fulvescens*) and the prehensile-tailed porcupine (*Coendou mexicanus*), were not recorded in the continuous forest.

In terms of the main diet type of the mammalian species found, in the continuous forest nine of the species were herbivorous, in the large fragment five species were herbivorous, and in the small fragment three species were herbivorous; the number of herbivorous mammals among the three sites did not differ statistically (Table 1).

Species found in the continuous forest had higher abundances than in the forest fragments, with the exception of the Desmarest´s spiny pocket mouse (*Heteromys desmarestianus*) was uncommon in the continuous forest, common in the large fragment, and abundant in the small fragment. The naked-footed mouse (*Peromyscus mexicanus*) was abundant in the three sites (Table 1).

Number of species of trees and understory plants: The number of species of trees did not differ significantly among the five study sites (Fig. 1). However, the number of species of plants in the understory was higher in the continuous forest than in the fragments (X^2 = 15.45; d.f. = 4; P = 0.004, Fig. 1).

Understory experimental plots: At the beginning of the experimental plots, in August 1999, the number of species of plants in all of the plots was higher in the continuous forest than in the fragments (F= 16.47; d.f.= 5, 30; $p < 0.0001$, Fig. 2). After six years, in November 2005, overall species richness was higher in the free – access plots than in the enclosure plots in both types of forest, continuous and fragmented (Fig 3). But the species richness in the continuous forest enclosed plots did not differ statistically when comparing with the free – access plots of the fragments, and these were richer than the enclosed plots in the two fragments (F= 27.93; d.f.= 5, 30; $p < 0.0001$, Fig. 3).

At the end of the experimental period, none of the free-access plots were dominated by one single species in both types of forest, continuous and fragmented. In the continuous forest four enclosures plots showed one dominant species: *Piper corrugatum* (*sensu lato*) (Piperaceae). In the large forest fragment (350 hectares), four enclosure plots showed dominance of saplings of *Inga* spp (Fabaceae). In the small forest fragment (20 hectares) all of the enclosed plots had a dominant species: *Psychotria quinquerradiata* (Rubiaceae) was dominant in four enclosed plots, *Conostegia oerstediana* (Melastomataceae) was dominant in one enclosed plot, and *Sorocea trophoides* (Moraceae) dominated the other enclosed plot.

DISCUSSION

Results have shown that continuous forest is richer in species of mammals. Although two species, the prehensile-tailed porcupine (*C. mexicanus*) and the pygmy rice mouse (*O. fulvescens*), were not recorded in the continuous forest, but were present in the fragments, both species have been recorded in the continuous forest site (Timm and LaVal 2000), supporting the expectation that continuous forest still being richer than forest remnants. However, the number of herbivorous mammals did not differ statistically among the three sites. This finding helps understand mammalian herbivory observed in forest fragments, the species of mammals absent in the fragments were mostly carnivores rather than herbivorous types. Two of these herbivores mammals found in both forest fragments were the prehensile-tailed porcupine, and the Hoffman´s two-toed sloth (*Choloepus hoffmani*), which are very inconspicuous and nocturnal animals.

It has been suggested that mammalian defaunation excludes from forested sites mostly medium/large sized herbivores, but does not affect small sized species (Mendoza and Dirzo 2007, Wright *et al*. 2007, Wright 2003, Dirzo 2000). However, it is important to add that the rare and inconspicuous species might be also less susceptible to disappear by contemporary defaunation. This may be the case of the prehensile-tailed porcupine and the Hoffman´s two-toed sloth found in the fragments, both species are medium/large important herbivorous. They are also followed by local poachers.

Although prehensile-tailed porcupines and Hoffman´s two-toed sloth were “rare” in the forest fragments, recorded on fewer than 10% of the visitis to these sites, according with the system by Hayes and LaVal (1989), it is important to notice that forest remnants are smaller forested sites than continuous forest, then, it is feasible to consider that rare mammalian herbivores present in small forested areas, could have higher impact in the vegetation than they could have in the continuous forest. This pattern must be evaluated; we could expect that the absence of several mammalian species in fragments can be off-set by the higher impact on the vegetation of the rare species of mammals potentially present in defaunated sites.

