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Biología reproductiva de plantas arbóreas en un ambiente fragmentado: Un análisis de las consecuencias de la fragmentación sobre el éxito reproductivo y la diversidad genética en *Astrocaryum mexicanum* Liebm. en Los Tuxtlas, Veracruz, México

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RESUMEN

Las selvas tropicales húmedas ocupan ~7% de la superficie terrestre, y albergan más de la mitad de todas las especies del planeta. Sin embargo, a pesar de ser el ecosistema con mayor riqueza biológica, también es el que presenta las mayores tasas de deforestación y fragmentación a nivel global, constituyendo uno de los cambios globales de mayor impacto sobre la biodiversidad. En la década de los 80´s América tropical perdió 74 millones de hectáreas de selva a una tasa de deforestación de 0.75% anual. Como consecuencia de ello surgen paisajes altamente modificados, compuestos de “islas” de vegetación original, inmersos en una matriz de vegetación altamente contrastante. A este proceso se le conoce como fragmentación del hábitat. En el sureste de México, en Los Tuxtlas, entre los años de 1979 a 1986 la cubierta vegetal disminuyó un 56%, lo que implica que el total de la selva original se había reducido a un 84%. Actualmente la fragmentación del hábitat en la región ha generado más de 1000 fragmentos con tamaños menores a 10 ha. El presente estudio analizó como la fragmentación afecta: i) la riqueza y composición florística en fragmentos de selva; ii) como se afecta la abundancia de una especie típica de selva madura (*Astrocaryum mexicanum*, Arecaceae) en ambientes que difieren en su estado de conservación, así como iii) el efecto de la fragmentación sobre la abundancia y diversidad de visitantes florales y polinizadores y el impacto sobre el éxito reproductivo femenino. Se encontró que la fragmentación afecta la riqueza, composición y similitud florística en seis fragmentos de tamaño contrastante (ámbito de 2-700 ha). Cuando se incluyeron plantas chicas ($\leq$ 1cm DAP) (plantas recién reclutadas) se detectó una disminución en la riqueza de especies en los fragmentos chicos. Asimismo se apreció un cambio significativo en la composición de especies: fragmentos chicos tuvieron ensambles distintos a los fragmentos grandes, esta diferencia fue debido a la presencia de especies pioneras. Se detectaron cambios en las espcies con diferentes estrategias de crecimiento (pioneras y tolerantes). Las primeras estuvieron sobre representadas en los fragmentos más chicos, mientras que las últimas incrementaron en los fragmentos grandes. Sin embargo, estos efectos desaparecen cuando se incluyen plantas grandes, las cuales estaban presentes antes de la fragmentación, esto podría indicar un efecto negativo en el reclutamiento en fragmentos chicos. En segundo lugar, utilizando tres paisajes con diferente estado de conservación se determino como era afectada la abundancia de una especie de selva madura: *A. mexicanum*. Se encontró que los sitios más chicos, aislados y con formas más irregulares tuvieron densidades más bajas de *A.*

mexicanum, probablemente debido a cambios en las condiciones ambientales en las orillas de los fragmentos, modificando la dinámica poblacional natural de la palma en estudio. El impacto de la fragmentación sobre la polinización mostró efectos negativos, disminuyendo los polinizadores en los fragmentos chicos, así como los visitantes florales en global, sin embargo no se detectaron efectos en el éxito reproductivo, muy probablemente debido a que si bien la cantidad de polinizadores disminuyen, estos son suficientes para fecundar las flores de *A. mexicanum*. Esto marca la pauta para llevar cabo estudios encaminados a determinar las consecuencias sobre la estructura genética de la especie en estudio.

La dificultad de predicción de las consecuencias de la fragmentación sobre las poblaciones de plantas parecería ser idiosincrática y se requiere de estudios que contemplen el efecto temporal (largo plazo) y metodologías comparables, asimismo la incorporación de más estudios con grupos de plantas y animales que han permanecido practicamente ignorados, como son las palmas. Estos estudios nos permitirán un mejor entendimiento de las consecuencias de la fragmentación del hábitat en los ecosistemas tropicales, además de ayudarnos a elaborar estrategias de conservación más eficientes en las áreas naturales remanentes.

ABSTRACT

The tropical rain forest have ~7% of the land cover and concentrate the major biodiversity in the earth. However the current rates of land use and cover change leading to deforestation and fragmentation of natural ecosystems has been recognized as one of the most pervasive global environmental changes. Currently, the predominant spatial configuration of tropical landscapes is that of an archipelago of vegetation remnants of different size immersed in a sea of transformed terrains consisting of agricultural fields, cattle grasslands, plantations or other human-dominated systems. In the first chapter I report changes in several plant diversity metrics associated to fragmentation in a Mexican rainforest. We examined richness; floristic composition and similarity as well as and richness/abundance of mature-forest and light-demanding plants, considering individuals of different size-categories across a range of fragment sizes and continuous forest. When we included small, recently recruited plants in the sample, we detected a linear decline in species richness, with a decrease of about 22% from continuous forest to the smallest fragment after 30 years from excision. We found a significant changes in species composition: small fragments had distinguishable assemblages compared to continuous forest. There was a shift in the relative representation of mature-forest and light-demanding species: the former decreased and the latter became overrepresented in small fragments. All these effects disappeared when considering the largest plants, which were present prior to fragmentation. In the second chapter I specifically the impact of forest fragmentation on a typical species of mature forest, *Astrocaryum mexicanum* in a wide landscape in the same region in Los Tuxtlas. I found that fragmentation affected the population size of *A. mexicanum*, with the smaller, most isolated and irregular forest fragments showing the lower number of individuals. The importance value index of *A. mexicanum* was greater in the most conserved landscape. Furthermore, palm density was positively correlated with species richness, density and basal area of old-growth

forest species, but negatively correlated with richness of secondary forest species. Overall, the strong decline in population size of adult reproductive palms may affect the regeneration and genetic diversity of this species increasing its probability of extinction. Finally, I evaluated the impact of fragmentation on a biological process (pollination) and the consequences on the reproductive success. Pollinator abundance was negatively affected by fragmentation, with a 4.2-fold average difference between small (< 35 ha) and large (114-700 ha) fragments. However, fruit set was relatively high (≥ 0.7) and not affected by fragmentation during three reproductive seasons. This could be explained because small fragments retained remarkably high numbers of pollinators (1191.4/inflorescence on average) and the high abundance of palms (and flowers) in fragments. Further research is needed, however, to assess if fragmentation restricts pollinator movements to plants within the fragments, leading to a reduction in genetic variation of the progeny present in forest remnants.

Our findings confirm, one the one hand, that fragmentation impacts tropical biodiversity and that the effect is differential and, on the other, that the remaining landscape retains a fraction of the floristic diversity from which restoration can be attempted. Finally is necessary more studies in other groups of plants and animals, include others biological processes such as dispersal of seeds (evaluating pre and post dispersal predation) and evaluate the consequences on genetic diversity of plants in the fragmented landscape.

INTRODUCCION GENERAL

a) La fragmentación tropical

Aunque las selvas tropicales húmedas ocupan tan sólo un 7% de la superficie terrestre, albergan más de la mitad de todas las especies del planeta (Wilson 1988). Por ejemplo, se tienen registros de 473 especies de árboles en una hectárea en la Amazonia Ecuatoriana (únicamente considerando individuos con un diámetro a la altura del pecho $\geq$ de 10 cm) (Valencia *et al.* 1994). En México para el área de la selva Lacandona se tienen registros de 3,400 especies de plantas vasculares, especificamente para la región de Chajul se han descrito 392 especies leñosas (194 especies arbóreas) (Martínez *et al*. 1994). Para el caso particular de la Estación de Biología Tropical "Los Tuxtlas", perteneciente a la UNAM, se tienen registros de 943 especies de plantas (545 géneros y 137 familias) de las cuales 278 especies son árboles lo que constituye el 31.7% de la flora dentro de la Estación Biológica (Ibarra-Manríquez & Sinaca 1995, Ibarra-Manríquez *et al.* 1997). Por otra parte, entre los insectos se tienen registros que en una sola especie de árbol en Panamá se colectaron 1200 especies de escarabajos (Erwin 1982). En un trabajo más reciente Ellwood y Foster 2004 hicieron una estimación de 1,160,000 invertebrados por hectárea asociados a una especie de helecho epífito (*Asplenium nidus*) en Borneo. Sin embargo, a pesar de ser la selva tropical húmeda el ecosistema con mayor riqueza biológica, también es el que presenta las mayores tasas de deforestación y fragmentación a nivel global, constituyendo uno de los factores de cambio global de mayor impacto sobre la biodiversidad (Orians *et al.* 1995, Sala *et al.* 1999, Myers *et al*. 2000, Dirzo & Raven 2003, Souza 2006).

En el año 2000 se estimó que existían en el planeta alrededor de 1172 millones de hectáreas de selvas tropicales, de las cuales 56%, 19% y 26% a corresponden a América, Africa y Asia Tropical, respectivamente (FAO 2001, Achard *et al*. 2003). Los patrones de uso de la tierra que impulsan la destrucción de estas selvas tropicales son principalmente la deforestación y la consecuente fragmentación de los hábitats naturales, que para el caso de los trópicos se debe básicamente a la conversión a potreros para la ganadería extensiva, la apertura de terrenos agrícolas y, en menor escala, la explotación forestal comercial masiva (Noble & Dirzo 1997, Lewis 2006). Entre los años 1981 a 1990 en la América tropical, en donde se ubica el área de interés del presente estudio, la selva perdió 74 millones de hectáreas de selva a una tasa de deforestación de 0.75% anual (Withmore 1997). Como consecuencia de ello surgen paisajes altamente modificados, compuestos de “islas” de vegetación original, inmersos en una matriz de vegetación altamente contrastante. A este proceso se le conoce como fragmentación del hábitat (Laurance & Bierregaard 1997). Un ejemplo muy claro lo podemos apreciar en la zona de “Los Tuxtlas” (Veracruz, México). En esta área se evaluaron las tasas de pérdida de cubierta vegetal en tres periodos de tiempo (1967, 1976 y 1986), mostrando que durante los 20 años que comprendió el estudio, la cubierta vegetal disminuyó un 56%, lo que implica que el total de la selva original se había reducido a un 84% hacia 1986 (Dirzo & García, 1992), trayendo consigo una notable fragmentación de la selva remanente. Recientemente Mendoza *et al*. (2005) llevaron a cabo un detallado análisis cuantitativo de la fragmentación en la región de Los Tuxtlas, encontrando que en 2005, dentro del ámbito de tamaños de fragmentos de la zona (0.5 a 9,356 ha) más de 1000 fragmentos presentan un área $\leq$ de 10 ha.

Las consecuencias directas de la deforestación y subsecuentemente fragmentación del hábitat son: i) disminución del área remanente de selva e ii) incremento en el aislamiento de los fragmentos. La disminución del área genera a su vez la aparición del efecto de borde, el cual puede originar cambios en los factores abióticos en las orillas de los fragmentos así como en fragmentos de tamaño pequeño, p. ej., modificando la temperatura, húmedad del aire y suelo, además de favorecer la llegada de especies exóticas o la invasión de patógenos o enfermedades, lo cual puede provocar también disminución en los tamaños poblaciones (Murcia 1996) (Figura 1).

b) Efectos ecológicos de la fragmentación

En la mayoría de los casos la reducción drástica del área de hábitat puede llevar por sí sola a la pérdida directa de especies. Por otro lado, el aislamiento de los fragmentos de selva produce una subdivisión de las poblaciones originales, con lo cual se generan reducciones en los tamaños poblacionales, modificando procesos biológicos y ecológicos. La Figura 1 presenta el marco conceptual que guía la presente tesis, enfatizando algunas de las posibles consecuencias de la deforestación y fragmentación del habitat sobre la pérdida de especies, en términos del impacto sobre un proceso biológico: la polinización y sus efectos sobre el éxito reproductivo, y las posibles consecuencias teóricas sobre la estructura genética de poblaciones de plantas.

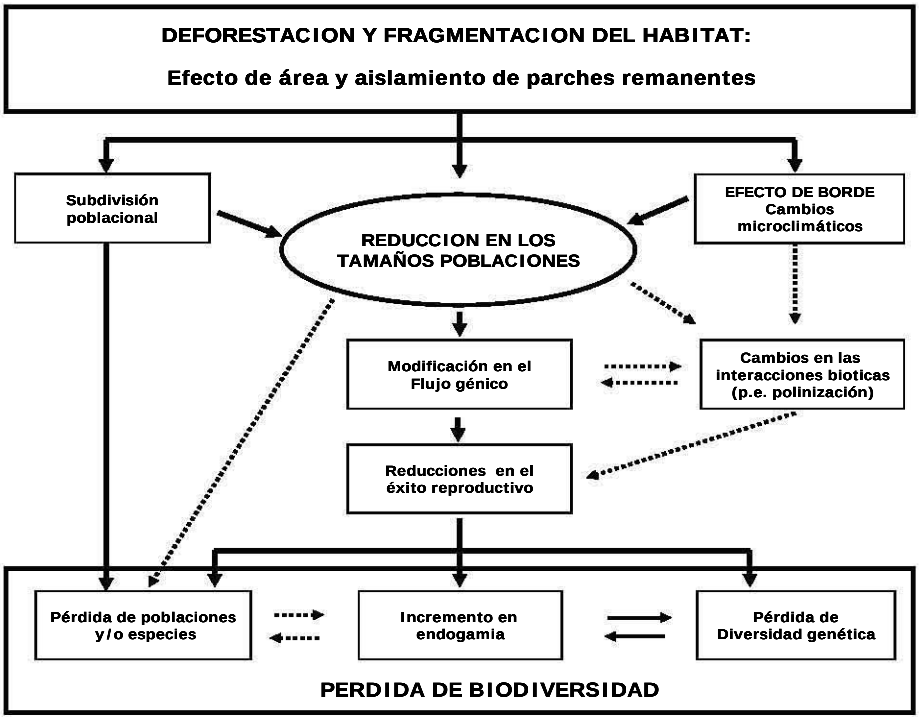

Figura 1. Representación esquemática de algunas de las posibles consecuencias de la fragmentación en el contexto de la polinización, éxito reproductivo y variabilidad genética de plantas. Las líneas gruesas ejemplifican los impactos directos, mientras que las flechas punteadas los posibles efectos indirectos.

Bajo este marco teórico se esperaría que estos factores pueden llevar de manera aislada o en conjunto a la pérdida de biodiversidad en las selvas tropicales. La fragmentación del hábitat puede afectar la riqueza y abundancia de especies, la dinámica del bosque, la estructura trófica de la comunidad, así como una gran variedad de procesos biológicos y del ecosistema (Laurance & Bierregaard 1997, Laurance 1999, Laurance *et al.* 2002, Lewis 2006). Asimismo, el efecto de borde presenta un impacto adicional sobre las poblaciones remanentes en fragmentos de tamaño pequeño, ya que su influencia puede llegar hasta más de 100 m dentro de la selva, con variaciones en sus efectos dependiendo del organismo o fenómeno estudiado (Murcia 1996, Ruíz-Guerra 2003, Chacoff & Aizen 2006, Laurance *et al.* 2006a).

La fragmentación generalmente tiene un impacto negativo directo sobre la dinámica y composición de especies de plantas en fragmentos de selva (Laurance *et al.* 1998*;* Laurance *et al*. 2000, Hill & Curran 2003) además de promover el establecimiento de especies pioneras en las orillas de los fragmentos de selva (Laurance *et al.* 2006b), así como un incremento en la abundancia de especies pioneras y de lianas en fragmentos o en los bordes de éstos (Laurance *et al*. 2000). Además de estos estudios que se enfocan principalmente a árboles, un análisis más reciente con plantas del sotobosque en Amazonia Central (Benítez-Malvido & Martínez-Ramos 2003) mostró que la fragmentación reduce significativamente la riqueza y densidad de especies, modificando la composición florística entre fragmentos, y que esos cambios afectaron plantas con diferentes formas de vida. Con base en estos antecedentes se requiere examinar cómo la fragmentación afecta la riqueza y composición de especies y su representación relativa en diferentes formas de vida o grupos funcionales, involucrando plantas con un amplio rango de tamaños, por ejemplo, plantas que han sido reclutadas recientemente en el sotobosque hasta árboles maduros, con lo cual podríamos tener un acercamiento al entendimiento de la dinámica de la selva en ambientes fragmentados.

c) *Fragmentación y polinización*

La fragmentación del hábitat no sólo afecta de manera aislada la riqueza y composición florística en los remanentes de selva, sino que también impacta varios procesos biológicos, por ejemplo, la polinización, la cual puede ser modificada debido a la disminución en la diversidad y/o abundancia de especies de polinizadores, así como a la capacidad de desplazamiento de dichos agentes entre fragmentos (Aizen & Feinsinger 1994, Murcia 1996, Kearns *et al.* 1998, Didham *et al.* 1996). Es de resaltar que más del 90% de las especies de árboles tropicales requieren agentes bioticos para ser polinizados, principalmente por insectos (Bawa 1990).

Varios estudios muestran cómo la fragmentación afecta negativamente a la polinización. Por ejemplo, Powell y Powell (1987) utilizando atrayentes químicos artificiales mostraron que la tasa de visita y abundancia de abejas euglossinas disminuye conforme decrece el tamaño del fragmento. Jennersten (1998) encontró resultados similares con los insectos visitantes de *Dianthus deltoides* en una pradera de Suecia, mostrando además consecuencias negativas sobre el éxito reproductivo. Steffan-Dwenter y Tscharntke (1999) mostraron qué el aislamiento entre pequeñas islas de habitat tuvo un impacto negativo disminuyendo la abundancia y riqueza de especies de abejas (Hymenoptera-Apidae). Sin embargo, también existen estudios que muestran resultados contrastantes. Tonhasca Jr. *et al*. (2002) utilizando también atrayentes químicos, no encontraron diferencias significativas en el número total de abejas en tres ambientes que diferían en el grado de conservación. Otro estudio muestra que los polinizadores nativos pueden ser reemplazados por especies exóticas, y que estas pueden ser más eficientes que las nativas (Dick 2001). Por otra parte, Wang *et al*. (2005) utilizando un sistema muy especializado (árboles del género *Ficus* y sus avispas polinizadoras *Agaonidae*) mostraron que en selvas altamente fragmentadas la comunidad de avispas polinizadoras disminuye mientras que la de avispas parásitas se incrementa y como consecuencia se presenta una mayor proporción de agallas en las flores femeninas en los sitios más fragmentados, sin embargo, el éxito reproductivo no presentó diferencias entre los hábitats estudiados. La fragmentación no solo puede afectar a la polinización *per se*, sino que además los efectos sobre ésta no son consistentes y pueden depender de varios atributos de las plantas, incluyendo el sistema reproductivo, densidad de individuos en floración, especificidad del mutualismo, o bien de la capacidad de desplazamiento de los polinizadores (Harris & Johnson 2004, Ghazoul 2005). Si bien se ha avanzado sustancialmente en el conocimiento de los posibles efectos de la fragmentación sobre la polinización, es notable la falta de estudios que involucren especies tropicales representativas de selva madura y que presenten polinización por animales, la cual es predominante en estas selvas, estos estudios nos permitirían evaluar mejor la magnitud del impacto de la fragmentación sobre el desempeño reproductivo de las plantas tropicales vía la interacción con sus polinizadores.

Al modificarse el proceso de polinización debido a la fragmentación se esperarían consecuencias sobre el éxito reproductivo de las plantas, disminuyendo la cantidad o calidad de los frutos o semillas producidos (Jennersten 1986, Aguilar *et al.* 2006). Sin embargo, la evidencia disponible no muestra resultados consistentes entre especies y entre estudios (Kolb & Lindhorst 2006). Aizen *et al*. (2002) evaluaron si los sistemas reproductivos de las plantas y el grado de especialización con sus polinizadores influyen en su respuesta reproductiva debido a la fragmentación del hábitat. Para ello analizaron 25 estudios que incluían a 46 especies diferentes de plantas. La mayoría de las especies mostraron efectos negativos, siendo la polinización y el éxito reproductivo en las especies auto-incompatibles más afectados por la fragmentación que en las especies auto-compatibles; además encontraron que el tener un polinizador muy especializado no incrementa el riesgo de extinción de las poblaciones de plantas inmersas en fragmentos de bosque, y concluyen que no se pueden hacer generalizaciones acerca de la susceptibilidad a la fragmentación con base en los sistemas de compatibilidad y en la especialización en la polinización. En este sentido Bruna y Kress (2002) no encontraron efectos sobre el éxito reproductivo en una hierba (*Heliconia acuminata*) en Amazonia Central. Resultados similares se reportan con *Ceiba aesculifolia* (Herrerias-Diego *et al*. 2006). Aguilar y Galetto (2004) encontraron que el éxito reproductivo (femenino y masculino) en una especie auto-incompatible (*Cestrum parqui*) decreció conforme disminuye el tamaño del fragmento. En Australia, Cunningham (2000) analizando flores de *Acacia brachybotria* y *Eremophila glabra* (Leguminosae) que crecen en remanentes de vegetación, encontró que ambas especies recibieron menos polen que las plantas ubicadas en sitios continuos. El autor encontró, además, mediante experimentos manuales, que la producción de frutos se incrementó en ambas especies cuando la deposición de polen es mayor. En un estudio más reciente Valdividia *et al.* (2006) evaluaron la polinización y el éxito reproductivo en zonas de bosque continuo y fragmentado en *Lapageria rosea* (Philesiaceae) en Chile, encontrando que la abundancia de flores, la tasa de visita de los polinizadores, así como la tasa de germinación de polen fueron menores en los sitios fragmentados. Esta incosistencia en los resultados de los posibles efectos de la fragmentación sobre el éxito reproductivo de las plantas puede estar afectado por multiples factores, incluyendo la modificación en la frecuencia de visita y abundancia de los polinizadores, la diversidad de sistemas reproductivos, una menor deposición de polen en los estigmas de las flores, menor dispersión de semillas y frutos, o bien menor densidad de flores en fragmentos de tamaño pequeño. Una característica de estos estudios es que se considera a la fragmentación como una variedad de conceptos, que van desde el de plantas aisladas, hasta fragmentos que no están totalmente aislados, asi como de remanentes de vegetación aislados por periodos de tiempo no controlados, o ubicados en diferenes condiciones ecológicas, entre otros. Lejos de ser desalentadores por la inconsistencia de los resultados, estos estudios enfatizan la necesidad de seguir explorando el tema, tratando de controlar, lo más posible, los probables factores de confusión.

Algunos efectos negativos de la fragmentación sobre la polinización y el éxito reproductivo pueden potencialmente provocar efectos genéticos deletéreos en las poblaciones de plantas (Alvarez-Buylla *et al.* 1996, Young *et al.* 1996, Goverde *et al.* 2002). Los efectos de la fragmentación sobre la diversidad genética han sido evaluados desde distintas perspectivas, desde evaluar cómo el flujo génico es afectado por la distancia que existe entre árboles aislados del continuo de selva (Fuchs *et al*. 2003, Rocha & Aguilar 2001; Cascante *et al.* 2002); o bien cómo el flujo génico se incrementa por la presencia de polinizadores exóticos (Dick 2001); estudios que muestran cómo la distancia no es un factor limitante en el movimiento de polen (Nason *et al.* 1998, Gaiotto *et al*. 2003), hasta los que simplemente muestran cómo el tamaño poblacional es fundamental en el mantenimiento de la diversidad genética de las poblaciones de plantas (Hall *et al*. 1996, Young *et al*. 1996). Dado este abanico de posibles consecuencias genéticas resulta interesante explorar estas tendencias, sin embargo, este tema es abordado solamente a través de una revisión bibliográfica detallada en este trabajo enfatizando los estudios que se han llevado a cabo con palmas.

La mayoría de los estudios que evaluan los efectos de la fragmentación del hábitat se han centrado principalmente en determinar i) cómo se afecta la riqueza y/o abundancia de especies, ii) cuáles son los efectos de la fragmentación sobre algunas interacciones bióticas (principalmente la polinización), y recientemente y con mayor énfasis, iii) las consecuencias en el éxito reproductivo de especies que quedan "atrapadas" en fragmentos de selva. En esos estudios, los temas mencionados, todos importantes, se han analizado de manera aislada. El presente trabajo, en contraste, intenta analizar estos aspectos de manera integrada; si bien centrada en las consecuencias finales sobre la biología reproductiva de una especie particular, esta tesis intenta analizar un gradiente de efectos de la fragmentación sobre las plantas, incluyendo: i) el impacto sobre la composición florística en fragmentos de selva, resaltando cómo la fragmentacion puede afectar diferencialmente a especies con diferente historia de vida (tolerantes a la sombra, típicas del bosque conservado, y pioneras demandantes de luz, típicas del bosque perturbado), ii) un análisis del potencial de permanencia de especies de selva madura en los remanentes de selva, utilizando como modelo a una especie dominante del sotobosque maduro, *Astrocaryum mexicanum* (Arecaceae), y iii) una explorarción de las consecuencias de la fragmentación sobre un proceso biológico: la polinización y sus posibles efectos sobre el éxito reproductivo en la palma *A. mexicanum*.

Una de las ventajas de utilizar esta especie como modelo de estudio es toda la información de base con la que se cuenta, tanto de historia natural (Martínez-Ramos 1997), biología reproductiva (Búrquez *et al.* 1987), demografía (Piñero *et al.* 1984), genética de poblaciones (Eguiarte *et al*. 1992; Eguiarte *et al.* 1993) y su dinámica en la comunidad (Piñero & Sarukhán 1982, Martínez-Ramos *et al*. 1998b).

Astrocaryum mexicanum (Arecaceae) es la única palma del género en México, el resto de las especies (47) se distribuyen en otras regiones del neotrópico (Uhl & Dransfield 1991). En México alcanza el límite de su distribución geográfica en la región de Los Tuxtlas, Veracruz, y se puede encontrar en un ámbito altitudinal de 0 a 700 m s.n.m. (Vite-González 1985). En la zona de Los Tuxtlas es la especie mas abundante del sotobosque, alcanzando densidades de más de 1000 palmas $\geq$1m de altura por hectárea (Piñero *et al.* 1977). La longevidad máxima de esta palma se ha estimado en 130 a 150 años (Piñero *et al.* 1984). La edad a la primera reproducción es a los 13 años aproximadamente (Piñero *et al.* 1982). Esta especie es monoica, pero protogínica (el primer día es viable la fase femenina, al segundo día la fase masculina). *A. mexicanum* presenta entre una y cinco inflorescencias por individuo, y cada inflorescencia tiene en promedio 27.8 flores femeninas y 4885 flores masculinas (Búrquez *et al.* 1987). La polinización es llevada a cabo por pequeños escarabajos (Coleoptera-Nitidulidae), sin embargo, presenta una alta diversidad de visitantes florales (Búrquez *et al.* 1987). Cada fruto mide de 3-5 cm de ancho y 4-6 cm de largo y esta totalmente cubierto por espinas. Este fruto es un recurso alimenticio para varias especies de animales, por ejemplo, ratones (*Peromyscus mexicanus* y *Heteromis desmarestianus*), seretes (*Dasyprocta punctata*), tepescuincles (*Agouti paca*) y ardillas (*Sciurus depeii* y *S. Aureogaster*) (Sarukhán 1980, Navarro-López 1982, Coates-Estrada & Estrada 1986, Martínez-Gallardo 1988). Estas últimas pueden ser depredadores de este fruto, sin embargo, también pueden funcionar como dispersores secundarios (Eguiarte *et al.* 1993). *A. mexicanum* presenta una dinámica poblacional muy peculiar en la selva de Los Tuxtlas, por ejemplo la probabilidad de muerte se incrementa para todas las categorias de edad en los claros de la selva, esto puede deberse a que esta palma posee un ciclo de vida que parece estar adaptado a condiciones de sombra (Martínez-Ramos & Samper 1998). El ambiente en los claros produce un aumento en la cantidad de individuos reproductivos pero disminuye la abundancia de palmas jóvenes. Por el contrario, en sitios cerrados se produce una disminución en la cantidad de individuos reproductivos y un incremento en la abundancia de palmas jovenes. Con altas tasas de producción de claros de gran tamaño de una manera constante, a largo plazo podría presentarse una disminución en la población, debido principalmente a una alta mortalidad de individuos adultos (Martínez-Ramos *et al.* 1988a, 1988b). Este escenario puede modificarse si la tasa de apertura de claros es alta pero temporal, de esta manera se incrementa la población de palmas adultas (Enríquez 1991). Resulta interesante que este incremento en la población de *A. mexicanum* se correlaciona con una disminución en la cantidad de árboles jóvenes de otras especies (Piñero *et al.* 1986). Esta dinámica en el sotobosque de la selva por parte de *A. mexicanum* lo puede señalar como un organizador importante en la comunidad de árboles (Sarukhán *et al.* 1985, Piñero *et al.* 1986, Dyer Leal 1990). Por último, resulta interesante destacar que *A. mexicanum* no sólo es importante por todos los atributos biológicos y ecológicos antes mencionados, sino que además es un recurso natural por parte de las comunidades locales, ya que tiene diferentes usos, uno de los cuales es el uso de las inflorescencias tiernas para cocinarlas de diferentes maneras (Alvarez-Buylla *et al.* 1989).

El sitio de estudio es la selva de Los Tuxtlas, esta región ha estado enmarcada desde tiempos remotos por intensa actividad humana, el cual comenzó con el proceso de colonización por los Olmecas hace aproximadamente 1,500 años. En el año de 1522 los españoles llegan a la zona, pero no es sino hasta mediados de los años cuarentas del siglo pasado que se mezclan con las etnias locales. Actualmente los asentamientos humanos son tanto urbanos como rurales, siendo las principales actividades económicas las agrícolas y ganaderas (Guevara *et al.* 1997). Como consecuencia de esta intensa actividad humana la zona ha reducido su cubierta de vegetación original hasta casi un 86% (Dirzo & García 1992), presentando ahora un paisaje altamente fragmentado (Dirzo & García 1992; Mendoza *et al.* 2005; Arroyo-Rodríguez & Mandujano 2006), lo cual resulta ideal para llevar cabo estudios sobre fragmentación del hábitat como lo es el presente trabajo.

Esta tesis consiste de cuatro capítulos. En el primero me enfoco a determinar cuáles son las consecuencias de la fragmentación del hábitat sobre la estructura y composición florística en cada fragmento de estudio. Existe evidencia que muestra cómo la diversidad florística puede ser afectada negativamente por la fragmentación favoreciendo el establecimiento de especies pioneras en los fragmentos de menor tamaño, y disminuyendo el establecimiento y permanencia de especies tolerantes a la sombra, como *A. mexicanum* (Benítez-Malvido & Martínez-Ramos 2003, Ross *et al*. 2002, Zhu *et al.* 2004, Laurance *et al*. 2006b). Con base en esta evidencia se espera que los fragmentos de menor tamaño presenten una abundancia mayor de especies pioneras (rápido crecimiento) que los fragmentos más grandes (Figura 2a), mientras que la abundancia de especies tolerantes a la sombra (lento crecimiento) disminuya conforme decrece el tamaño del fragmento (Figura 2b).

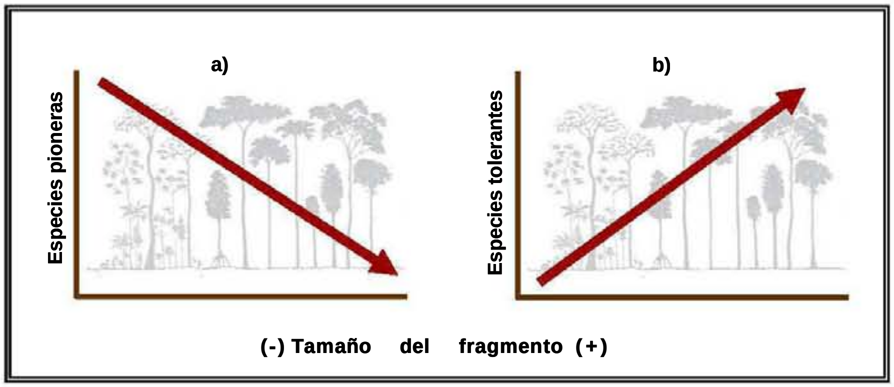

Figura 2. Representación de la hipótesis que propone que en fragmentos de menor tamaño habrá un incremento de especies pioneras, las cuales disminuirán conforme se

incrementa el tamaño del fragmento (a). Por otro lado, se hipotetiza que las especies tolerantes a la sombra disminuirán en fragmentos chicos con una tendencia a incrementarse conforme aumenta el tamaño del fragmento (b).

El segundo capítulo evalúa cómo diferentes atributos del paisaje (superficie de selva conservada, tamaño del fragmento, forma del fragmento y aislamiento) afectan la abundancia de *A. mexicanum* una especie representativa de las tolerantes a la sombra, típica de la selva madura. Para ello se utilizaron sitios que difieren en su estado de conservación y se contrastaron con una selva continua en la reserva de Los Tuxtlas, de la UNAM. La hipótesis a investigar fue si la abundancia de *A. mexicanum* sería menor en los paisajes que presenten menor estado de conservación (Figura 3).

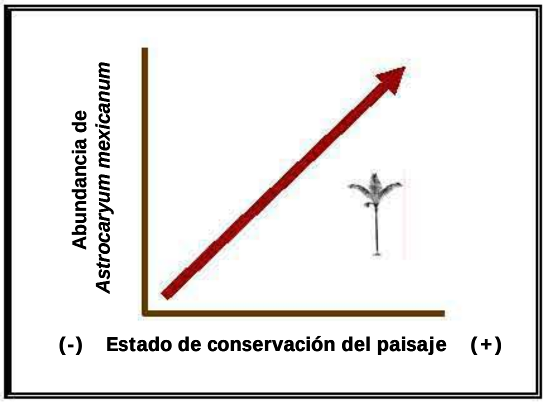

Figura 3. Representación de la hipótesis que propone que la abundancia de una especie típica de selva madura (*A. mexicanum*) será más abundante en sitios más conservados.

En el tercer capítulo evalúo el efecto del tamaño del fragmento sobre la diversidad y abundancia de visitantes florales y polinizadores de *A. mexicanum* así como el posible impacto sobre el éxito reproductivo femenino ("*fruit set*") de esta palma.

Para esto colecté y cuantifiqué la fauna de visitantes en global, así como los principales polinizadores asociados a las inflorescencias de *A. mexicanum*. Las predicciones fueron que en fragmentos de tamaño pequeño habrá una menor diversidad y abundancia de visitantes florales y de polinizadores comparado con los fragmentos más grandes, con lo cual se esperarían tendencias similares en el éxito reproductivo femenino (Figura 4).

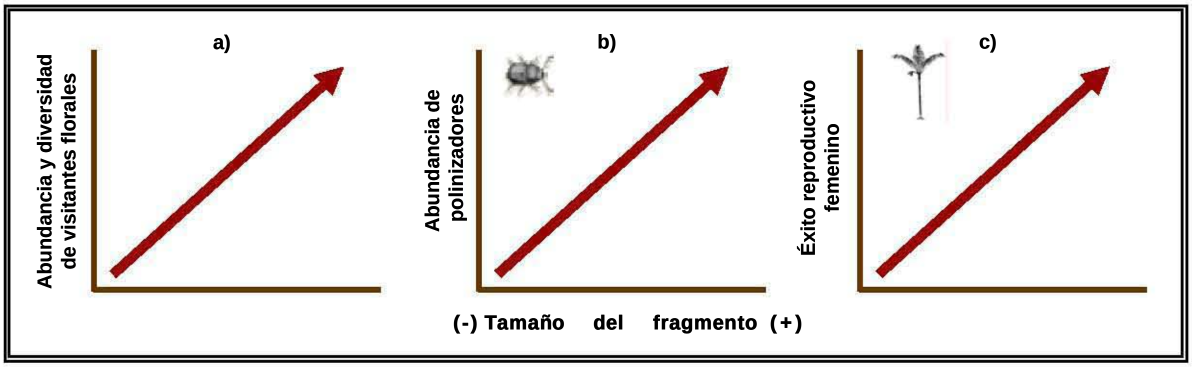

Figura 4. Representación de la hipótesis que propone que la abundancia y diversidad de visitantes florales en global se incrementará conforme aumenta el tamaño del fragmento (a); la misma tendencia se espera para los polinizadores (b). Asimismo se esperaría que el cuajado de frutos ("*fruit set*") sea mayor en los fragmentos más grandes (c).

Por último, el cuarto capítulo presenta las conclusiones generales de esta tesis, así como una revisión bibliográfica de las consecuencias de la fragmentación sobre aspectos de genética de poblaciones en palmas, y finalmente presento las perspectivas de estudio en este campo de investigación.

El presente estudio intenta producir un avance en el conocimiento de las consecuencias de la fragmentación sobre la comunidad de plantas, enfocándose después sobre una especie característica de selva madura y sus consecuencias en el mantenimiento de esta especie con sus polinizadores, asi como las consecuencias sobre el éxito reproductivo femenino, poniendo además en perspectiva las posibles consecuencias genéticas.

Desde el punto de vista formativo, la meta fué acercarme a la biología de la conservación desde una perspectiva amplia, incluyendo la ecología de comunidades y de poblaciones aplicada a la conservación.

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CAPITULO I

Efecto de la Fragmentación Sobre la Diversidad Florística en una Selva Tropical en México

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Fragmentation-related Changes in Floristic Diversity Metrics in a Mexican Tropical Rain Forest

Fragmentation-related changes in floristic diversity metrics in a Mexican tropical rain forest

ABSTRACT

We report changes in several plant diversity metrics associated to fragmentation in a Mexican rainforest. We examined richness; floristic composition and similarity as well as and richness/abundance of mature-forest and light-demanding plants, considering individuals of different size-categories across a range of fragment sizes and continuous forest. When we included small, recently recruited plants in the sample, we detected a linear decline in species richness, with a decrease of about 22% from continuous forest to the smallest fragment after 30 years from excision. We found a significant changes in species composition: small fragments had distinguishable assemblages compared to continuous forest. There was a shift in the relative representation of mature-forest and light-demanding species: the former decreased and the latter became overrepresented in small fragments. All these effects disappeared when considering the largest plants, which were present prior to fragmentation. Our findings confirm, one the one hand, that fragmentation impacts tropical biodiversity and that the effect is differential and, on the other, that the remaining landscape retains a fraction of the floristic diversity from which restoration can be attempted.

Keywords: Floristic diversity, floristic similarity, fragmentation, species decline, tropical rain forest, Los Tuxtlas, compositional shifts, regeneration strategies

1. INTRODUCTION

The current rates of land use and cover change leading to deforestation and fragmentation of natural ecosystems has been recognized as one of the most pervasive global environmental changes. This is because it can drive, as an indirect forcing, the only practically irreversible anthropogenic global change—massive biological extinction (Dirzo and Raven 2003) affecting biodiversity in terms of genetic erosion (Young 1996), population extinctions (Hughes et al. 1997), local or global species loss (Pimm 2000) and, potentially, even entire ecosystems loss (López and Dirzo 2007). The risks of biodiversity loss associated to land use change are particularly critical in tropical ecosystems, since they concentrate a disproportionate amount of the Earth's biodiversity and they are being, at the same time, heavily impacted (Dirzo and Raven 2003). Currently, the predominant spatial configuration of tropical landscapes is that of an archipelago of vegetation remnants of different size immersed in a sea of transformed terrains consisting of agricultural fields, cattle grasslands, plantations or other human-dominated systems. While the massive conversion of tropical forests into cleared lands for agriculture and cattle grazing will lead to a rapid loss of populations or species, the remaining fragments have the potential to retain at least some of the indigenous species. However, our understanding of the relationships between forest fragmentation and biodiversity loss is still rudimentary (Fahrig 2003), particularly in tropical regions. Turner´s (1996) pioneer analysis and a comprehensive compilation of our knowledge of the patterns and biological consequences of tropical fragmentation (Laurance and Bierregaard 1997) show that most of the studies have been carried out in the neotropics, particularly in Central Amazonia (Laurance and Bierregaard 1997; Laurance et al. 2001) and most of the studied organisms are vertebrates (particularly birds), with a lower representation of studies dealing with other organisms. In the case of plants, studies in Central Amazonia and some additional, recent investigations have documented effects of fragmentation on the dynamics and species composition of forest fragments (e.g., Laurance and Bierregaard 1997; Laurance et al. 1998*a;* 1998*b;* Laurance et al. 2000, Hill and Curran 2003), increased mortality rates of canopy trees in fragments as compared to unfragmented forest (Laurance and Bierregaard 1997, Laurance et al. 199*8a,* 1998*b*), and increased abundance of pioneer trees and lianas in fragments or near fragment edges (Laurance et al. 1998*a,*1998*b*; Laurance et al. 2000). Apart from these studies, largely focusing on trees, a recent analysis with understory plants in Central Amazonia (Benítez-Malvido and Martínez-Ramos 2003) showed that fragmentation significantly reduced species richness and density and shifted the species composition among fragments and these changes affected plants in different life forms. This suggests that by affecting the plants of the understory, fragmentation has the potential to disrupt forest regeneration and overall plant species diversity. The authors of this study indicate that lack of replication prevents extrapolation of their findings and apart from this study and other isolated studies elsewhere (e.g., Zhu et al. 2004), work investigating the consequences of fragmentation on plant recruitment is limited.