The omnivorous gray fox (*Urocyon cinereoargenteus*) is also a species interesting to discuss. Gray foxes have been observed in Monteverde eating small seedlings and fresh plant sprouts, in forested areas and open pastures (personal observations). In this study it was rare, present in the continuous forest and the large (350 hectares) fragment. *U. cinereoargenteus* is able to arrive to fragments from surrounded areas, as important seed dispersers, as well as facultative herbivores, should be considered as one of the mammalian species maintaining ecological interactions with plants in forest fragments.

The number of species of trees in continuous forest and fragments was similar, but the number of species of understory plants was lower in the forest fragments. Being forest remnants of smaller area, it is expected to find less species, but it is interesting to notice that the change in species richness have been observed in the understory level, but not yet in the canopy level of the forest. The tree richness could be considered as a reflex of the continuous situation where actual forest fragments were in the past. These forest fragments in Monteverde were created 40 to 55 years ago, according to the respective land owners, when environs were changed to cattle pastures. This period of time might be not long enough to observe changes in the tree species richness in the fragments.

The important occurrence of mammalian herbivores in continuous forest and fragments seems to be strongly related with the consistent pattern of lower number of species of plants in the enclosed plots. While in the free-access plots the interactions between plants and mammalian herbivores maintain higher species richness, while enclosed plots were missing these interactions, allowing some species of plants to take over the space (Dirzo and Miranda 1991). In the long run, the dominance of some species of plants in the enclosure plots prevails and decreases species richness. In this study there were not obvious higher – order interactions that could compensate the lack of interactions between plants and mammals in the enclosed plots.

The dominant plants in enclosed plots were species of different families, rather than only one species, as found by Dirzo and Miranda (1991). It is interesting to evaluate why some species become dominant and others do not. Besides the differential seed predation based on the seed size, proposed by Mendoza and Dirzo (2007), other particular circumstances such as soil type, seed bank composition or differential dispersion mechanisms could contribute to determine which species will dominant in mammalian defaunated conditions.

ACKNOWLEDGMENTS

An earlier version of this paper was greatly improved by Rodolfo Dirzo. I thank Gerardo Ceballos, Igancio Méndez and Rodolfo Dirzo for their guidance and logistical support. Luisa Moreno, Frank Joyce, Allison Deines, Mauricio García, Edgardo Arévalo, Joaquín Sánchez, Alfredo Cascante, Armando Estrada, Yuber Rodríguez and Gladys Valencia provided valuable help. Thank to Mariano Arguedas, Eduardo Arguedas and Franklin Arce for permissions to work in their properties. Thank to Oscar Brenes, Marvin Hidalgo, Wally VanSikle, Barbara Lewis and Johnny Rosales for logistical support. The Institute of Ecology of the National Autonomous University of Mexico (UNAM), Idea Wild, Monteverde Biological Station (EBM), Organization for Tropical Studies (OTS), WWF-Central America through the Mesoamerican Biological Corridor Program (CBM), and Monteverde Conservation League (MCL) provided financial and logistical support.