Clearly, we still need to examine how fragmentation affects species richness, composition and the relative representation of plants in different life forms or functional groups, involving individuals of a wide range of sizes—from plants recently recruited in the understory to mature trees, and this is the main aim of the present study. The rational for our comparison of a range of sizes is that assemblages of mature, large trees, should have been equally diverse throughout the forest prior to fragment excision and therefore fragmentation should not have as marked an effect on the diversity of this size class, unless significant edge-related mortality (Laurance et al. 1998*a,* 1998b; Laurance et al. 2000) has proceeded. In contrast, small sized plants, reflecting post-excision recruitment should show a greater species richness decline (Benítez-Malvido and Martínez-Ramos 2003), particularly in the case of mature-forest species, many of which should be particularly vulnerable to changes in the physical environment (Turner 1996; Scariot 1999; Benítez-Malvido and Martínez-Ramos 2003) and in their biotic environment, including interactions with pollinators or dispersal agents which in turn affect population recruitment (e.g., Cordeiro and Howe 2001). This latter expectation is consistent with available information on the negative impact of fragmentation on animals that play such roles (see discussion in Mendoza et al. 2005, for the specific case of our study site). In contrast, light-demanding species are less likely to be affected by the physical changes brought about by fragmentation and have the potential to recruit in small fragments or fragment edges of larger fragments. Conceivable, if such enhanced recruitment compensates for the expected recruitment reduction of the mature-forest plants, overall species richness decline may not be as marked.

Here we report on changes in several metrics of plant diversity associated to fragmentation in a tropical rainforest area in southeast Mexico. We aimed to specifically answer the following questions: i) Is there significant variation in species richness across a range of fragment sizes representative of the current fragmentation in the area, and if that is the case how does it vary with plant size? In addressing this question we hypothesized that if forest fragmentation reduces plant species richness, the effect should be more pronounced when including the young (recruited post-fragmentation) plants, and that such effect should be diluted or not evident in the larger trees. ii) To what extent is species composition and floristic similarity affected by forest fragmentation? For this question we hypothesized that if plant species differ in their ability to recruit or withstand the effects of fragmentation, species composition should change with fragmentation, and floristic similarity should decrease with the contrast in size among fragments. iii) Does habitat fragmentation affect the relative representation of species with different regeneration patterns? In addressing this question we hypothesized that if we separate species according to their light requirements for regeneration, considering light-demanding versus shade-tolerant species, the former should be better represented in the smaller or smallest fragments while the latter should have a greater relative representation in the largest fragments or continuous forest.

2. MATERIALS AND METHODS

2.1. Study site

This study was carried out in Los Tuxtlas, Veracruz, Mexico. This area is the easternmost extension of the Mexican Volcanic Transbelt and constitutes the northernmost limit of tropical rainforest distribution on the Americas (Dirzo and Miranda 1991). Topography is complex, with elevational changes from sea level to1600 m a.s.l. within a short distance. Given its latitudinal position (18°39') and location, adjacent to the Golf of Mexico (Dirzo et al. 1997), the area experiences a high precipitation—around 4,700 mm/year and mean annual temperature is 25ºC (Dirzo and García 1992). The predominant vegetation is tropical rain forest in the lowlands, with variations along the elevational range, including cloud forest and mixed forests at higher elevations. Floristic diversity in the area includes a total of 950 known vascular plants (Ibarra et al. 1997). The flora is largely composed of plants of neotropical origin but higher elevation sites include combinations of neotropical and neartic taxa (Dirzo and Mendoza 2004).

The area has a long history of human occupation. Significant anthropogenic impacts became apparent starting in the 16th century with the Spanish colonization (Dirzo and Mendoza 2004). Recently, the predominant land use in the area is conversion of forest to cattle grasslands. Rates of deforestation in the decades of the 60's-late 80's were ca. 4%/year (Dirzo and García 1992). Current deforestation rates have decreased because forest remnants are restricted to the most inaccessible areas of the region. A recent study of fragmentation (Mendoza et al. 2005) shows that the spatial configuration of the landscape consists of a large number (92% out of 1005 in an area of ca. 1000

km^2) of small/very small fragments (< 10 ha) with only a few extensive areas still remaining. In the northern part of Los Tuxtlas, corresponding to our study site, the only remnant of continuous forest corresponds to the Los Tuxtlas Research Station and its extension towards the San Martín Volcano, encompassing an area of ca. 9,500 ha. For details of the natural history of the region see González-Soriano et al. (1997).

2.2. The selected fragments

Given that the skewed frequency-distribution of fragment sizes in Los Tuxtlas (Mendoza et al. 2005), we chose a group of fragments of the predominant small size and a continuous forest site. We chose isolated fragments which: i) bore the same vegetation type, tropical rain forest, and therefore were located within a restricted elevation (0-150 m a.s.l.); ii) were of a similar age, but long enough to contain recruited plants beyond the seedling stage. Our selection included five fragments of 2 (F1), 4 (F2), 19.4 (F3), and 34.6 (F4) ha and an extensive area of relatively continuous forest (CF) (Fig. 1).

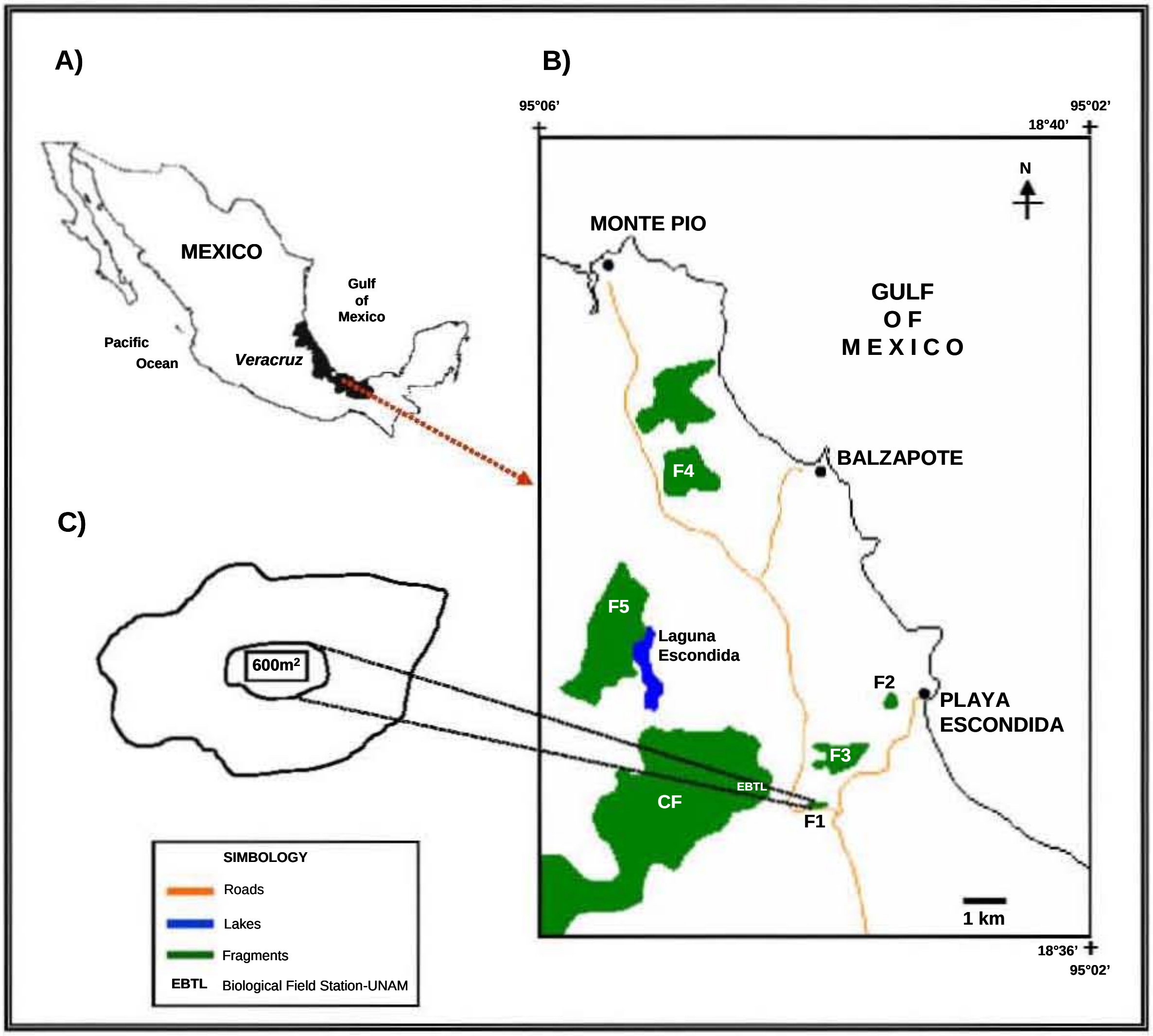


Figure 1. Location of the study site in the State of Veracruz, Mexico (A), including the specific location of the fragments (F1-F4) and continuos forest (CF) within the area (B) and the sampling design of plants within permanent observation plots in the fragments.

The latter corresponds to an area which extends from the lowlands westward towards the San Martín Volcano, encompassing an area of over 9,000 ha. For the purposes of this study, which emphasized floristic diversity in lowland tropical forest, we will consider the latter site as an area of 700 ha which contains the same vegetation type. We will refer to this as continuous forest (CF). In CF we used three independent sampling locations to quantify species richness. These sampling points were considered independent as they were established in three separate hills, each one of them with a different orientation (north, east, and south). All sites were selected using a satellite image (year 2000) and an aerial photograph, scale 1:75,000 (year 1991, INEGI). This was digitized using ILWIS 2.4 to calculate areas of each fragment and distances between fragments and the continuous forest. With this and complementary exploration on the ground we insured that the fragments, all of ca. 20 years of separation, were within the required elevation and that the vegetation was lowland tropical rainforest with similar structure and composition typical of such forest in the region.

2.3. Sampling protocol

We used the method developed by Gentry (1982, 1988) to assess plant species diversity, with some modifications. An area of 2 ha (corresponding to the smallest fragment of our sample) was used to establish ten independent, randomly selected, 50 x 2 m transects located in the physical center of each fragment. This insured that the vegetation in the sampling area was experiencing, simultaneously, a gradient of the effects of fragment size and edge, two predominant factors associated to fragmentation in the area. For all variables the total area sampled per fragment was 0.1 ha, except in the case of species richness in CF, in which we used the three independent 0.1 ha sites. Within each transect, we recorded all rooted plants with diameter at breast height (DBH, at 1.3 m height) ≥ 1.0 cm. For all trees we measured their DBH except in the case of trees with large buttresses (≥ 1.3 m height), in which we measured diameter immediately above the buttresses. For lianas we measured the diameter at the base of the stem. For hemiepiphytic plants we measured (at 1.3 m) the thickest trunk that reached the ground. With these measurements we established three plant categories: all plants, including individuals with DBH ≥ 1.0 cm; plants with DBH ≥ 2.5 cm; and large trees, plants with DBH ≥ 10.0 cm. All plants were identified to species. Nomenclature follows Ibarra and

Sinaca (1997). Voucher specimens were deposited in the herbarium of the Los Tuxtlas field station. The minimum diameter included in this study, 1.0 cm, is smaller than Gentry's (1982, 1988) of 2.5 cm. This modification not only allowed us to incorporate a larger number of plants, but also allowed us to include plants that most likely colonized and recruited into the study sites post-fragmentation.

2.4. Metrics of floristic diversity

With the obtained data set we calculated the following diversity metrics:

i) Species richness, defined as the number of plant species/0.1 ha considering the three size categories. To examine the variation of species richness across fragments we used regression analyses. Given our field sampling effort of only 0.1 ha we calculated non-parametric estimates of species richness using the EstimateS 7.5 program (Colwell 2005). We calculated three non-parametric estimators: ICE, Chao2, and Jacknife2. All of them yielded similar results and we only report that of Jacknife2, one of the best estimators of plant species richness (Chazdon et al. 1998).

ii) Changes in floristic composition among fragments. With the identity of the species in the ten transects of each fragment we developed a matrix of presence/absence and performed a principal component analysis (PCA) using MVSP version 3.11 (MVSP 2000). This analysis provides a visual representation of clusters of floristic assemblages, if present. In addition, with the species identity and their relative abundances we estimated the floristic similarity of all possible pairs of fragments, using a modification of the classical indices of compositional similarity recently proposed by Chao et al. (2005). The proposed estimators consider species abundance, the effect of unseen/rare species (as is the case of tropical forests in general and of our study site in particular (see Ibarra et al. 1997), and produce values that are considerably less biased than the classical indices. We calculated modified Sorensen’s indices (Chao-Sorensen) using the EstimateS 7.5 software (Colwell 2005). Further details of the advantages and accuracy of the modified indices are described by Chao et al. (2005). In order to analyze possible groups of Chao-Sorensen indices we applied a grouping analysis, UPGMA, using MVSP version 3.11 (MVSP 2000).

iii) Relative representation of mature forest (shade-tolerant) species as compared to early successional, disturbed-site (light demanding) species. The definition of the two regenerating strategies was based on our knowledge of the regeneration strategies of the species of this forest, as well as on published information for plants from Los Tuxtlas (Bongers et al. 1988; Martinez-Ramos 1985; Ibarra et al. 1997; Van Breugel et al. 2007). This analysis was performed with both the number of species and the number of individuals (regardless of species identity) of the two strategies across fragment sizes. The relative representation of each of the two types of regeneration strategy, considering both species number and abundance was tested for independence from fragment size using contingency analyses.

iv) Value of importance (VI) of the species. We calculated, for each of the species: density (no. plants/0.1 ha), frequency (the number of transects, out of ten, in which a given species appeared in each fragment/CF) and dominance (the sum of basal areas obtained form DBH). The relative values of these three measures were summed to calculate a VI for each of the species (Curtis and McIntosh 1951). We used the ten species with the highest VI for each of the fragments to assess changes in relative dominance of pioneer/shade-tolerant species with fragmentation.

All of these parameters were obtained from the sampling of 0.1 ha plots in the fragments of 2, 4, 19.4, and 34.6 ha, and in one of the three sites of CF. Species richness, in contrast, was calculated from all fragments and the three independent locations within CF.

3. RESULTS

3.1. Changes in floristic diversity

Considering plants of DBH ≥ 1.0 cm, the number of plant species per 0.1 ha plot (i.e., fragment) ranged from 102 (in the second smallest fragment) to 135 (in one of the sites of CF). The corresponding values for plants ≥ 2.5 cm DBH were 79 (second smallest fragment) and 95 (one of the CF sites). For plants with DBH ≥ 10.0 cm the range of variation was 31 (smallest fragment) to 40 species (second largest fragment).

The observed variation was consistent with our expectation of a significant reduction in species diversity as remaining habitat area decreases in plants with DBH ≥ 1cm (F = 138.47, $P < 0.0001$) (Fig. 2A) and fragment size explained 74% of the variation in species richness. When we considered the non-parametric estimate of species richness, Jacknife2, the estimated values ranged from 165 to 225. A regression of these values on fragment size reveals a closely similar pattern to that of observed with observed richness (Fig. 2A); this non-parametric estimator was also significantly related to fragment size (F = 10.53, P = 0.04) (Fig. 2A), which explained 78% of the variance in Jacknife2. The slope of the corresponding equation is notably similar to and statistically indistinguishable from that of the observed species richness (Fig. 2A; t = 0.14, P = 0.55).

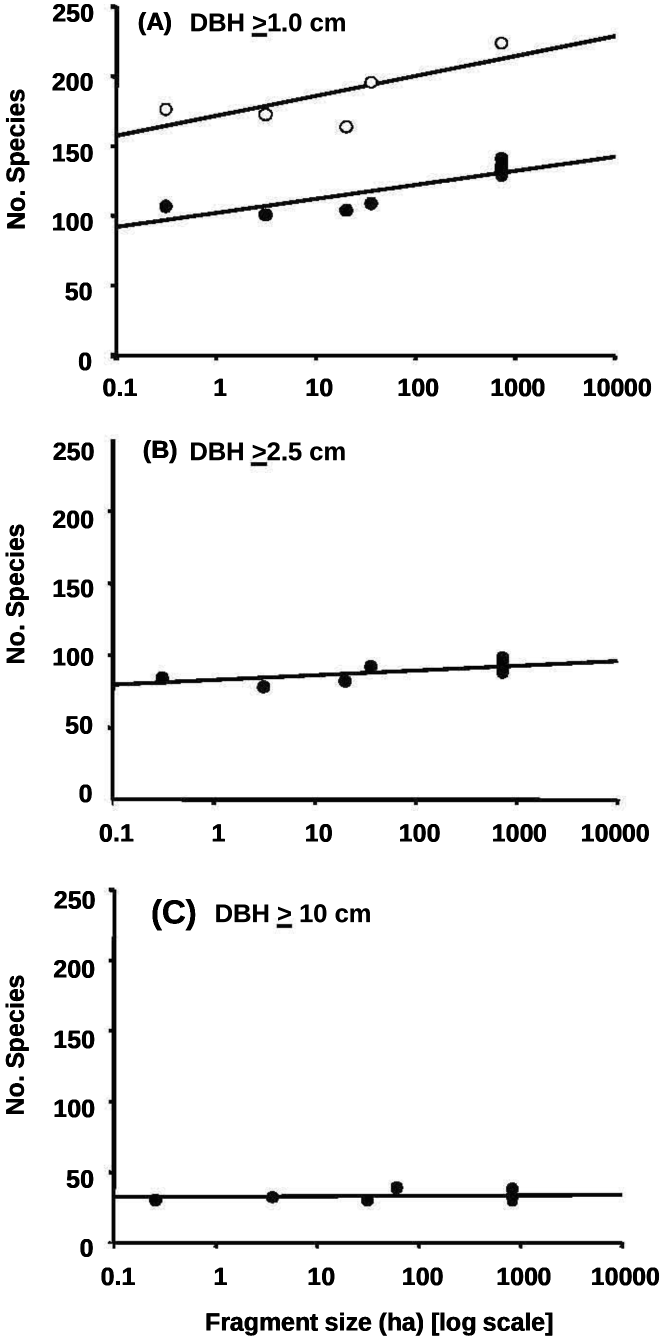


Figure 2. The relationship between area of fragment/site and number of species per 0.1 ha (●) in lowland tropical rain forest in the area of Los Tuxtlas, southeast Mexico. Relationships correspond to plants in three size categories: A) DBH ≥ 1.0 cm, B) DBH ≥ 2.5 cm, C) DBH ≥ 10.0 cm. The relationship for the first group includes also species numbers as derived from a non-parametiric estimator, Jacknife2 (○). For details of statistical analyses of the relationships see text.

A similar trend in the observed species was detected when we eliminated the smallest plants and only considered plants with DBH ≥ 2.5 (Fig. 2B), but this relationship is only marginally significant (*F* = 4.90, *P* = 0.08), although 54% of the variation in species richness was explained by fragment size. Finally, when we considered only the largest plants (DAP ≥ 10.0) (Fig 2C), the relationship fragment area-species richness became non-significant (*F* = 0.23, *P* = 0.65).

3.2. Changes in species composition

A first quantitative assessment of the variation in species composition was attempted using a PCA, using all plants $\geq$ 1 cm DAP (Fig. 3). This analysis detected a clear differentiation of CF from the rest of the fragments along axis 2. This is largely due to the presence of a set of mature-forest plant species (*Astrocaryum mexicanun, Chamaedorea* spp., *Pychotria* spp., *Mortoniodendron guatemalense*). The rest of the fragments constituted a constellation of points situated on the right-hand side of axis 2 and encompassing a wide space along axis 1, although the smallest fragment insinuates itself as a distinct unit on axis 1. This is largely due to the presence of a contingent of light-demanding species such as *Myriocarpa longipes, Acalypha* spp., *Eupatorium galeotti, Bursera simaruba,* and *Robsinsonella mirandae*, in addition to some shade-tolerant species.