Resumen: Se ha sugerido que la pérdida de mamíferos herbívoros debida a su explotación directa por cazadores locales, disminuye la diversidad de plantas en los sotobosques tropicales, produciendo “alfombras mono-específicas de plántulas”. Esta mayor densidad de plantas podría también desencadenar más cambios en otros niveles de la estructura trófica, aumentando la herbivoría por insectos, lo que podría compensar la ausencia de mamíferos herbívoros, evitando la disminución en la riqueza de especies. Estudié si los efectos de la ausencia de mamíferos (defaunación) sobre la riqueza de plantas del sotobosque se mantienen en el tiempo. Evalué la riqueza de plantas en bosque continuo y fragmentado. La riqueza de especies de árboles fue similar en ambos tipos de bosque. Sin embargo, la riqueza de plantas del sotobosque fue menor en los fragmentos. También evalué los cambios en la riqueza del sotobosque en parcelas protegidas de los mamíferos (bajo exclusión condición defaunada) y parcelas de libre acceso (control) durante seis años. Ninguna de las parcelas con libre acceso presentó dominancia de alguna especie de planta, ni en el bosque continuo ni en los fragmentos; la riqueza de especies no fue diferente a la riqueza encontrada seis años antes. Sin embargo, en el bosque continuo cuatro parcelas bajo exclusión fueron dominadas por la especie *Piper corrugatum* (Piperaceae); en el fragmento más grande (350 hectáreas) solo cuatro parcelas bajo exclusión fueron dominadas por plántulas de *Inga* sp (Fabaceae); en el fragmento pequeño (20 hectáreas) todas las parcelas bajo exclusión fueron dominadas por *Psychotria quinquerradiata* (Rubiaceae) en cuatro parcelas, *Conostegia oerstediana* (Melastomataceae) en una parcela y *Sorocea trophoides* (Moraceae) en otra parcela. En seis años, la ausencia de interacciones con mamíferos disminuye la diversidad de plantas en el sotobosque con mayor severidad en los fragmentos de bosque que en el bosque continuo. Aparentemente, no ocurren interacciones de segundo orden que compensen los efectos de la ausencia de mamíferos en el sotobosque.

Palabras clave: Riqueza de plantas, paisaje fragmentado, defaunación contemporánea.

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Table 1. Mammals abundance[1] found at each study site in Monteverde, Costa Rica.

Species	Presence evidence	Continuous forest	Fragment (350 hectares)	Fragment (20 hectares)
Peromyscus mexicanus [2]	Traps	A	A	A
Scotinomys teguina	Traps	C		
Oryzomys albigularis	Traps	U		
Oryzomys alfaroi	Traps	R	R	
Oligoryzomys fulvescens	Traps		R	
Nyctomys sumichrasti	Traps	R		
Tylomys watsoni	Traps	R		
Heteromys desmarestianus	Traps	U	C	A
Reithrodontomys gracilis	Traps	C	U	
Didelphis marsupialis [2]	Seen	U		
Choloepus hoffmani [2]	Seen	C	R	R
Dasypus novemcintus	Seen/tracks	A		
Cebus capucinus [2]	Seen	C	U	
Ateles geoffroyi [2]	Seen	R		
Alouatta palliate [2]	Seen	C		
Sciurus variegatoides	Seen	A	A	C
Sciurus granatensis	Seen	A	U	
Coendou mexicanus [2]	Seen		R	R
Agouti paca	Seen/tracks	U		
Dasyprocta punctata	Seen	C	U	
Urocyon cinereoargenteus [2]	Seen	R	R	
Nasua narica	Seen	U	R	
Procyon lotor	Seen	R		
Mustela frenata	Traps	R	R	R
Potos flavus	Seen	R	R	
Puma concolor	Tracks	R		
Herpailurus yaguaroundi	Seen/tracks	R		
Leopardus pardalis	Tracks	R		
Leopardus wiedii	Tracks	R		
Pecari tajacu [2]	Seen/tracks	C		
Mazama americana [2]	Seen/tracks	R		

[1] Abundance: **A** = Abundant species recorded (observed and/or captured) one or more times on at least 80% of the visits to the site. **C** = Common species recorded on 40 – 80% of visits. **U** = Uncommon species recorded on 10 – 40% of visits. **R** = Rare species recorded on fewer than 10% of visits.

[2] Species with herbivorous diet.