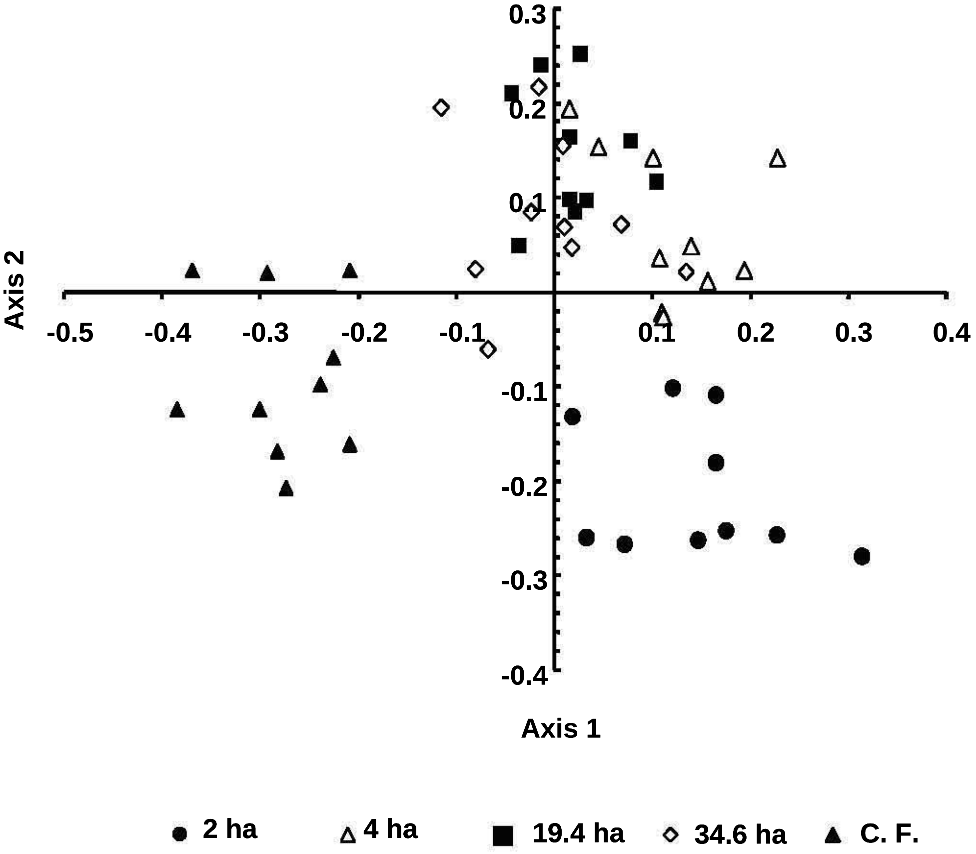


Figure 3. A principal component analysis based on the presence-absence of species in the 10 transects from each fragment and continuous forest in lowland tropical rain forest in Los Tuxtlas, Mexico.

A visual inspection of the analysis of compositional similarity based on the Chao-Sorensen's similarity index for all possible pairs suggested consistent patterns of variation. For example, the highest similarity corresponds to a comparison involving two fragments, while the lowest value was that of CF and one of the fragments. In order to more objectively visualize this apparent tendency, we performed the grouping analysis (UPGMA) shown in Figure 4. The resulting dendrogram reveals two distinguishable groups (*a* and *b* in Fig. 4) with no overlapping of similarity values: group *b* has values greater than 0.84 while those of group *a* are all lower than 0.81. In addition, values in group *b* do not include a single paired comparison involving CF; we refer to this as “the fragments group”. In contrast, 4 out of 6 paired comparisons in group *a* involve CF, suggesting that the lowest floristic similarity in this group is largely explained by the comparisons between CF and forest fragments. We refer to this as “the continuous forest group”. Although two of the paired comparisons in this group do not involve CF, a *U*-test showed that the median floristic similarity is significantly lower in the CF group than in the fragments group (*Z*=2.56, *P*=0.01) (see Fig. 4) indicating that, in general, similarity was greater among fragments than between fragments and continuous forest.

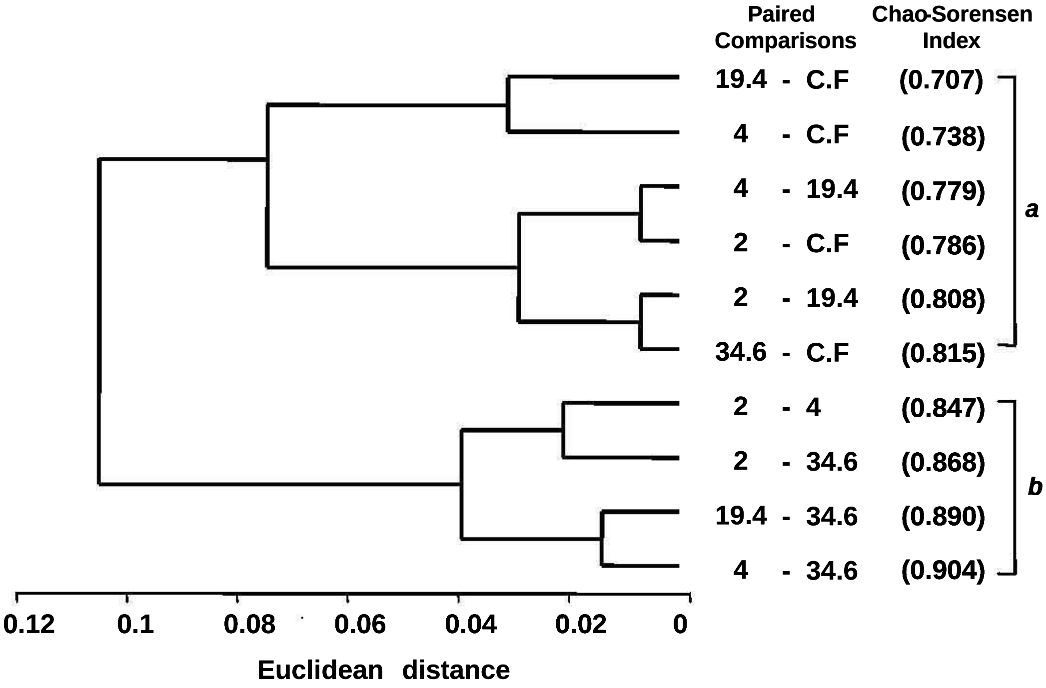


Figure 4. A grouping analysis, UPGMA, of the Chao-Sorensen similarity indices applied to all possible pairs of fragments and continuous forest (CF). Letters *a* and *b* denote the two major clusters corresponding to the continuous forest group of pairs and the fragments group of pairs. In addition, *a* and *b* denote statistically significant differences in Chao-Sorensen values. See text for details.

3.3. Changes in species representation according to regeneration strategy

The number of species belonging to the two regeneration strategies varied across fragments and such heterogeneity also differed in their magnitude as a function of plant size category (Fig. 5, left-hand side panels). Considering all plants with DBH ≥ 1.0 cm (Fig 5A), the relative representation of plant types showed an overrepresentation of shade-tolerant species in CF as compared to light-demanding species. Such contrast in the proportion shade-tolerant:light-demanding species is considerably lower in the smallest fragment, as well as in fragments of intermediate size. A contingency test showed a significant heterogeneity in the distribution of regeneration strategy across fragment sizes ($X^2 = 11.6$, $P = 0.02$). In the case of plants with DBH ≥2.5 cm (Fig. 5B) a similar tendency was observed: the overrepresentation of shade-tolerant species as compared to the light demanding taxa was considerably greater in CF than in all forest fragments ($X^2 = 32.0$, $P < 0.00001$). Consistent with previous results, plants of the larger size category (DBH ≥ 10.0 cm) (Fig. 5C) did not show a contrasting relative representation across fragment sizes ($X^2 = 3.1$, $P = 0.54$).

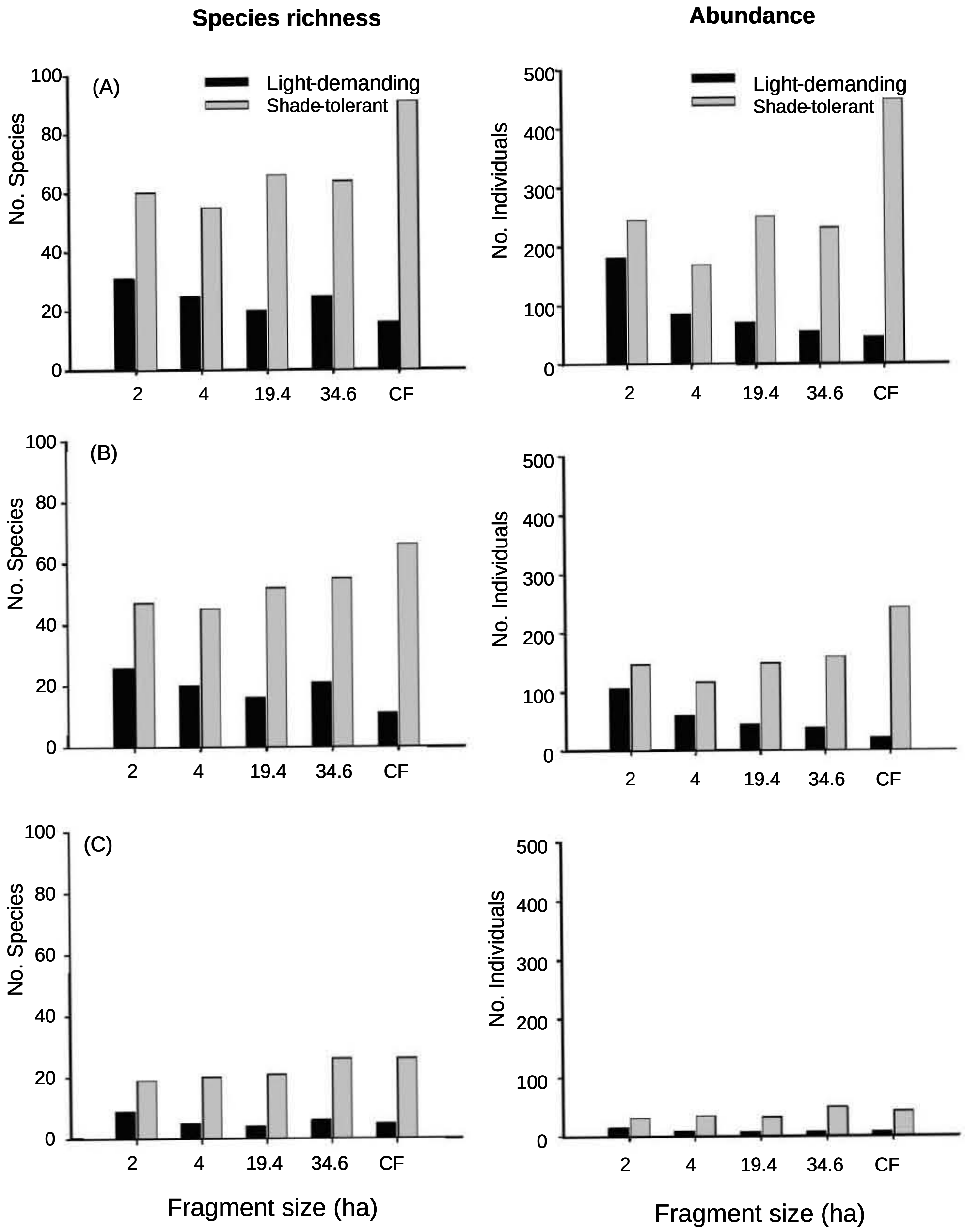
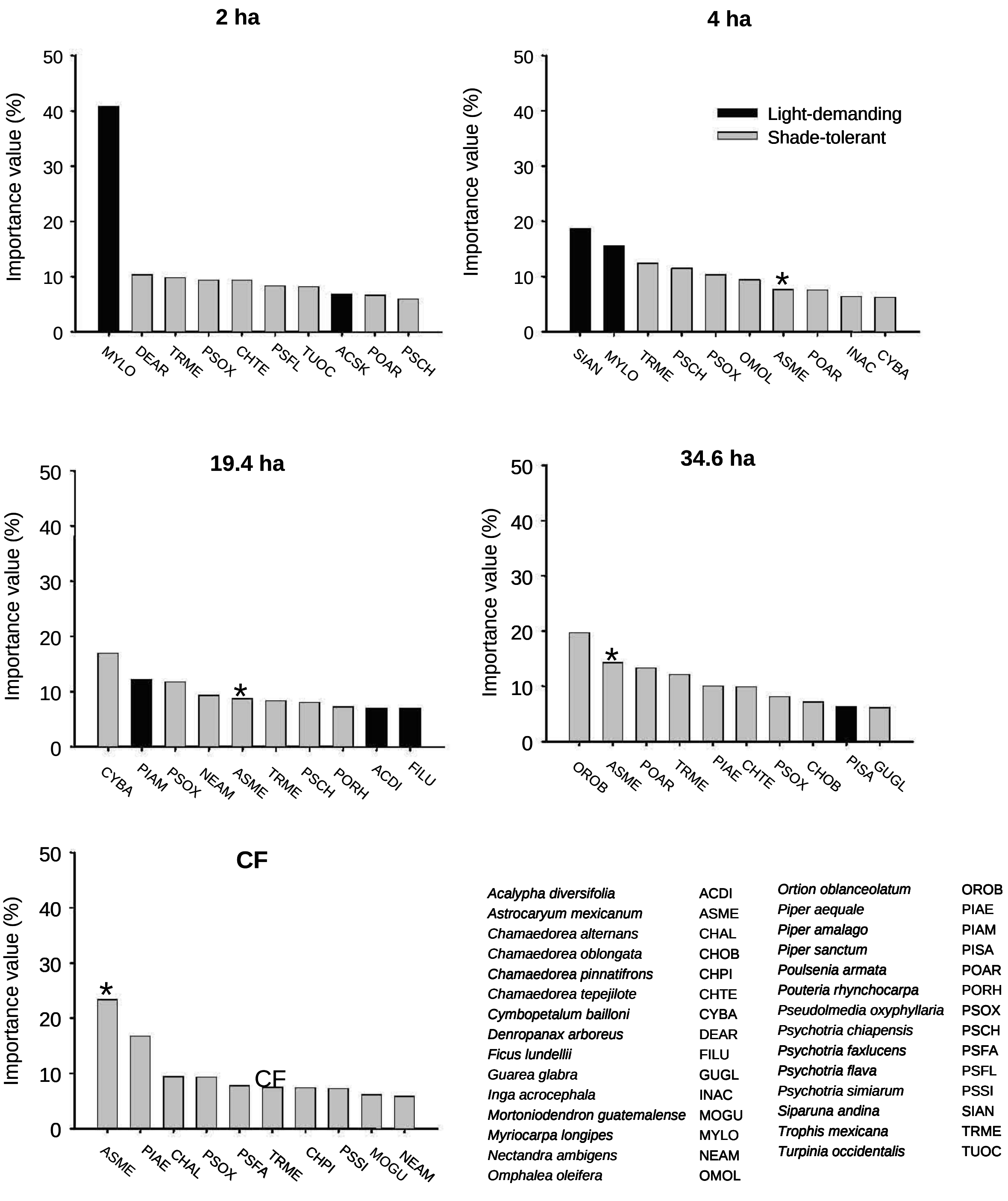


Figure 5. Relative representation of the number of shade-tolerant and light-demanding species in fragments of different size and continuous forest (CF) from lowland tropical rainforest of Los Tuxtlas, separated according to plant size category: A) DBH ≥ 1.0 cm, B) DBH ≥ 2.5 cm, C) DBH ≥ 10 cm. Panels on the left correspond to species richness (number of species per 0.1 ha) and panels on the right correspond to abundance (number of individuals per 0.1 ha). For details of contingency analyses comparing the distribution of both plant types in relation to fragment size see text.

The observed pattern of relative representation of plants of the two regeneration modes becomes more evident when considering plant abundance, as defined by the number of individuals, regardless of species identity (Fig. 5, right-hand side panels). The magnitude of overrepresentation of shade-tolerant species in the continuous forest as compared to the fragments, but particularly the smallest fragment, shows a decreasing gradient as plant size increases. In the smallest size category the contrast was highly significant (X^2 = 156.6, $P < 0.00001$), followed by a still highly significant heterogeneity in the case of plants ≥ 2.5 DBH (X^2 = 91.0, $P < 0.00001$), while the relative representation of the two strategies does not differ significantly with fragment size in plants ≥ 10.0 cm DBH (X^2 = 6. 5, $P = 0.16$).

To further illustrate the representation of shade-tolerant and light-demanding species in the different fragments we present the VI corresponding to the ten most important species in all sites (Fig. 6). A contrasting pattern is readily evident when comparing the two extremes of fragment size. In the smallest fragment, two light-demanding species were among the ten most important taxa. Collectively, these two species accounted for 48% of the total sum VI of this site. Moreover, the most important species, *Myriocarpa longipes*, accounts for 35% of the accumulative VI of this group of ten species. *M. longipes* has, in fact, a VI over four times greater than the species ranked in second position. In great contrast, no light-demanding species is present among the ten most important taxa of CF. Furthermore, its ten most important taxa showed a comparatively more even distribution as compared to the histogram of the smallest fragment.



Acalypha diversifolia	ACDI
Astrocaryum mexicanum	ASME
Chamaedorea alternans	CHAL
Chamaedorea oblongata	CHOB
Chamaedorea pinnatifrons	CHPI
Chamaedorea tepejilote	CHTE
Cymbopetalum bailloni	CYBA
Denropanax arboreus	DEAR
Ficus lundellii	FILU
Guarea glabra	GUGL
Inga acrocephala	INAC
Mortoniodendron guatemalense	MOGU
Myriocarpa longipes	MYLO
Nectandra ambigens	NEAM
Omphalea oleifera	OMOL
Ortion oblanceolatum	OROB
Piper aequale	PIAE
Piper amalago	PIAM
Piper sanctum	PISA
Poulsenia armata	POAR
Pouteria rhynchocarpa	PORH
Pseudolmedia oxyphyllaria	PSOX
Psychotria chiapensis	PSCH
Psychotria faxlucens	PSFA
Psychotria flava	PSFL
Psychotria simiarum	PSSI
Siparuna andina	SIAN
Trophis mexicana	TRME
Turpinia occidentalis	TUOC

Fig. 6. The ten species with the greatest value of importance in each of the studied fragments, including shade-tolerant and light-demanding species. Species codes correspond to the first two letters of the genus and species and the corresponding names are given in the lower right panel. *Astrocaryum mexicanum* is represented by (*).

In CF the ten most important species included two understory palms and eight tree species typical of mature forest. The other three fragments insinuated a gradient of dominance of light-demanding species. Overall, the sum of the VI of the ten most important light-demanding species shows a clear gradient across fragment sizes in the direction 2 ha (47.6%) > 4 ha (34.3%) > 19.4 ha (26.2%) > 34.6 ha (6.2%) > CF(0%).

4. DISCUSSION

Our study, based on the accurate identification, measurement of size and analysis of the distribution of 3200 plants in 282 species across fragments and continuous forest provided consistent information regarding our three major questions.

We found that species richness, considering the plants of all sizes, significantly decreased from CF to the smallest fragment. The regression equations of both the observed species richness and the Jacknife2 estimate vs. fragment size show that floristic diversity decreased by about 22% from CF to the smallest fragment in a lapse of ca. 20 years. Species richness decline may be related to the prevalence of species with low local population size (rare species) and inability to withstand the effects of fragmentation, as is typical in tropical forests (Hubbell and Foster 1983). This is a likely mechanism of species loss in fragments of Los Tuxtlas, as a large proportion of the species we sampled (45%) was singletons and singletons plus doubletons constituted an even larger proportion (65.2%). Even if a moderate proportion of these species is intolerant of the environmental changes brought about by fragmentation, this would translate into a significant decline in species richness in fragments.

We detected a consistent, decreasing gradient of strength of the relationship between fragment size and species richness as plant size category increases. This finding is consistent with our expectation that the effect of forest fragmentation should be diluted in the case of the largest plants, which include a contingent of species present prior to fragmentation. Although winds can be strong in this region (see González-Soriano et al. 1997), wind throw does not seem to have affected large trees yet, as has been observed in Amazonia (Laurance et al. 1998b, 2000). Although our findings of a lack of relationship between species richness and fragment size in the case of the large plants is contrasting with that of other authors (Turner 1996 and refs. therein; Hill and Curran 2003; Zhu et al. 2004), it remains to be seen whether the lack of effect in the large trees is just a transient state of a trajectory of species richness decline already in motion. Clearly, there is a need for studies of long-term monitoring and comparisons among fragments that have been excised for longer periods (Turner 1996, Hill and Curran 2003).

The observed gradient of response may reflect the situation likely to result after the "filtering" of the seed and seedling bank, as we considered the plants that have become established in the fragments. Our findings may represent a next stage in the decline of seedling species richness detected by Benitez-Malvido and Martinez-Ramos (2003). This study and the species diversity decline we observed at Los Tuxtlas when considering plants with DBH ≥ 1 cm, suggests a connection between seedling species richness decline and overall plant species richness reduction, but this needs to be corroborated by an equivalent study with seedlings at Los Tuxtlas.

In addition to the quantitative changes in species richness we detected a shift in species composition. In general, the species from CF defined a floristic group distinguishable from the assemblages of the fragments and such shifts were associated to the prevalence of light-demanding species in the fragments. On the other hand, our analysis of floristic similarity among fragments and CF suggested that, in general, similarity was greater among fragments than between fragments and continuous forest (see Scariot 1999; Benitez-Malvido and Martinez-Ramos 2003). However, floristic composition/similarity can be influenced by distance among fragments but we argue that this is not a determining factor of our results. When we examined if floristic dissimilarity is positively related to distance among fragments we found that floristic differentiation is occurring in our study site independently of the effect of distance/spatial location of fragments (rank correlation distance-similarity, Sperman's r_s=0.127, P=0.726), despite the fact the study sites were all located within a restricted range (0.298 and 4.29 km). We conclude therefore that fragmentation may be setting the vegetation in a trajectory of floristic differentiation, and we can also attempt to identify the taxa responsible for such shifts. Our comparison of plants of the two regeneration strategies consistently reflected differential susceptibility to fragmentation with an impoverishment of mature-forest species and proportionally increased richness of pioneer species in fragments. In particular, pioneer species have ecologies that reflect many generations of selection for resistance to fragmentation-like effects. In contrast, shade-tolerant species reflect adaptation to mature, continuous forest, with less selective pressure for tolerance to fragmentation-like effects. Therefore, when we analyzed the ranking of value of importance across fragments and CF, we found that while the dominant species in CF were typical shade-tolerant, mature-forest species, the smallest fragment had a marked dominance of light-demanding plants. This suggest that the future physiognomy of the fragmented landscapes will not be given only by the prevalence of secondary species in edges, roadsides, and clearings; it appears that, in the absence of compensatory effects, the forest remnants may be dominated by such species.

The greater susceptibility to fragmentation of the mature-forest species may also reflect an indirect effect consisting of the decline of animals important for plant recruitment, including pollinators, dispersal agents and even herbivores that mediate plant-plant interactions. The dramatic pace of defaunation in Los Tuxtlas and its consequences for plant diversity are analyzed elsewhere (Dirzo 2001; Mendoza et al.

2005) but those and other studies underscore the importance of such higher-order effects impacting plant diversity.

Another aspect directly related to higher-order effects, is the likelihood of invading exotic species, widely recognized as a driver of local species loss (Sala et al. 2000). Remarkably, out of the 3200 plants we observed, not a single one was an exotic species, even in the case of transects located close to the edge of the smallest fragment. An apparent resistance to invasions in diverse ecosystems has been referred to in other studies in which the undisturbed community is considered (Withmore 1991, Sala et al. 2000). Our findings are surprising, given the magnitude of disturbance and fragmentation of Los Tuxtlas and the fact that the surrounding matrix contains abundant herbaceous, shrubby, and arboreal exotics, including species from tropical regions (e.g., *Terminalia catalpa*, *Delonix regia*, etc.). The resistance of diverse ecosystems to invasions is an aspect of the relationship biodiversity-ecosystem functioning that warrants further research (see Rejmaneck 1996) but our observations in Los Tuxtlas lend support to that contention and suggest that other types of underlying mechanisms may be of greater significance than invasions.

In conclusion, our study adds to the still limited wave of ongoing investigations in the realm of the realistic conditions in which plants and animals are being exposed to the conditions of the real-world fragmented landscapes. Our main findings, including a significant reduction in species richness; a significant shift in species composition and a shift in the relative representation of the types of regeneration strategies associated to forest fragmentation confirm that this global environmental change is critical to the maintenance of tropical biodiversity. Finally, although our emphasis was on diversity metrics based on species or functional groups, implicit in our findings is another critical but largely ignored aspect of biodiversity loss, namely, the loss of local populations (see Hughes et al. 1997). This is where the most critical pulse of extinction due to tropical deforestation and fragmentation is likely to be occurring and we need to pay attention to it; yet this study suggests that the populations of mature-forest species are at greater risk.

These rapidly changing floristic configurations may have profound effects on our efforts to conserve, manage, and restore ecosystems. Although we typically deploy conservation and management efforts based on the composition and structure of relatively intact ecosystems, we need to consider how to preserve biodiversity and ecosystem services amid anthropogenic change. There is an increasing need to focus our research on the rapid biological change unfolding in human-dominated landscapes.

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CAPITULO II

Impacto de la Fragmentación de la Selva Sobre el Tamaño Poblacional de una Especie de Palma Estructuralmente Importante: *Astrocaryum mexicanum* en Los Tuxtlas, México

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Impact of Rain Forest Fragmentation on the Population Size of a Structurally Important Palm Species: *Astrocaryum mexicanum* at Los Tuxtlas, Mexico

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Impact of rain forest fragmentation on the population size of a structurally important palm species: *Astrocaryum mexicanum* at Los Tuxtlas, Mexico

ABSTRACT

Forest fragmentation changes the structure of natural landscapes causing shifts on the distribution and abundance of plant species that could lead to population extinctions. The tree palm *Astrocaryum mexicanum* is one of the most abundant plant species in the Los Tuxtlas region, Mexico. Nevertheless, 95% of the original rain forest in this region has disappeared, and remaining palm populations are present within landscapes that differ in their conservation status. To identify the landscape (e.g., amount of forest cover, fragment size, fragment shape and isolation) and vegetation (e.g., plant species richness, density and basal area) attributes that could influence the adult population size of *A. mexicanum*, we analyzed 45 forest fragments (< 1 - 266 ha) distributed in three landscapes that encompassed different levels of fragmentation, and compared with the population inhabiting the Los Tuxtlas Field Station (700 ha). Fragmentation affected the population size of *A. mexicanum*, with the smaller, most isolated and irregular forest fragments showing the lower number of individuals. The importance value index of *A. mexicanum* was greater in the most conserved landscape. Furthermore, palm density was positively correlated with species richness, density and basal area of old-growth forest species, but negatively correlated with richness of secondary forest species. Overall, the strong decline in population size of adult reproductive palms may affect the regeneration and genetic diversity of this species increasing its probability of extinction. The loss of this species from the remaining fragments may have dramatic consequence for the ecological functioning of this system.

Keywords: Arecaceae; common species; edge effect; forest fragmentation; isolation.

1. INTRODUCTION

Deforestation and fragmentation of natural ecosystems are some of the most pervasive global environmental changes, particularly affecting old-growth forests in tropical regions (Achard et al., 2002). Tropical rain forests are characterized by the presence of many tree species with low population densities, and very rarely one or two tree species are much more abundant than the rest (Richards, 1952; Hubbell and Foster, 1986). Such as in the case of the legume tree *Pentaclethra macroloba* at La Selva, Costa Rica (Hammel, 1990), the laurel tree *Nectandra ambigens* and the palm *Astrocaryum mexicanum* in the canopy and in the understory of Los Tuxtlas, Mexico, respectively (Sarukhán, 1978; Bongers et al., 1988), or the tree Family Dipterocarpaceae in South East Asia, that has a particularly large number of species and individuals (Whitmore, 1984). These abundant species are important constituents of these rain forests as many of their other features may be directly dependent on them. Because their importance on tropical rain forest structure and function it is relevant to study the effect of human disturbances such as forest fragmentation on abundant tree species.

The reduction of forest cover, coupled with shifts in landscape patterns (e.g., increase number of forest fragments, reduction in fragment size, increase of fragment isolation; Fahrig, 2003) can directly affect vegetation related ecological processes such as pollination, seed dispersal, seed predation, forest regeneration, and competition (Kearns et al., 1998; Wright and Duber, 2001; Aizen et al., 2002; Benítez-Malvido and Martínez-Ramos, 2003; Dupuy and Chazdon, 2006; Fleury and Galetti, 2006; Galetti et al., 2006), which in turn influence the distribution and abundance of several plant species (Turner et al., 1996; Hill and Curran, 2003; Arroyo-Rodríguez and Mandujano, 2006) that could lead to the loss of genetic diversity (Young, 1996) and extinction of numerous populations within the remaining forest patches (Turner et al., 1996; Hughes et al., 1997; Pimm and Brooks, 2000; Ferraz et al., 2003).

The forest edge is the most drastically altered zone of a fragment (Laurance and Yensen, 1991; Saunders et al., 1991; Murcia, 1995). Increments in the incidence of light and wind near edges may cause high tree mortality (Laurance et al., 1998, 2000), with the most damage suffered by large and emergent old-growth forest species (Benítez-Malvido, 1998; Hill and Curran, 2003; Arroyo-Rodríguez and Mandujano, 2006). However, our understanding of the impacts of forest fragmentation on plant populations is still rudimentary (Fahrig, 2003), and largely focused on woody trees, leaving aside other plant growth forms that are important components of forest structure and biodiversity (Laurance et al., 1998, 2000; Scariot, 1999; Zhu et al., 2004).

Palm species are important components of tropical rain forests being present at all forest strata (canopy, subcanopy and understorey). Furthermore, palms are important food resource for many animal species and have an important economic value for human populations (Scariot, 1999; Vormisto, 2002; Henderson, 2006). Despite of their abundance, because many palm species are obligate outcrossing (Murcia, 1996, Eguiarte et al. 1992), and pollination frequently depends on highly specialized insect species (Henderson, 1986; Listabarth, 2001) their populations are extremely susceptible to fragmentation. However, research on the effect of fragmentation on palms have reported contrasting results with some species and ontogenetic stages such as seedlings being particularly susceptible to forest fragmentation (Svenning, 1998; Scariot, 2001; Souza and Martins, 2002; Benítez-Malvido and Martínez-Ramos, 2003).

In this paper we present data on the palm *Astrocaryum mexicanum* Liebm. (Arecaceae) inhabiting rain forest fragments in the Los Tuxtlas Biosphere Reserve, Mexico. This species is very representative of the forest understorey of Los Tuxtlas, with around > 1,000 adult palms per hectare (Piñero et al., 1977). Although there is a lot of information concerning different aspects of its demography (Sarukhán, 1978; Piñero et al., 1984; Martínez-Ramos et al., 1988b), gap dynamics (Martínez-Ramos, 1985;

Martínez-Ramos et al., 1988a,b; Martínez-Ramos et al., 1989), and population genetics (Eguiarte et al., 1992, 1993), all studies have been conducted within the Los Tuxtlas Field Station (LTFS, 700 ha), and little is known about the effects of forest fragmentation on the abundance of this important palm species across the landscapes integrating the Biosphere Reserve.

We analyzed adult populations of *A. mexicanum* within 45 rain forest fragments distributed in three landscapes that encompassed different levels of fragmentation and addressed following questions: 1) What are the density patterns of *A. mexicanum* within the three landscapes?; and 2) What are the habitat attributes (i.e., fragment size, shape and isolation) with stronger influence on the density patterns of *A. mexicanum*.

In the Los Tuxtlas region 95% of the original tropical rain forest has already disappeared (Castillo-Campos and Laborde, 2004; Guevara et al., 2004). Therefore, our study is relevant for the conservation of this palm species because Los Tuxtlas holds the northern most *A. mexicanum* populations of the Neotropics, this species is very representative of this rain forest region and is involved in many ecological processes (Martínez-Ramos, 1997).

2. METHODS

2.1. Study Site

Los Tuxtlas is located in the southeast of the Veracruz State, Mexico (18º 8´-18º45´ N, 94º 37´-95º 22´ W (Fig. 1).

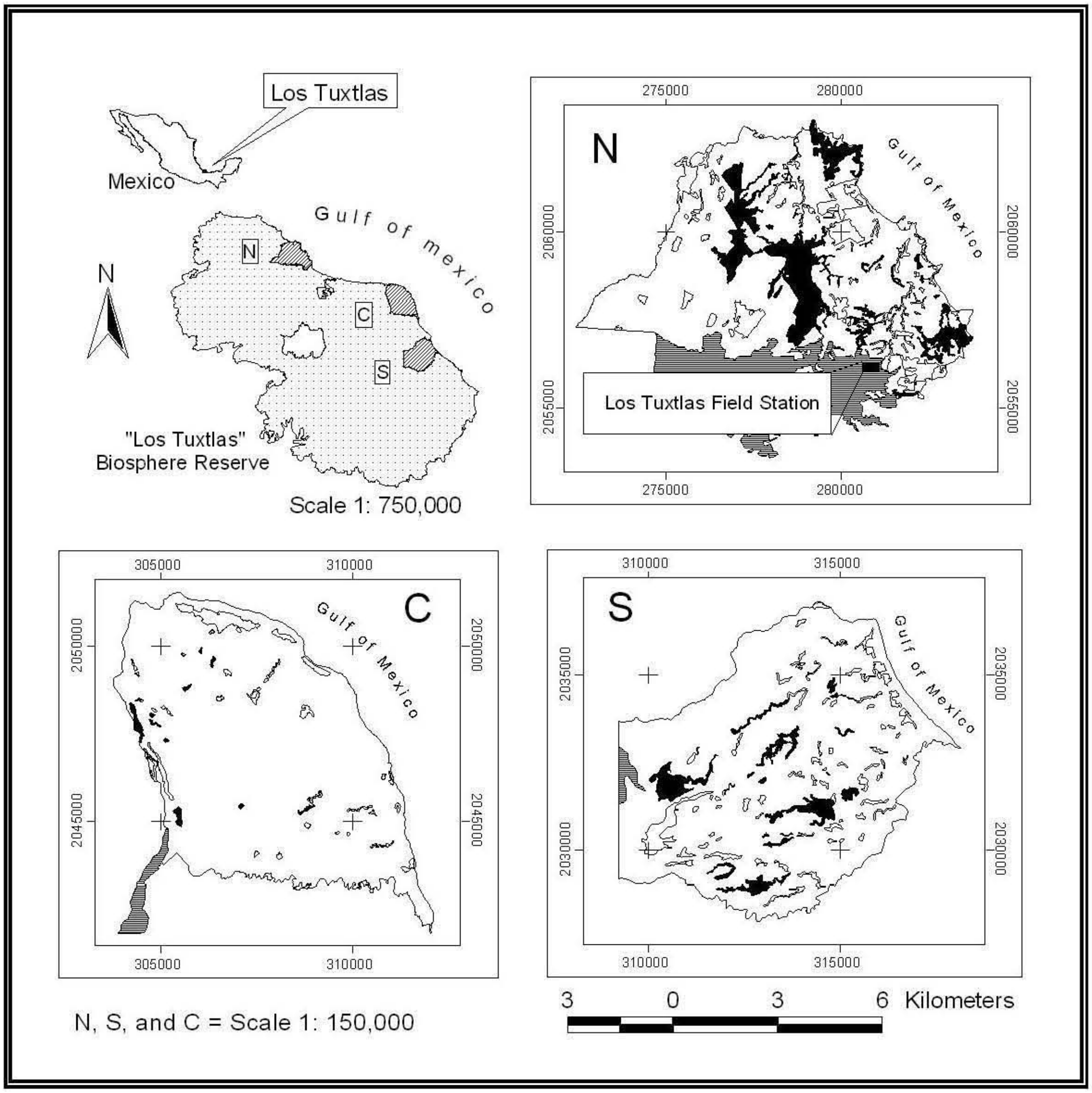


Figure. 1. Location of the three landscapes (N = Northern, S = Southern and C = Central) studied in the Los Tuxtlas Biosphere Reserve, southeastern Veracruz, Mexico. Nearest continuous forest (striped polygons), the Los Tuxtlas Field Station, fragments occupied (black polygons) and unoccupied (white polygons) by adult individuals of the palm *Astrocaryum mexicanum* are indicated on the map.

The climate is warm, with a mean annual temperature of 25ºC, and annual rainfall between 3,000 – 4,600 mm; elevation ranges from 0 to 1,780 m a.s.l. (Guevara et al., 2004). The region was heavily deforested and fragmented between 1972 and 1993 (Guevara et al., 2004), but Los Tuxtlas was decreed a Special Biosphere Reserve in 1998 (Diario Oficial de la Federación, 1998), as it represents the northern limit of tropical rain forest distribution in the Neotropics with high and unique biodiversity (Dirzo and Garcia, 1992; Castillo-Campos and Laborde, 2004). The Reserve covers an area of 155,122 ha, and it is naturally divided in three regions: the northern San Martin Tuxtla Volcano landscape; the central Sierra de Santa Marta landscape; and the southern San Martin Pajapan Volcano landscape (Guevara et al., 2004). The original dominant vegetation type (below 700 m a.s.l.) was tropical rain forest, but it is actually highly fragmented and surrounded by a matrix of pastures and croplands (Castillo-Campos and Laborde, 2004).

2.2. The study species

The tree palm *A. mexicanum* is the only species of the genus in Mexico (Henderson, 1986). In Los Tuxtlas it is distributed between 0 and 700 m a.s.l. (Martínez-Ramos, 1997). Its reproductive stage starts at the age of about 40 y and in certain individuals lasts for more than 100 y. Adult palms can hold more than five inflorescences in a reproductive season (Búrquez et al., 1987), which are highly appreciated by the local people as a food resource (fruits and flowers; Martínez-Ramos, 1997). The species is monoic (with dicogamy) and obligate outcrossing (Búrquez et al., 1987; Eguiarte et al., 1992). Pollination is throughout small beetles (Coleptera: Nitidulidae) (Búrquez et al., 1987). The principal dispersal mode is by gravity although there is evidence of secondary dispersion by small mammals (Eguiarte et al., 1993). The species is shade-tolerant and individuals could be drastically affected if exposed to the intense solar radiation present in forest gaps and edges (Martínez-Ramos, 1997). Despite of its commonness, the combination of these attributes makes *A. mexicanum* a particular sensitive species to habitat loss and fragmentation (see Henle et al., 2004).

2.3. Data collection

We selected three landscape units considering that they: 1) represent a gradient of habitat loss and fragmentation; 2) are situated between 0 and 400 m a.s.l.; and 3) each has an approximate area of 5,000 ha (Table 1; Fig. 1). The landscapes were digitized through ArcView 3.2 (ESRI®) software using aerial photographs (1:20 000, INEGI, 1999), ortophotos (INEGI, 1996), digital data (INEGI, 1990) and field information. The northern landscape covers 4,656 ha, 24% of which correspond to rain forest distributed among 74 fragments (0.5 to 266 ha); the southern landscape covers 4,965 ha, 11% of which correspond to forest distributed among 88 fragments (0.5 to 76 ha); and the central landscape covers 5,046 ha, with only a 4% of remaining rain forest in 46 fragments (0.5 to 68 ha).

We randomly selected 45 forest fragments (15 per landscape). Information on fragment size, isolation, and shape was calculated for the 45 fragments using the Patch Analyst 2.2 extension for Arc View 3.2 (Rempel and Elkie, 1999). Isolation distances were measured considering the nearest fragment, nearest road, and the nearest village, as these variables may be related to dispersion patterns and several human disturbances (Hill and Curran, 2003; Arroyo-Rodríguez and Mandujano, 2006). Fragment shape was calculated using the shape index suggested by Forman and Godron (1986) as: $IF = P/\sqrt{A\pi}$; where *P* and *A* are the fragment perimeter and area measured in meters, respectively. The index takes values equal to 1 when the fragment is circular, and goes up to a maximum of 5 when the fragment shape is highly irregular. The largest forested area (ca. 700 ha) comprises the Los Tuxtlas Field Station (LTFS). The vegetation type at LTFS is the same as in the fragmented landscapes and located at the same altitude (Ibarra-Manríquez et al., 1997; Castillo-Campos and Laborde, 2004).

On each fragment and in LTFS, we randomly located ten 50 x 2 m transects (0.1 ha) (Gentry, 1982). Thereafter, we recorded all adult individuals of *A. mexicanum* (> 1.3 m tall; Piñero et al., 1986). To relate the population size of palms with the vegetation present in each transect, we also recorded all species of trees, shrubs and lianas with ≥ 2.5 cm d.b.h. Because the dominance of different functional groups can be indicative of forest disturbances (Benítez-Malvido, 1998; Laurance et al., 1998, 2000, 2006; Hill and Curran, 2003), plant species were classified into three groups according to their light requirements for germination as (Hill and Curran, 2003): old-growth species, secondary species, and non-secondary light demanding (NSLD) species. Old-growth species establish mainly under forest shade and persist in old-growth forests. Secondary species need intense light during the first stages of growth, establishing only under canopy gaps and at the forest edge and they do not persist in the old-growth forest. Finally, NSLD species grow under similar light requirements as secondary species, and during the first growth stages they can be found together with secondary species, but they have longer life cycles, and grow to become species characteristic of the old-growth forest canopy. The classification was based on *Flora de Veracruz* and *Flora Neotropica*; as well as from several species lists (for further details see Arroyo-Rodríguez and Mandujano, 2006).