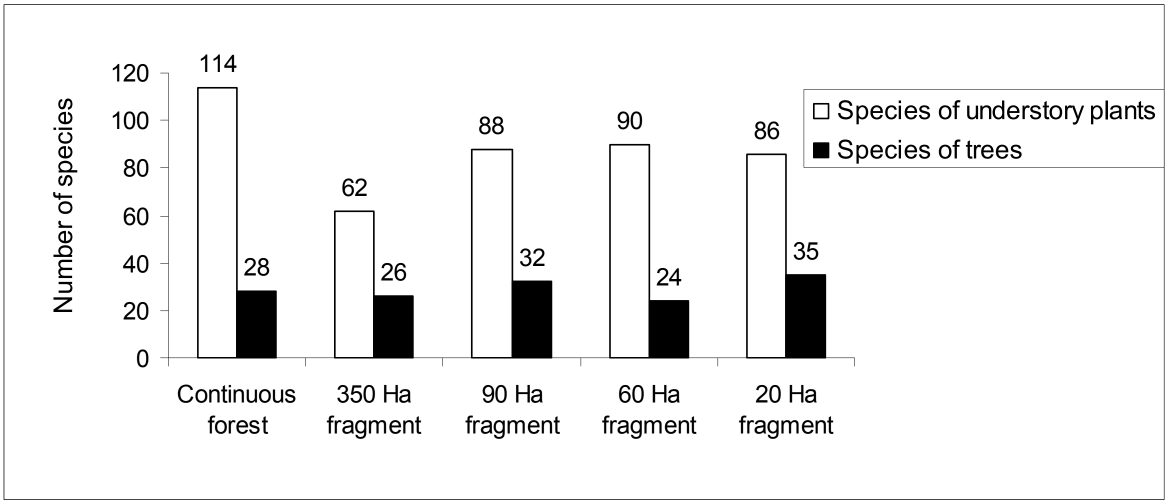

Figure 1. Number of species of trees in 300 m^2, and number of species of understory plants in 30 m^2, at each study site.

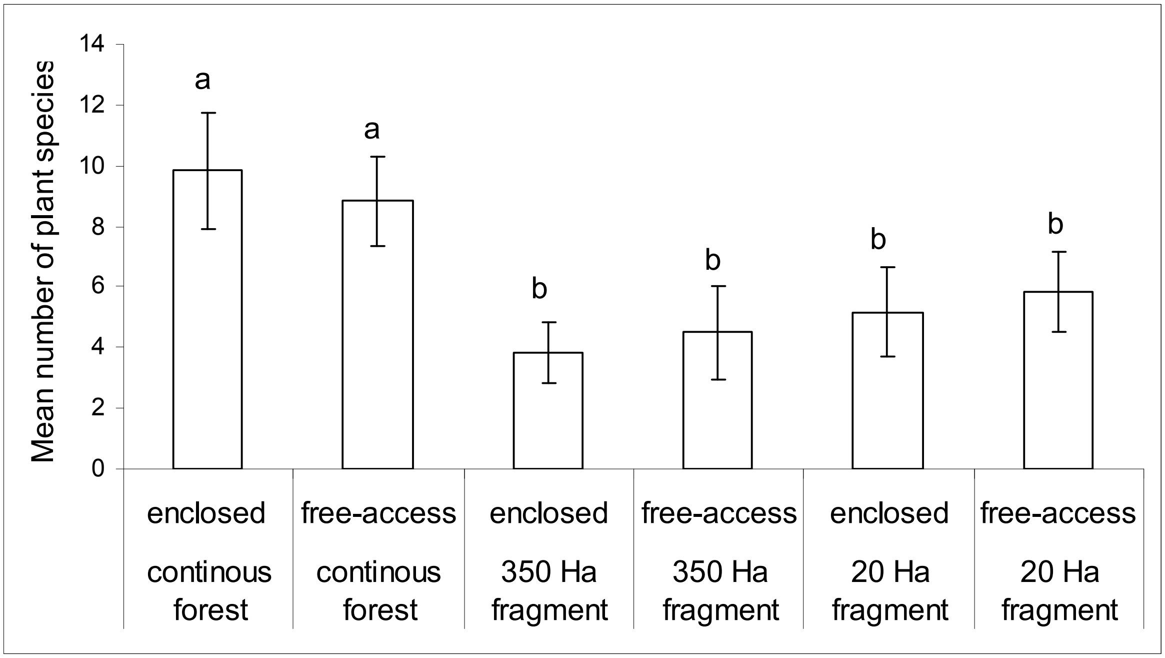

Figure 2. Mean number of species of plants in enclosed and animal free – access plots (n = 12 per site) in August 1999 starting the experiment. Different letters denote statistically different groups ($p < 0.05$, ANOVA test, Tukey post hoc comparisons). Vertical lines are standard deviations.