	Northern	Southern	Central	χ²
Total area (ha)	4,656	4,965	5,046	-
Total forest cover (ha)	1,107	542	216	-
Percent of forest cover	23.8%	10.9%	4.3%	-
Number of forest fragments	74	88	46	-
Fragment size (ha)	15.2 (40.3)	6.1 (12.7)	4.7 (10.3)	6.7*
Shape index[a]	2.2 (1.0)	1.9 (0.7)	1.8 (0.6)	9.3**
DNF (m)	102.7 (172.0)	112.7 (99.9)	288.7 (299.8)	34.6**
DNR (m)	423.5 (519.0)	443.9 (518.3)	333.0 (435.1)	1.6 n.s.
DNV (m)	1,462.5 (1,240.4)	889.8 (662.6)	1,725.3 (1,175.7)	24.7**
Number of villages	4	8	3	

Table 1. Characteristics of the three fragmented landscapes studied at Los Tuxtlas, Mexico. Fragment size (ha), shape, and isolation distances (mean ± SD) to the nearest forest fragment (DNF), to the nearest road (DNR), and to the nearest village (DNV), are reported. Differences among landscapes were analyzed with generalized linear models (d.f. = 2, for all cases). * $p < 0.05$; ** $p < 0.01$; n.s. = not significant

2.4. Data analysis

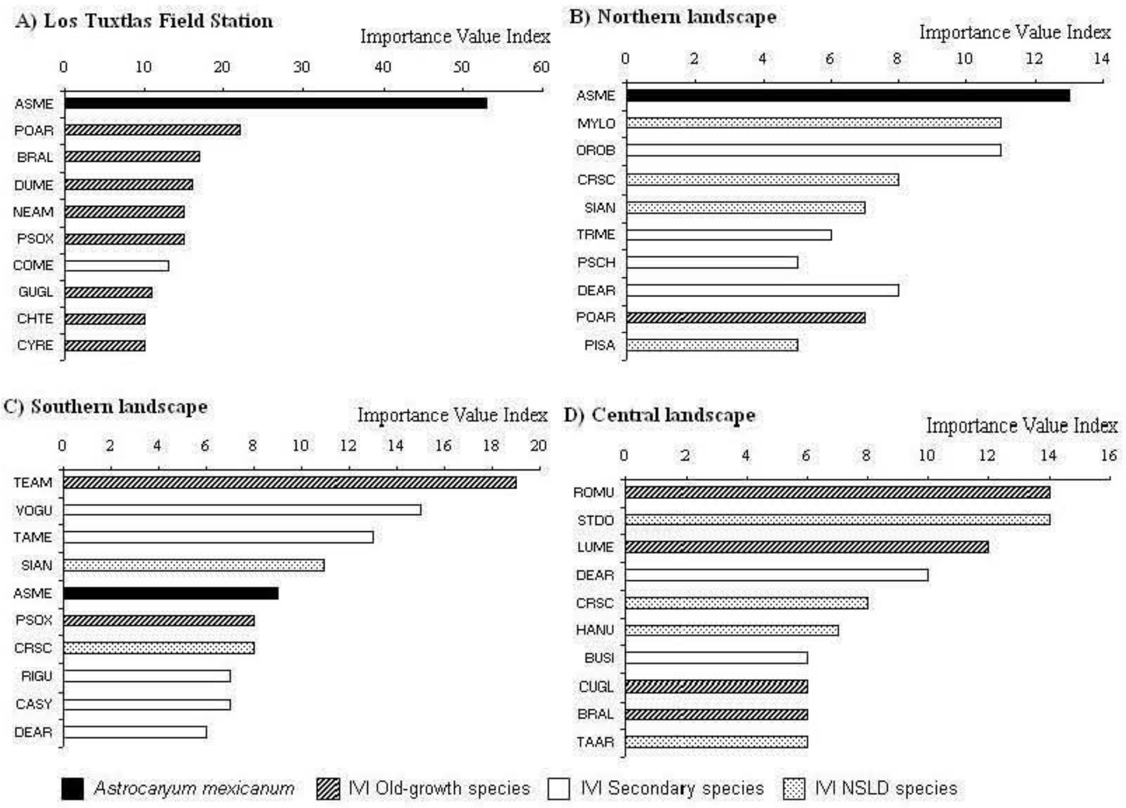
For each fragment we quantified the adult population size of *A. mexicanum*, as well as species richness, density, and basal area (m^2) for each functional group. On the basis of the sum of density, frequency and basal area, the importance value index (IVI) was calculated for each species on each fragment (Moore and Chapman, 1986). To test differences in population size between landscapes we used an analysis of deviance with generalized linear models (GLM). We fixed a Poisson error (to a count dependent variable) and corrected for overdispersion (Crawley, 2002). As fragments differed in size within landscapes (Table 1), and this may affect the structure and composition of the vegetation (Hill and Curran, 2003; Arroyo-Rodríguez and Mandujano, 2006), fragment size was included as a covariable in the model (Crawley, 2002).

To identify the landscape attributes (i.e., fragment size, shape and isolation) affecting the density of palms we used multiple regression analysis with GLM (Crawley, 2002), considering LTFS as the largest (700 ha), most regular fragment (shape index = 1), with zero isolation. We used Akaike's information criterion (AIC) to objectively select the most parsimonious model, i.e., the minimal adequate model (Motulsky and Christopoulos, 2003). To test whether or not palm density was related to the richness, density and basal area of old-growth, secondary and NSLD species, we used the Pearson correlation analysis. All analyses were performed using the S-Plus Program for Windows, version 2000. Significance was set at $p < 0.05$.

3. RESULTS

Adults of *A. mexicanum* were present in 38 out of 45 fragments, summarizing a total of 552 individuals. Six of the fragments presented only one individual per 1,000 m^2, 15 fragments presented between 2 and 10 individuals, six fragments between 11 and 20 individuals, five between 21 and 30 individuals, and six fragments between 31 and 49 individuals. In contrast, the LTFS presented 90 individuals per 1 000 m^2.

Taking fragment size as a covariate, the density of palms was not significantly different among landscapes (Wald, $\chi^2 = 1.94$, d.f. = 2, $p = 0.38$). However, IVI analysis showed that *A. mexicanum* was the most important species in the LTFS, as well as in the fragments within the best preserved northern landscape (Fig. 2). In the southern and central landscapes this palm species ranked fifth and eleventh in the IVI, respectively (Fig. 2). For these landscapes, secondary species such as *Siparuna andina*, *Stemmadenia donnell-smithii*, and *Croton schiedeanus*, and NSLD species such as *Vochysia guatemalensis*, *Tapirira mexicana* and *Bursera simaruba*, hold IVI greater than *A. mexicanum* (Fig. 2).



Astrocaryum mexicanum	(Arecaceae)	ASME	*Nectandra ambigens*	(Lauraceae)	NEAM
Brosimum alicastrum	(Moraceae)	BRAL	*Orthion oblanceolatum*	(Violaceae)	OROB
Bursera simaruba	(Burseraceae)	BUSI	*Piper sanctum*	(Piperaceae)	PISA
Casearia sylvestris	(Flacourtiaceae)	CASY	*Poulsenia armata*	(Moraceae)	POAR
Chamaedorea tepejilote	(Arecaceae)	CHTE	*Pseudolmedia oxyphyllaria*	(Moraceae)	PSOX
Cordia megalantha	(Boraginaceae)	COME	*Psychotria chiapensis*	(Rubiaceae)	PSCH
Croton schiedeanus	(Euphorbiaceae)	CRSC	*Rinorea guatemalensis*	(Violaceae)	RIGU
Cupania glabra	(Sapindaceae)	CUGL	*Rollinia mucosa*	(Annonaceae)	ROMU
Cynometra retusa	(Caesalpinaceae)	CYRE	*Siparuna andina*	(Monimiaceae)	SIAN
Dendropanax arboreus	(Araliaceae)	DEAR	*Stemmadenia donnell-smithii*	(Apocynaceae)	STDO
Dussia mexicana	(Fabaceae)	DUME	*Tabernamontana arborea*	(Apocynaceae)	TAAR
Guarea glabra raza *bijuga*	(Meliaceae)	GUGL	*Tapirira mexicana*	(Anacardiaceae)	TAME
Hampea nutricia	(Malvaceae)	HANU	*Terminalia amazonia*	(Combretaceae)	TEAM
Lunania mexicana	(Lauraceae)	LUME	*Trophis mexicana*	(Moraceae)	TRME
Myriocarpa longipes	(Urticaceae)	MYLO	*Vochysia guatemalensis*	(Vochysiaceae)	VOGU

Figure. 2. The ten plant species with the highest importance value indices (IVI) in Los Tuxtlas Field Station, and in 45 forest fragments in three fragmented landscapes (northern, southern and central; 15 patches per landscape) at Los Tuxtlas, Mexico. The ecological group of each plant species (NSLD = non-secondary light demanding species) is indicated.

The density of *A. mexicanum* was positively and significantly related to fragment size (Wald, $\chi^2 = 10.1$, d.f. = 1, $p < 0.01$), being the most irregular (Wald, $\chi^2 = 4.4$, d.f. = 1, $p < 0.05$) and isolated fragments (Wald, $\chi^2 = 3.9$, d.f. = 1, $p < 0.05$) the ones with the lowest density (Table 2). Furthermore, density was positively and significantly correlated with species richness (r = 0.39, $p < 0.01$), density (r = 0.62, $p < 0.001$) and basal area (r = 0.55, $p < 0.001$) of old-growth forest species, but negatively and significantly correlated with the richness of secondary species (r = -0.37, $p < 0.05$).

Predictor factors	Parameters	SE	χ^2	*p*
Fragment size	0.32	0.10	10.1	0.002
Shape index	-0.66	0.31	4.4	0.035
Distance to nearest forest fragment	-0.33	0.17	3.9	0.049
Distance to nearest road	0.11	0.08	1.9	0.160
Intercept	3.21	0.90	12.8	0.000

Table 2. Results from the generalized linear model to test for the effect of five fragment attributes (size, shape, and distance to the nearest fragment, road, and village) on the population density of *Astrocaryum mexicanum*. The minimal adequate model was constructed using the Akaike Information Criterion.

4. DISCUSSION

Our results showed that in the Los Tuxtlas region, Mexico, the adult population size of *A. mexicanum* is strongly affected by habitat loss and fragmentation, with the smaller, most isolated and irregular forest fragments showing the lower number of individuals. The reduced population size in fragments could be explained by a complex interplay of factors of two kinds: those that increase palm mortality (e.g., edge effects), and those that reduce palm recruitment (e.g., reduced dispersal).

4.1. Fragment size, shape and edge effects

Small and more irregular fragments presented lower densities of palms. Fragments with such characteristics have greater edge effects that may increase tree mortality and the number of tree fall gaps (Laurance and Yensen, 1991; Murcia, 1995; Laurance et al., 1998, 2000). Furthermore, the studied fragments were surrounded by pastures and croplands which make edge effects stronger than when surrounded by secondary regrowth (Mesquita et al., 1999; Laurance et al. 2006). Previous studies in the closed canopy of the LTFS showed that more than one-third of adults *A. mexicanum* deaths were by falling trees and canopy debris (Martínez-Ramos et al., 1989). Therefore, palm mortality risks by mechanical damage and exposure to high light levels could increase within forest fragments as tree falls are common within and along fragments edges (Martínez-Ramos et al., 1988a; Martínez-Ramos, 1997).

The density of *A. mexicanum* was positively correlated to species richness, density and basal area of old-growth forest species suggesting that the abundance of *A. mexicanum* is greater in larger fragments that present a closer canopy and are less affected by edge effects than the small ones (Murcia, 1995). In the northern landscape and in the LTFS, we found that *A. mexicanum* was the most important plant species (greater IVI). The northern landscape presents the greatest forest cover, with larger and less isolated fragments, and with fewer human settlements. In contrast, for the southern and central landscapes, with a low amount of forest cover, the IVI of *A. mexicanum* decreased notably. These observations support the idea that fragmentation tends to change forest's species composition (Benítez-Malvido, 1998; Harrison and Bruna, 1998; Benítez-Malvido and Martínez-Ramos, 2003; Arroyo-Rodríguez and Mandujano, 2006; Laurance et al., 2006), largely due to differences between species sensibility to forest fragmentation (see Henle et al., 2004; Ewers and Didham, 2006).

4.2. Fragment isolation, dispersal and recruitment

The low dispersal capacity of *A. mexicanum* could explain why the most isolated fragments presented the lowest density of palms. The seeds of *A. mexicanum* are large and principally dispersed by gravity (Búrquez et al., 1987). Nevertheless, some rodents act as secondary dispersers moving seeds up to 15 m away from the parent (Eguiarte et al., 1993). Increase fragment isolation, the type of surrounding matrix (pastures and croplands), and the severe defaunation (several species of mammal dispersers have disappeared; Dirzo and Miranda, 1991) at the Los Tuxtlas region, may be modifying the dispersal and colonization potential of *A. mexicanum*, as well as for other plant species (Arroyo-Rodríguez and Mandujano, 2006), affecting the composition and structure of the vegetation within the fragments.

As for most large-seeded species, successful recruitment of *A. mexicanum* may be highly affected by the spatial variations in the distribution and abundance of both seed and seedling predators and seed dispersers (Smythe, 1989; Wright and Duber, 2001; Fleury and Galetti, 2006; Galetti et al., 2006). The negative effects of forest fragmentation and defaunation on the abundance of seedlings have been reported for several plant species including palms (Scariot, 1999; Benitez-Malvido and Martínez-Ramos, 2003; Fleury and Galetti, 2006; Galetti et al., 2006). For example, studies on the palm species *Attalea* in central Panama and southeastern Brazil (Wright and Duber, 2001; Souza and Martins, 2002) and *Astrocaryum aculeatissimum* in the Atlantic forest of Brazil (Galetti et al., 2006), showed that the absence of scatter-hoarding rodents as a consequence of anthropogenic disturbances such as hunting and habitat fragmentation, reduces seed dispersal (Wright and Duber, 2001; Souza and Martins, 2002; Galetti et al., 2006). Therefore, limited dispersal in addition to unfavorable environmental conditions makes the recovery of *A. mexicanum* populations within fragments very difficult.

4.3. Decrease in population size and implications for conservation

Overall, we found that forest fragmentation caused an important decline in the adult population size of *A. mexicanum*. Previous studies within the LTFS showed that this palm species was the most conspicuous component of the understorey vegetation with more than 1,000 individuals per hectare (Piñero et al., 1977). Based on its density and population dynamics previous studies suggested that the populations of *A. mexicanum* were numerically stable (Martínez-Ramos et al., 1988a), and our findings on palm density for the LTFS are consistent with those reported 30 y ago (Piñero et al., 1977). However, *A. mexicanum* was absent in seven out of the 45 fragments considered; whereas 6 fragments presented only one individual, suggesting a drastic decline in population size for some fragments.

The decline in the adult population size was more severe in small, more irregular and isolated fragments. Similar results were reported for the Brazilian Amazon with greater density and species richness of young palms in old-growth continuous forest than in forest fragments (Benítez-Malvido and Martínez-Ramos, 2003, Scariot 1999, 2001); whereas in a forest fragment of Singapur, shade tolerant palm species (rattans) were particularly vulnerable to extinction (Turner et al., 1996). The reduction in population size within fragments may decrease the “seed rain” (see Benítez-Malvido, 1998) and increase demographic stochasticity and the extinction probability (Álvarez-Buylla et al., 1996). Furthermore, as *A. mexicanum* is obligate outcrossing and requires biotic pollination, decrease population size may increase the loss of genetic diversity and may favor endogamy (Eguiarte et al., 1992, 1993). Estimations have suggested that the effective population size of *A. mexicanum* in Los Tuxtlas is around 300 individuals per hectare (Eguiarte et al., 1993). In our study only six (13%) of the 45 fragments presented abundances above 300 individuals per hectare. Therefore, it is likely that the populations of *A. mexicanum* in most of the studied fragments are not genetically viable.

Our findings suggest that the natural regeneration (few reproductive individuals) and therefore the permanence of *A. mexicanum* are compromised in the forest fragments at Los Tuxtlas region. Considering that *A. mexicanum* is one of the most important structural components of the forest in Los Tuxtlas (Martínez-Ramos, 1997), its loss may have dramatic consequence for the ecological functioning of this system. Fruits of *A. mexicanum* represent an important food source for numerous mammal species (e.g, *Sciurus depeii*, *S. aureogaster*, *Peromyscus mexicanus*, *Heteromys desmarestianus*, *Dasyprocta punctata*, *Agouti paca*) (Martínez-Ramos, 1997), and their inflorescences sustain a diverse arthropod fauna (ca. 60 species), which are also negatively affected by fragment size (Aguirre and Dirzo, 2007). Therefore, the decline of *A. mexicanum* populations can also reduce biodiversity of these fragments in the Los Tuxtlas region.

Finally, some actions that could be implemented to reduce the decay of *A. mexicanum* at Los Tuxtlas region, could be: (1) the protection of the largest fragments within the reserve to maintain the last viable populations of this palm species in the region; and (2) direct seed sowing and planting of seedlings and juveniles from different populations of *A. mexicanum* in the most isolated fragments that may not be naturally colonized by the species. However, smaller and most irregular forest fragments should not be considered for this, as they are probably under abiotic and/or biotic effects not only on the edge, but in their entire extension, and these effects are probably acting as a bottleneck on *A. mexicanum* survival. In this regard, more research is needed in evaluating each step on *A. mexicanum* establishment. On the other hand, in Los Tuxtlas region the largest fragments are mainly found above 600 m a.s.l. As altitude increases, the rain forest gives way to cloud and scrub forests (Castillo-Campos and Laborde, 2004). Consequently, the most preserved and protected areas of the reserve are not actually protecting the main habitat of *A. mexicanum* (Martínez-Ramos, 1997). This highlights the need to increase conservation efforts in the most deforested and fragmented areas at the lowlands.

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CAPITULO III

Efecto del Tamaño del Fragmento Sobre la Abundancia de Polinizadores y Exito Reproductivo de una Palma Abundante del Sotobosque en una Selva Mexicana

Effects of Fragmentation on Pollinator Abundance and Fruit Set of an Abundant Understory Palm in a Mexican Tropical Forest

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Effects of Fragmentation on Pollinator Abundance and Fruit Set of an Abundant Understory Palm in a Mexican Tropical Forest

ABSTRACT

Tropical forest fragmentation affects both biodiversity and plant reproductive success when small, isolated fragments sustain a reduced diversity or abundance of pollinators. Fragmentation-related effects have been poorly investigated in the case of palms, an important structural and functional component of tropical forests. To examine the relationships between fragment size, diversity and abundance of flower visitors, and palm reproduction, we quantified the total arthropod fauna associated to 86 inflorescences of *Astrocaryum mexicanum* (Arecaceae), and the possible consequences on its fruit set. The sample yielded a remarkable total of 228,772 arthropods (10 orders, 60 species). Coleoptera was the predominant group (≥ 50% of the species), followed by Hymenoptera (20%), while the remaining (30%) was distributed among the other eight orders. We found a predominance of pollinating insects (Coleoptera-Nitidulidae), representing 85 % of all visitors. Pollinator abundance was negatively affected by fragmentation, with a 4.2-fold average difference between small (< 35 ha) and large (114-700 ha) fragments. However, fruit set was relatively high (≥ 0.7) and not affected by fragmentation during three reproductive seasons. This could be explained because small fragments retained remarkably high numbers of pollinators (1191.4 / inflorescence on average) and the high abundance of palms (and flowers) in fragments. Further research is needed, however, to assess if fragmentation restricts pollinator movements to plants within the fragments, leading to a reduction in genetic variation of the progeny present in forest remnants.

Keywords: *Astrocaryum*, Coleoptera, fragmentation, Los Tuxtlas, palms, pollination.