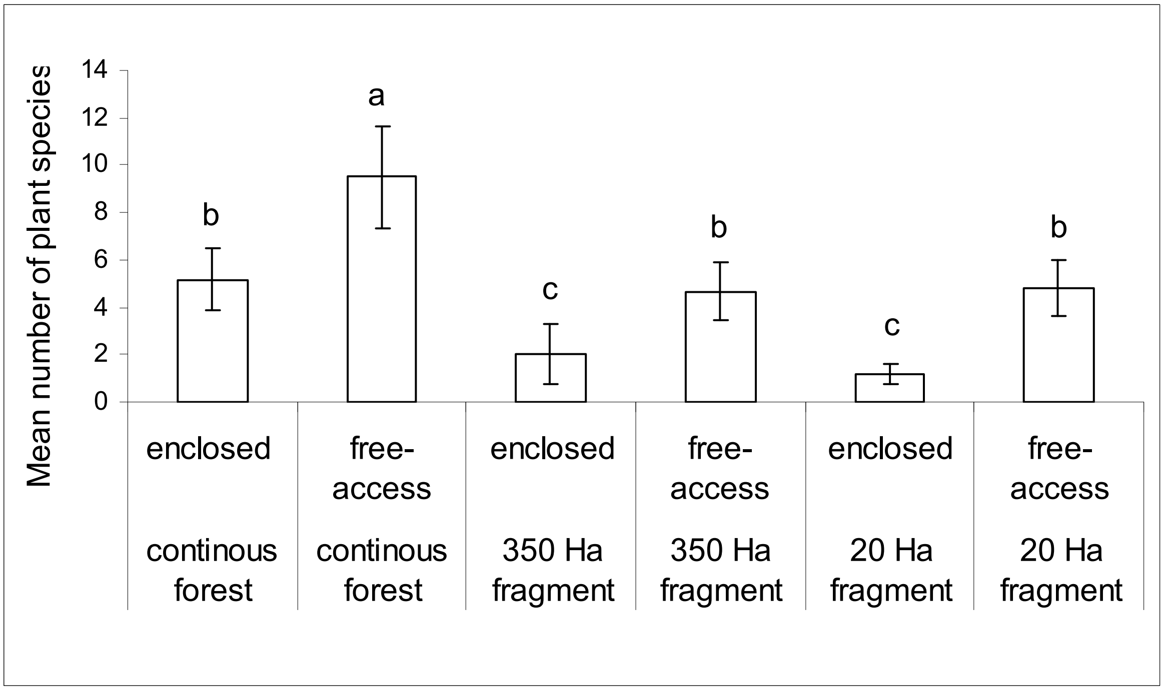

Figure 3. Mean number of species of plants in enclosed and animal free – access plots (n = 12 per site) in November 2005 at the end of the experiment after six years. Different letters denote statistically different groups ($p < 0.05$, ANOVA test, Tukey post hoc comparisons). Vertical lines are standard deviations.

DISCUSIÓN GENERAL

Como se desprende de los capítulos anteriores, la fragmentación del bosque y la cacería ha tenido efectos negativos en la riqueza de especies de mamíferos en la región de Monteverde, pues los fragmentos mantienen menos especies que el bosque continuo. Sin embargo, en la zona todavía se encuentran casi todas las especies nativas conocidas históricamente. Solo han sido extirpadas del área dos especies: el hormiguero gigante (*Myrmecophaga tridactyla*) y el chancho de monte (*Tayassu pecary*). Otras especies como el mono colorado (*Ateles geoffroyi*) y el jaguar (*Panthera onca*) son ahora muy raras, y solo se pueden encontrar en el bosque continuo, pero estas especies podrían desaparecer de la zona de Monteverde en un futuro cercano. Sin embargo en los fragmentos de bosque, especialmente los de mayor tamaño, se encuentran al menos el 50% del total de especies de mamíferos nativos de la zona. En este sentido los fragmentos de bosque en Monteverde resultaron ser valiosos para la conservación de los mamíferos. De cualquier modo, el bosque continuo resultó tener un valor único, al mantener la gran mayoría de especies nativas de la región.