1. INTRODUCTION

Current patterns of land use in tropical forests (i.e., their conversion to grasslands for cattle ranching or agricultural fields) generate a landscape mosaic of fragments of different size, imbedded in a matrix of transformed lands (Dirzo, 2001; Mendoza et al., 2005; Arroyo-Rodríguez et al., 2007). Research on the biodiversity consequences of tropical fragmentation has focused on changes in species diversity or abundance of some groups of organisms, particularly birds and mammals (e.g., Ferraz et al., 2007; Corlett, 2006; Lees and Peres, 2006) and plants (Scariot, 1999; Laurance et al., 2000; Hill and Curran, 2005; Cagnolo et al., 2006; Laurance et al., 2006). In contrast, other groups of organisms, such as insects, have received comparatively less attention (see Didham et al., 1996; Driscoll and Weir 2005; Grimbacher et al., 2006; Vasconselos et al., 2006). This is so despite the fact that insects are critical in myriad ecological processes susceptible to be affected by fragmentation (see review in Didham et al., 1996; Tscharntke and Brandl, 2004; Valladares et al., 2006), including pollination (Kearns et al., 1998; Harris and Johnson, 2004; Ghazoul, 2005; Kremen et al., 2007). It is known that more than 90% of tropical tree species require of biotic agents, particularly insects, for their pollination (Bawa, 1990). Furthermore, a large proportion of all tropical plants are self-incompatible (Bawa, 1992), or have some mechanism to avoid selfing (dichogamia and herkogamy) (Kress and Beach, 1994). Thus, we could expect that in out-crossing plants remaining in isolated fragments the possibilities of receiving pollen from other compatible individuals would be low or even null, making them more vulnerable to the loss of genetic variation (Murcia, 1996; 2002; Honnay and Jacquemin, 2007). Aguilar et al., (2006) recently reviewed 54 publications (89 plant species, 45 families) and found that reproduction is negatively affected by habitat fragmentation, and that pollinators are crucial in these effects. However, most of the studies involved herbaceous perennial species and only a few were tropical tree species. Lowe et al.,

(2005) found that in seven out of ten studies of tropical trees there were negative consequences on seed set associated to a variety of habitat disturbances related to tree isolation. Likewise, Aizen et al. (2002) reviewed 25 studies involving 46 different species of plants and found that, in the case of herbaceous species, fragmentation had a negative effect on pollination and fruit or seed set in 92% and 76% of the studies, respectively. The corresponding numbers for trees were 50% and 56%. Nevertheless, most of the studies in their review involved herbaceous species from temperate ecosystems and only a minor fraction (10% of the studies) looked at species from tropical zones. In the case of trees, only three species were from tropical forests and, surprisingly, two of them (*Embothrium coccineum*, Proteaceae, and *Symphonia globulifera*, Butifferae) showed a positive effect of fragmentation on pollination, and only one (*Spondias mombin*, Anacardiaceae*)* showed negative effects. While the former two species are pollinated by birds, the latter is pollinated by insects. These results are intriguing, but studies are still too few to speculate whether in the tropics insect pollination is more affected than vertebrate pollination, and whether fragmentation has limited or no negative effects on pollination.

Fragmentation may be particularly critical for insect-pollinated plants since many important pollinators, including wasps, bees, and beetles, are of relatively small size (Ghazoul and McLeish, 2001; Listabarth, 2001; Ghazoul and Shaanker, 2004) and restricted capacity of movement and search range relative to the spatial configuration of the remnant forest fragments (but see Nason et al., 1996; 1998; Nason and Hamrick, 1997). Many tropical insects important for tree pollination are known to experience reduced abundances within small or isolated forest fragments (Aizen and Feinsinger, 1994; Didham et al., 1996; Murcia, 2002; Valdivia et al., 2006).

Palms, a group of floristically and structurally important plants in tropical forests, have received limited attention from the point of view of the effects of fragmentation on their reproductive biology. In their reproductive stage, palms are a diverse or abundant component of the upper and medium strata of tropical forests (Scariot, 1999), and a suite of species are also present in the understory as mature individuals. The study of the effects of fragmentation on palm reproductive biology is also important since many of them are obligate out-crossers (58% of the species) or dioecious (45% of the species) (Murcia, 1996) and many of them are of economic importance (Vormisto, 2002). Regarding their pollen vectors, Henderson (1986) distinguishes three pollination syndromes: cantharophily (beetle pollination), mellitophily (bee pollination), and miophily (fly pollination). Although most palms do not seem to exhibit a marked morphological fit and specialization in their flowers relative to pollinator morphology and behavior (Uhl and Dransfield, 1987), some cantharophilous species do (Bernal and Ervik, 1996; Listabarth, 1996; 2001; Henderson et al., 2000), and it is suggested that cantharophily is the predominant syndrome among understory palms (Kahn and de Granville, 1992; Henderson, 1995; Nuñez et al., 2005). Given that cantharophily generally involves small-sized insects, we would expect for fragmentation to have a negative impact on pollination of understory palms (Blanche and Cunningham, 2005).

Here we quantify the community of arthropods visiting the inflorescences of a tropical palm *Astrocaryum mexicanum* Liebm. to examine to what extent fragment size affects its flower visitors and, potentially, its reproductive success. This plant is a useful model to investigate fragmentation-related changes in pollination, given that it is an abundant plant in continuous forest and fragments and a previous study (Búrquez et al. 1987) reported details of its pollination biology and identify the main pollinators. We used this system to ask: i) what are the main visitors and pollinators to the inflorescences of *A. mexicanum* in forest fragments of different size? ii) to what extent is the abundance of the main pollinators affected by fragmentation? and, iii) if fragmentation affects pollinator abundance, to what extent does this in turn affect fruit set?

2. METHODS

2.1. Study site and selection of fragments

The area of the study site, Los Tuxtlas, is a mountainous region located in the State of Veracruz, SE Mexico (Fig. 1, Cap. I), and represents the northernmost limit of tropical rainforest distribution in the Americas (Dirzo and Miranda, 1991). The predominant vegetation in the lowlands is tropical rain forest, with considerable variations along the elevation range, including cloud forest and mixed (conifer and broadleaf) forests at higher elevations. Its latitudinal position and elevation range determine the existence of remarkable combinations of species of tropical and boreal origin (González-Soriano et al., 1997). In addition to the diversity of habitats, species richness in various groups of organisms is considerable, including a total of 950 known vascular plants (Ibarra et al., 1997). Characteristics of the region's physical environment, flora, fauna and natural history are described in detail in González-Soriano et al. (1997).

Although the area has been occupied by humans for a long time, the most extensive conversion, mostly to grasslands for cattle ranching, has occurred in the recent decades (Mendoza et al., 2005). Rates of deforestation corresponding to the decades of the 60's-late 80's were of the order of 4.3% per·year (Dirzo and García, 1992). Currently, forest remnants are restricted to the most inaccessible areas of the region and the spatial configuration of the landscape consists of a large number of small to very small fragments (< 1.0 ha) with only a few extensive areas still remaining (Mendoza et al., 2005).

For this study we chose isolated fragments of similar age (isolation time of continuous forest), with the same vegetation type, lowland tropical rain forest, and generally similar ecological conditions (ie, within a restricted elevation, same climate and edaphic characteristics). With these criteria, we selected five fragments of 2, 4, 19.4, 34.6, and 114.6 ha with ~30 years from excision, and an extensive tract of lowland forest (Table 1). The latter, corresponding to the Los Tuxtlas research station, extends westwards, towards the San Martin Volcano (~1600 m a.s.l.), encompassing a much larger area of relatively continuous forest, although tropical rain forest is restricted to the lowlands, representing an area of *c*. 700 ha.

Fragment code	**Area (ha)**	**Elevation (m a.s.l)**	**Geographic location (Lat-Long)**
F1	2	59	18°34’40.14”N – 95°03’58.84”W
F2	4	187	18°35’24.39”N – 95°03’32.14”W
F3	19.4	61	18°35’02.01”N – 95°03’43.66”W
F4	34.6	205	18°37’12.20”N – 95°05’04.61”W
F5	114.6	100	18°36’31.94”N – 95°05’40.60”W
F6	700	322	18°34’57.27”N – 95°05’02.78”W

Table 1. The selected study fragments in the area of Los Tuxtlas, Veracruz.

For the purposes of this study we considered this as a “large fragment” of 700 ha. Fragments were selected from direct exploration in the field and using an aerial photograph (scale 1:75,000) which was digitized using ILWIS 2.4 software to calculate the areas of each fragment (Fig. 1B, Cap. I).

2.2. Study system

Astrocaryum mexicanum Liebm. (Arecaceae) is a monoecious palm distributed in tropical rainforest areas of Southeast Mexico, and the only species of the genus in the country (Henderson, 1986). Its distribution in the region's altitudinal range is between 0 and 700 m a.s.l. In the forest of Los Tuxtlas this is the most abundant species in the understory, with an average density of 1000 palms ≥ 1 m height·ha (Martínez-Ramos, 1997). The reproductive stage of *A. mexicanum* begins at about 40 years of age and lasts for more than 100 years in certain individuals, with most of the reproductive individuals being in the height class of 2 to 6 m (Sarukhán, 1978; Piñero et al., 1984). The tallest individuals grow to a height of *c.* 8 m (Búrquez et al., 1987). Throughout the reproductive season a reproductive palm can have up to 5 inflorescences, each with an average of 4885 male flowers and 28 female flowers (Búrquez et al., 1987). Female flowers open synchronously on a given day, lasting until the morning of the following day, when opening of the male flowers begins. The male and female functions overlap for a short period in the same inflorescence, but at this time stigmatic receptivity is very low and the pollen is largely unviable (Búrquez et al., 1987) thus pollination requires the spatio-temporal coincidence of individuals in the two flower phases.

2.3. Insect sampling protocol

Within each fragment we established a 600 m^2 (30 x 20 m) permanent plot of plant observations, located in the center of each fragment. In each plot, used for a long-term demographic analysis, we located and tagged all plants of *A. mexicanum.* From these we selected a group of reproductive plants of a similar height (~age) to sample flower visitors.

Visitors to the inflorescences were collected during the flowering season (March-May) of 1999. The greatest concentration of male and female flowers per inflorescence during this period translated into the greatest availability of the reward offered to this plant (pollen grains) to flower vistors. Our sampling therefore included most visitors to flowers and not just a small sample that may not reflect the pollinator fauna. Within each plot we collected the inflorescences of 10 randomly selected palms in the female phase, and five in the male phase. With the aid of a ladder, we reached the inflorescence of each plant and using a thick-paper bag we rapidly encapsulated the inflorescence, without disturbing it, and removed it by cutting the peduncle with clippers. No visual evidence of insect escape was detected, and application of the same exact protocol insured that sampling was comparable among sites. All inflorescences were collected between 0700 and 0800 AM, the time in which we observed the most intense insect activity, consistent with observations by Búrquez et al. (1987). Upon collection, we placed a ball of cotton wool soaked in ethyl acetate in the bags with the inflorescences. The bags were transported to the laboratory for arthropod separation, quantification and individual identification. Insects, but particularly Coleoptera were the most abundant flower visitors. Sorting and identification was carried out with the assistance of Coleopterologist Dr. S. Zaragoza (Entomology Department, Institute of Biology, UNAM).

A first approximation to describe the arthropod communities visiting the flowers of *A. mexicanum* and the possible fragmentation-related changes in the identity and composition of the community was to sort insects by order. We calculated the number and percentage of individuals for all orders. From this we then defined the species richness and determined, based on a previous study on the pollination of *A. mexicanun* at Los Tuxtlas (Búrquez et al., 1987), and from direct observations in the field, which of them were the pollinators of this palm. Following Búrquez et al., (1987), we defined flower visitors as pollinators when, in addition to their massive, readily evident pollen loads, we observed that their behavior consisted of both collecting pollen from the flowers in the male phase and transfering it onto the receptive flowers in the female phase.

2.4. Fruit set calculation

At the fruiting peak of 1999 we collected one of the infructescences from a random sample of reproductive plants present within each of the permanent plots (*N*= 10 plants in years 1999 and 2000 and *N*= 20 in 2002, for a total of 60, 60 and 120, respectively)**.** We estimated fruit set as the ratio of the number of fruits/number of female flowers per infructescence/inflorescence. The number of flowers per inflorescence was defined by carefully counting the female flower scars from the mature infructescences. To insure reliability of flower counting, each of the scars in the rachis of the infructescence was tallied and a mark was placed with an indelible marking to avoid repeated or missed counting. The number of fruits was counted directly from the mature infructescences. To prevent that fruits that could have fallen off the infructescences would be missing in our counting, we placed a fruit trap (a basket made of cloth mesh held with wire) directly under the inflorescence. Such traps were firmly tied to the palms' trunks. Given that this year we did not find variation in fruit set across sites the same procedure was applied on the reproductive seasons of 2000 and 2002 to asses if this result was consistent among years.

3. RESULTS

3.1. Fauna associated to inflorescences of *A. mexicanum*

Our sampling collectively detected a remarkable abundance of arthropods: 228,772 individuals associated to all sampled inflorescences (and considering both male and female phases) of *A. mexicanum*. The vast majority of the observed animals were insects. Collectively, we found 10 orders (nine of Insecta and one of Arachnidae), 12 families and 60 species. On average, an inflorescence of *A. mexicanum* bears 2660.13 arthropods, including those present in the male and female phases of the inflorescence.

A quantitative evaluation of the distribution of the fauna associated to the inflorescences of *A. mexicanum* across fragments showed that, in each site, a minimum of 50 percent of the insect species corresponds to Coleoptera (Fig. 2A). Another important proportion corresponds to Hymenoptera (~20 %), while the remaining (~30 %) is distributed among two to four additional orders (Fig. 2A). The four smallest fragments (2, 4, 19.4, and 34.6 ha) had between five and six orders, while the two largest sites (114.6 and 700 ha) had four orders each. The total number of species per fragment ranged from 24 to 39, with the second smallest fragment (4 ha) showing the greatest number of species, 39, while the lowest number (24), was found in the smallest fragment (Fig. 2A). Apart from Coleoptera, many of the species present in the smallest fragments included visiting taxa that do not operate as pollinators.

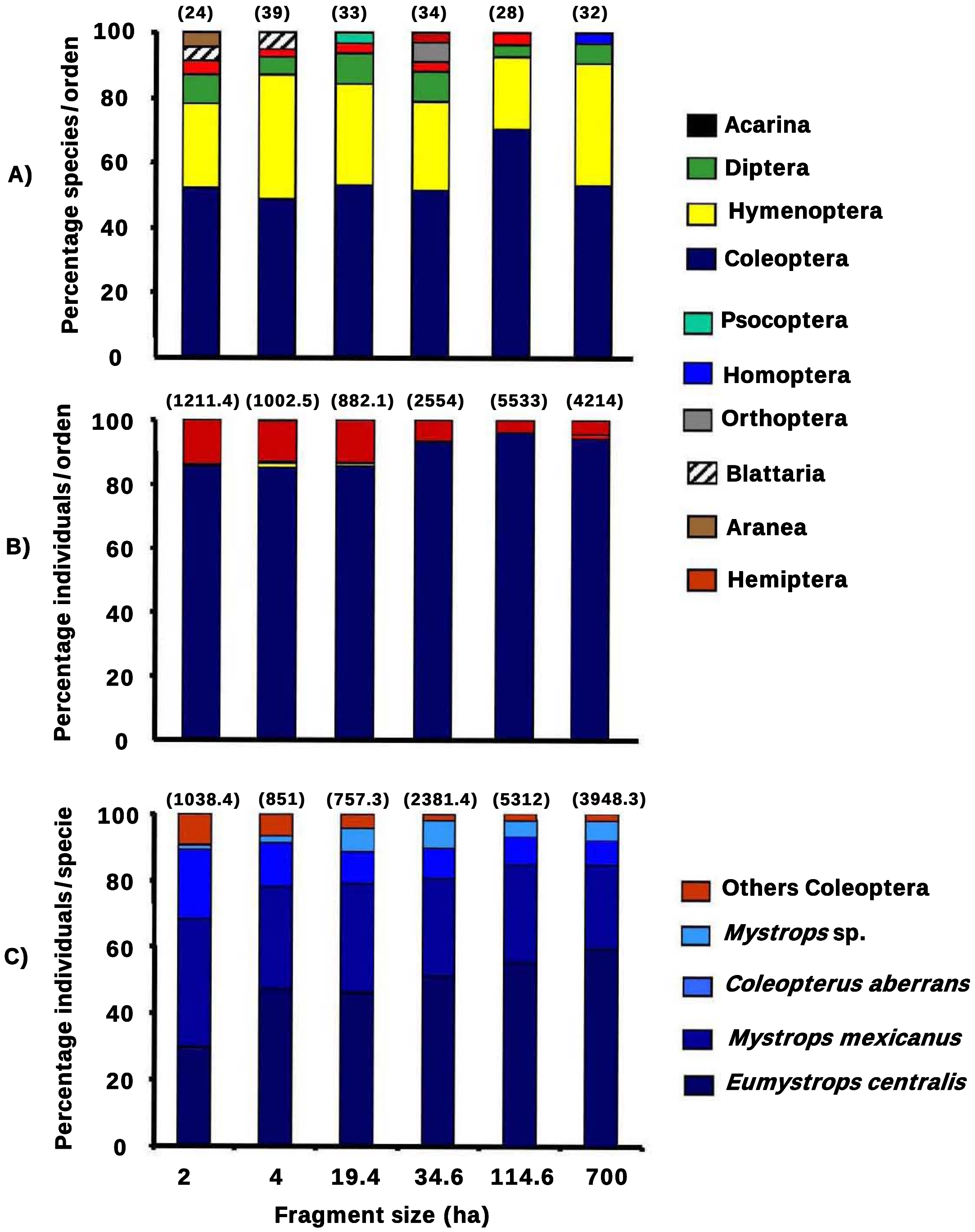

Figure 2. Arthropod fauna associated to the inflorescences of *Astrocaryum mexicanum*. A) Percent of species per order in each fragment; B) Abundance, as percentage of individuals per order; C) Abundance of beetles of the four species detected as the important pollinators. Numbers above the bars (in parenthesis) represent the total number of species (A), and the mean number of individuals (B and C) per inflorescence in each fragment.

The predominance of Coleoptera is even more noticeable when considering insect abundance (Fig. 2B). Overall, better than 85 % of the individuals collected in each fragment were Coleoptera, with abundances of 851 to 5312 beetles per inflorescence in each fragment. The abundance of Coleoptera is even more marked in the three largest fragments. Hemyptera was the second most abundant group (~10 %); the rest of the orders only represents a small proportion, in some cases with a single individual.

Among the Coleoptera, four species were identified as the most important pollinators, *Mystrops mexicanus*, *Coleopterus aberrans*, *Mystrops* sp. and *Eumystrops centralis*. This was determinated by our direct observation of their capacity to move within an inflorescence as well as among plants, and their pollen loads (determined by Búrquez et al. 1987), ranging from 430 to 711 pollen grains/animal. In addition, two of these four species (*E. centralis* and *M. mexicanus*) were the most abundant in all fragments, and the other two pollinators were present in abundances of 10-23 % (Fig. 2C). The rest of the species of Coleoptera appeared not to be important in the pollination in this palm (lack of pollen loads and limited mobility; A. Aguirre, pers. obs.) and these represented a very small proportion, of the order of up to 5-10 % in all fragments. Thus, the rest of our results focus on the pollinators.

3.2. Effects of fragment size on pollinator abundance

Pollinator abundance varied in relation to fragment size (cf. Fig. 2), with a trend of reduction in abundance in the smallest fragments. The trend, however, is not linear. Instead, a threshold is insinuated, in which the three or four smallest fragments present numbers of pollinators which were considerably smaller (1270-3879 pollinators/plant) than those of the other, largest (6383-9893) fragments. With the aim of a rigorously examining this trend, we ran a grouping analysis, UPGMA (Unweighted Pair Group Method) (MVSP, version 3.1) using the total number of pollinators per inflorescence. The results, using the first divise Euclidian distance (c. 3500), showed the definition of two major clusters: one composed of the two largest fragments (114.6 and 700 ha), which separates completely from the rest of the fragments. The second cluster is constituted by a well defined group of fragments of 2, 4 and 19.4 ha, which in turn join the 34.6 ha fragment at a Euclidean distance of 1600. Therefore subsequently data are analized with two-sample comparison tests, instead of regression-type analyses.

Using this approach, the effects of fragment size on the abundance of pollinators of *A. mexicanum* become readily evident. In the case of the total number of pollinators (all four species) and lumping the data for both phases of the inflorescences, we observe a 4.2 fold reduction in the number of pollinators in the small fragments (Fig. 3A) (*t*-test = 4.28, df = 4, *P* = 0.01). The results are consistent in both phases of the inflorescences although the difference is greater in the male (a 8.8 reduction) than in the female phase (a 3.4 reduction) (data not shown). An independent analysis considering *E. centralis* in both phases of the inflorescences (Fig. 3B) showed that the mean number of these pollinators is 6-times smaller in the small fragments (*t*-test = 6.11, df = 4, *P* = 0.003); contrasts were similar in the male (a 8.9 ratio) and female (a 5.1 ratio) phases (data not shown). Finally, in *M. mexicanus* (Fig. 3C) there was a 3.6-fold reduction in abundance in the small fragments (*t*-test = 3.67, df = 4, *P* = 0.02), with a greater contrast in the male phase (a 11.4 difference) than in the female phase (a 2.7 reduction) of the inflorescences (data not shown). Given this consistent and significant reduction in the abundance of pollinators in the smaller fragments, we would expect a concordant reduction in plant reproductive success associated to fragmentation.