La vegetación del sotobosque es menos rica en especies en los fragmentos que en el bosque continuo. Sin embargo, el número de especies de árboles en los fragmentos de bosque resultó ser igual al número de especies de árboles del bosque continuo. Posiblemente el tiempo transcurrido desde que se crearon estos fragmentos (55 años) es relativamente corto para poder observar cambios en la composición de árboles. Sin embargo, se puede esperar que esa composición de especies de árboles en los fragmentos también cambie con el tiempo, hacia una menor riqueza de especies, pues en el sotobosque de la actualidad, que es menos rico, están presentes los árboles del futuro dosel.

En este estudio, durante los seis años que permanecieron las parcelas experimentales en el campo, no ocurrieron mecanismos de compensación que mantuvieran o restauraran la diversidad de plantas del sotobosque en los fragmentos defaunados, ni tampoco en las parcelas bajo exclusión (condiciones de defaunación experimental). La riqueza de plantas dentro de parcelas bajo exclusión disminuyó más que la riqueza de las parcelas abiertas con libre acceso para los mamíferos. Existen especies de mamíferos herbívoros muy poco abundantes, de hábitos nocturnos, como el puercoespín (*Coendou mexicanus*) y el perezoso de dos dedos (*Choloepus hoffmani*), que pueden estar escapando de la cacería por ser difíciles de encontrar, y que tampoco requieren de un área muy extensa de bosque; otras especies son capaces de llegar hasta los fragmentos, desde otros sitios con bosque, como el zorro gris (*Urocyon cinereoargenteus*), que es un omnívoro – herbívoro facultativo. Estos tres ejemplos, son de especies que podrían estar manteniendo cierto nivel de herbivoría sobre la vegetación de los fragmentos. Su efecto podría estar influyendo en la mayor riqueza de plantas encontrada dentro de las parcelas con libre acceso de los fragmentos, en contraste con la menor riqueza de plantas en las parcelas bajo exclusión. Otras especies también podrían ser capaces de llegar a los fragmentos desde sitios boscosos, como murciélagos (Chiroptera, los cuales no fueron evaluados en este estudio), mapaches (*Procyon lotor*) y pizotes (*Nasua nasua*), que representan llegada y salida de semillas, y que podría permitir que, en cierta medida, en los fragmentos continúen ocurriendo interacciones entre plantas y animales.

Por otra parte, la riqueza de pequeños roedores fue menor en los fragmentos que en el bosque continuo, pero la abundancia de las especies que se encuentran en los fragmentos fue mucho mayor. Por ejemplo, *Heteromys desmarestianus*, que es un importante granívoro del suelo del bosque, presentó una abundancia de 4 individuos por hectárea en el bosque continuo, y más de 20 individuos en la misma área en bosques fragmentados. Es necesario evaluar si la mayor densidad de granívoros de talla pequeña podría compensar la menor cantidad de especies de mayor tamaño, haciendo que la depredación de semillas sobre las cuatro especies de árboles evaluadas, sea similar entre los fragmentos y el bosque continuo.

La información proveniente de estudios de varios años, aunque puede seguir siendo parcial, por ejemplo, un cambio significativo en la riqueza de árboles en los fragmentos de bosque de Monteverde requiere más de 50 años, es sin embargo información necesaria para entender el curso temporal de los efectos de la fragmentación, y contar con mayor información al conservar las poblaciones nativas que aún se mantienen en paisajes fragmentados.

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