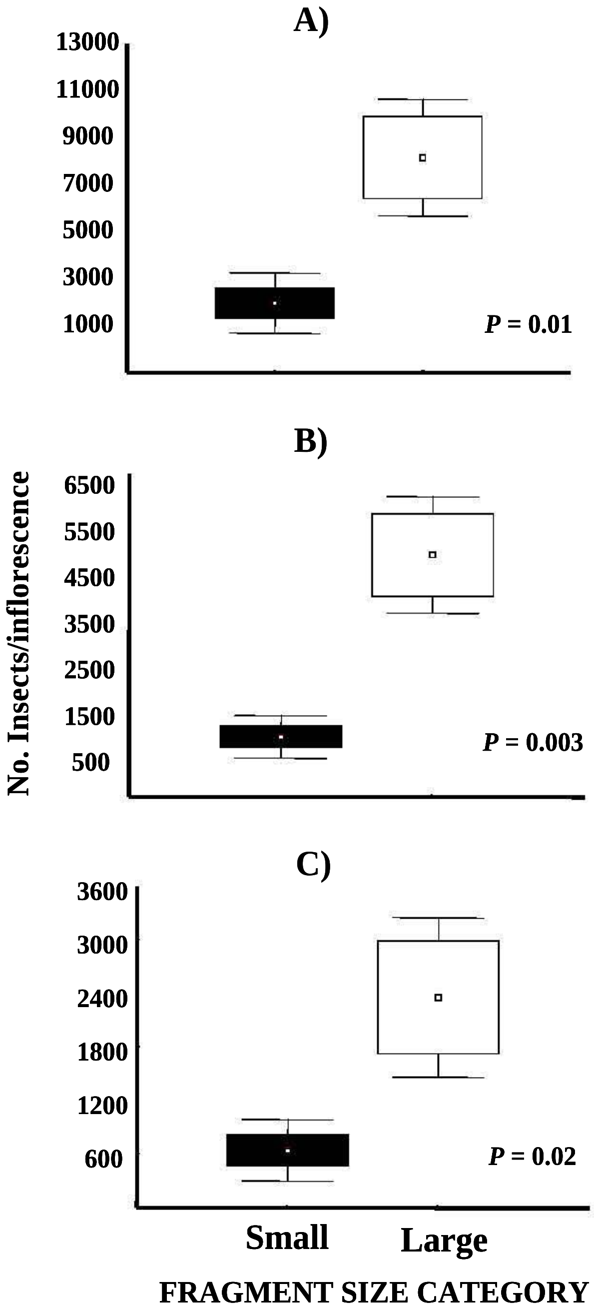

Fig. 3. Comparisons of pollinator abundance between fragments of contrasting size (small, large) in both sexual phases of the inflorescences of *Astrocaryum mexicanum*. A) corresponds to all four pollinators; B) *Eumystrops centralis*; C) *Mystrops mexicanus*. Box plots represent the mean, standard error and standard deviation of four (small) and two (large) fragments.

3.3. Effect of fragment size on fruit set

Fruit set was relatively high, at least 0.7 in all three years that we measured it. Variation among plants was noticeable, both in the small and large fragments (Fig. 4). In 1999, the year in which we observed the changes in pollinator abundance associated to fragment size, mean fruit set in small and large fragments was almost the same. When we quantified fruit set in two additional reproductive seasons, 2000 and 2002 we found remarkably consistent results and in no case were differences statistically significant (*t*-test*;* *P* > 0.233 in all three cases). In addition, we did not observe variation in the proportion of viable fruits per plant (*t*-test = 0.08, *P* = 0.94) and germination percentage (*t* test = 0.33, *P* = 0.74) across fragments.

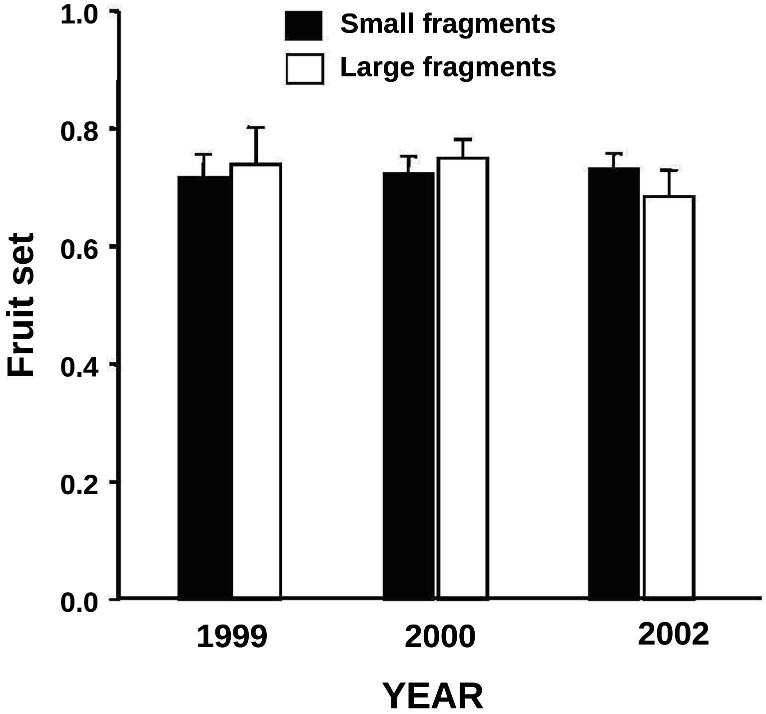

Fig. 4. Mean fruit set of plants from the two categories of fragment size in three different years. Lines above the bars represent standar error.

4. DISCUSSION

4.1. The contingent of arthropods associated to palm inflorescences

Taking into account the extremely high density of *A. mexicanum*, of *c*. 1,000 plants ≥ 1 m height·ha^{-1} (Piñero et al., 1977; Martínez-Ramos, 1997), and that in a given year the number of reproductive plants is around 300·ha^{-1} (Martínez-Ramos, 1997), our finding of an average of 2660.13 arthropods per inflorescence translates into a number of 798,039 arthropods·ha^{-1} associated to this palm. This number is conservative, since reproductive palms may produce up to five inflorescences in a given reproductive season. Using a median value of 2.0 inflorescences per reproductive palm, the abundance of arthropods associated to the inflorescences of *A. mexicanum* in Los Tuxtlas is an astonishing number of 1.596 million arthropods·ha^{-1}. Furthermore, given the relatively small size of the inflorescences (only ~40 cm length and 24.95 ± 1.04 g dry weight), the density of arthropods is remarkable: our data suggest an animal load of 106.6 animals·g^{-1} of inflorescence. These findings underscore the importance of *A. mexicanum* in particular, and of palms in general, as a resource, either trophic, or habitat, or both, for insects in tropical forests. A recent paper (Ellwood and Foster, 2004) reported an estimated abundance of 1.16 million invertebrates·ha^{-1} associated to an abundant epiphytic fern (*Asplenium nidus*) in Borneo. Such striking number was used to argue that, by including the fauna of epiphytes, we can more than double the estimates of total invertebrate biomass in an entire tropical rain forest canopy. It is thus remarkable that our study yielded a similar estimate of abundance (biomass data not available) based only on the arthropod fauna associated to the inflorescences of a single, dominant palm.

From a taxonomic perspective, the highlight was the marked predominance of Coleoptera, which consistently represented *c*. 50 % of the sampled animals in all fragments. Species richness is similar to that found on other palms, including *Bactris* *bifida*, *B. monticola* and *B. gasipaes* (Listabarth, 1996); *Geonoma irena* and *G. cuneata* (Borchsenius, 1997), *Hyospathe elegans* (Listabarth, 2001), *Astrocaryum vulgare* (Consiglio and Bourne, 2001), *Attalea alleni* and *Wettinia quinaria* (Nuñez *et al.* 2005) in natural forests, and on *Elaeis guineensis* in crop plantations (Mayfield, 2005). This data set underscores the importance of palms as reservoirs of tropical biodiversity.

Although a relatively diverse arthropod fauna visited the inflorescences of *A. mexicanum,* only a few had the appropriate attributes to function as pollinators: i) the large amount of pollen transported on their body (range: 430 to 711 pollen grains/animal; Búrquez et al., 1987) and ii) their activity patterns, consisting in both collecting pollen from the flowers in the male phase, and the transfer of pollen onto the receptive flowers during the female phase (Búrquez et al., 1987; Anderson et al., 1988; Núñez et al., 2005). Such contingent of species included those previously reported by Búrquez et al. (1987) and the two aditional species (*E. centralis* and *M. mexicanus*) we detected in this study.

The additional contingent of non-Coleoptera taxa we observed largely corresponds to arthropods that do not seem to play a role in palm pollination (see Henderson, 1986; Búrquez et al., 1987; Listabarth, 1996). Furthermore, it is known that several of these animals can have a negative impact on the flowers. Some Orthopterans, for example, operate as flower consumers. This is the case of *Melanonotus* sp., a large phytophagous Tettigonid that, although of low abundance, is frequently found in the inflorescences of *A. mexicanum* (R. Dirzo, unpubl. data); likewise, some species of Diptera, Apidae and Vespidae were found carrying pollen but they are unlikely to have a positive role as pollinators of *A. mexicanum* given that, in addition to their low abundance, their relatively large size (particularly in the case of wasps and bees) prevents them from reaching the female flowers at the base of the inflorescences.

4.2. Fragment size and pollinator abundance

The abundance of Coleoptera in general, and of the pollinator beetles in particular, was high in all fragments, but there was significant variation associated to fragment size. Considering either all four species of pollinators or each species individually, we detected a marked numerical reduction in the smaller fragments. These trends are consistent with those reported in other systems (see Murcia, 1996 for a review), including woody plants in Argentinean dry forest chaco (Aizen and Feinsinger, 1994), herbs in temperate forests (Jennersten, 1998) and bee visitation rates (using chemical attractants) in Amazonia (Powell and Powell, 1987). Furthermore, Wang et al. (2005) found that the abundance of the wasps responsible for the pollination of *Ficus racemosa* decreases with fragmentation, while the abundance of non-pollinating, parasitic galling wasps, increases. Such differential change resonates with our findings of a decrease in the abundance of pollinators and an increase in the abundance of non-pollinating arthropods (including phytophagous insects that damage the inflorescences, and carnivorous arthropods that may prey on other visitors, including pollinators) in the smallest fragments or near the fragments' edges (Chacoff and Aizen, 2006).

A noticeable fact of the impact of fragment size on pollinator abundance was the insinuation of a threshold. Although our resolution is limited given that we did not have sufficient fragments to represent all the size-variation across the range, in general fragments smaller than 35 ha had pollinator abundances that were 3.6- to 6.0-times lower than those of the fragments ≥ 100 ha. Reductions in pollinator abundance associated to fragmentation have been noticed in other studies with long-lived plants, including in semi-tropical ecosystems (e.g., Aizen and Feinsinger, 1994; Donaldson et al., 2002; Ghazoul and McLeish, 2001) but we are not aware of other studies in which such a magnitude of fragmentation-related reduction in pollinator abundance has been detected.

4.3. Fragment size and plant reproductive success

Although the significant and consistent reduction of pollinator abundance in both phases of the inflorescences in the smallest fragments opened the possibility of an indirect negative impact of fragmentation in terms of plant reproductive success, we found that there was no effect on the fruit set of the plants of the same study sites in the same year of the observations of pollinators. Furthermore, when we repeated the measurements of fruit set in two additional years, the results were the same. Although some studies have found evidence consistent with the expectation of negative effects of fragmentation on plant female reproductive success (seed set and/or fruit set) (Aizen and Feinsinger, 1994; Murcia, 1996; Gigord et al., 1999; Cunningham, 2000; Ghazoul and McLeish, 2001; Murren, 2002; Quesada et al., 2003; Harris and Johnson, 2004; Kolb, 2005), other researchers have reported findings similar to ours (Cascante et al., 2002; Aguilar and Galetto, 2004; Herrerias-Diego et al., 2006; Ramos and Santos, 2006). In a recent review, Ghazoul (2005) found that 21 of 51 studies analyzing the effect of patch size do not show detectable effects on pollination or some attribute of plant reproductive success.

A possible explanation for our results is that, even when pollinator reduction was substantial, the numbers of pollinators observed to be present in the plants of the small fragments were still considerably high (an average of 1191.4 pollinators, considering the four pollinator species). In addition, pollinators have considerably high pollen loads (Búrquez et al., 1986). Such pollinator abundances and pollen loads reflect the existence of several thousand pollen grains potentially available for deposition on an *A. mexicanum* inflorescence in the female phase. For example, this number is 1825 pollen grains/female flower/inflorescence, considering *Mystrops* sp. alone, the least abundant of the four pollinators. In general, male function in flowers of animal-pollinated plants needs repeated visits for the complete dispersion of pollen, while female flowers can cover all their pollen needs with a single visit (Bell, 1985, Stanton et al., 1986). Thus, since the female flower of *A. mexicanum* has only one ovule to pollinate, and there are few female flowers per inflorescence relative to male flowers (4885 male flowers: 28 female flowers; Búrquez et al., 1987), we can expect that most of the female flowers will be pollinated. These observations and the consistently high values of fruit set, suggest that our finding of a lack of effects of fragmentation on fruit set is probably due to the abundance of the remaining pollinators. Indeed, with the palm densities in this area, it seems fragments of almost any size would have sufficient numbers of neighboring palms to cross with. However, from the pollination point of view, effective densities are low because not all palms in a given patch reproduce at the same time and, furthermore, not all reproductive plants operate as pollen donors and receptive plants at the same time. This implies that with the extremely high abundances of pollinators we detected, fruit set could still be achieved even in the smallest fragments, although with pollen flow restricted to those plants co-ocurring within the fragments. This may have genetic consequences, as we discuss below.

4.4. Implications and further work

Our result of undetectable effects of fragmentation on fruit set is significant, yet it does not necessarily imply that fragmentation has an innocuous effect on plant reproductive biology, particularly from the genetic diversity point of view. Although we have observed that pollinators can actively fly among neighboring palms in the forest understory, we have not observed them flying over long-distances, especially not across the extensive cattle grasslands that surround the fragments. We therefore posit that most or all of the pollination and fruit set that takes place within the small fragments is likely to involve the few neighboring reproductive plants present therein. This is consistent with the fact that Eguiarte et al., (1993) found that *A. mexicanum* pollen can be dispersed only up to 20 m.

In addition, these authors found that gene flow via seed dispersal is even more restricted, up to about 3 m. We therefore predict that gene flow onto small fragments is restricted and that genetic diversity of the plants that are being recruited in the small fragments is likely to be reduced. We are currently investigating the indirect effects of fragmentation on genetic diversity using genetic and ecological performance analysis of progenies of *A. mexicanun* from small and large fragments in Los Tuxtlas. Research is needed to assess if fragmentation leads to a reduction in genetic variation of the progeny present in forest remnants, even in those systems in which pollination and fruit or seed set appear not to be affected.

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CAPITULO IV

DISCUSION Y CONCLUSIONES GENERALES

En el primer capítulo he descrito cómo la fragmentación afecta la composición florística en fragmentos de selva en un ámbito de tamaños contrastante (2-700 ha) y las implicaciones que tiene en la permanencia de especies con distintos requerimientos de luz (especies pioneras y tolerantes) en la selva de Los Tuxtlas, Veracruz. Las predicciones teóricas sugieren que la deforestación y fragmentación del hábitat llevan consigo a una subdivisión poblacional y que eventualmente tiene el potencial de llevar a una pérdida de poblaciones y/o especies. Con los resultados obtenidos muestro algunos procesos que pueden contribuir a la probable pérdida de poblaciones y/o de especies de plantas (Fig. 1).

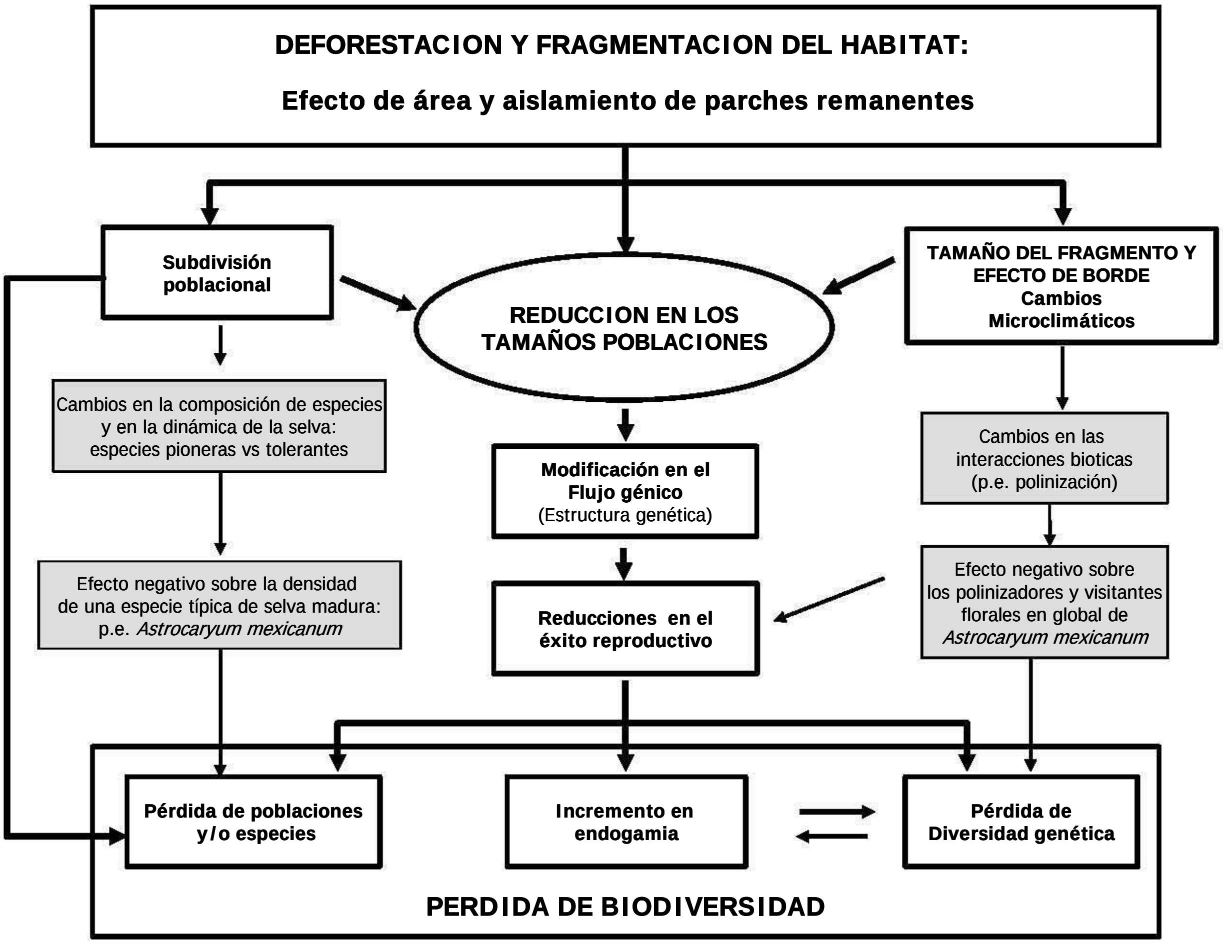

Figura 1. Marco conceptual de algunas de las consecuencias de la deforestación y fragmentación del hábitat que pueden dirigir a la pérdida de biodiversidad. Las cajas en color gris muestran los efectos detectados en este estudio.

En primer lugar detecté cambios en la abundancia y riqueza de especies, menos especies en fragmentos chicos *vs* grandes (considerando plantas ≤2.5 cm de DAP), sin embargo, no hubo cambios cuando analicé plantas con un DAP ≥10 cm (Fig. 1). Esto podría indicar que plantas en estadíos jóvenes (plantas post-fragmentación) son afectadas negativamente en fragmentos chicos, muy probablemente por modificaciones en las condiciones ambientales en las orillas de los fragmentos, ya que en fragmentos de menor tamaño la influencia al efecto de borde es mayor (Mendoza *et al.* 2005), afectando negativamente el establecimiento y permanencia de plantas jóvenes e incluso de árboles adultos (Didham & Lawton 1999, Laurance 2000, Benítez-Malvido & Martínez-Ramos 2003, Harper *et al.* 2005). Considero importante señalar que el empleo de plantas ≥1.0 cm de DAP (consideradas plantas jóvenes) es crucial, ya que se disminuyen posibles variables de confusión en el caso de considerar estadíos aún más jóvenes, comos sería el caso de plántulas, y en las cuales sabemos que ocurren tasas muy altas de mortalidad, no necesariamente asociadas con la fragmentación del hábitat, de tal forma que nuestros resultados estarían reflejando un efecto negativo sobre plantas que se han establecido posteriormente a la fragmentación en Los Tuxtlas.

La composición florística en los remanentes de selva parece seguir un patrón, en fragmentos chicos la composión de especies corresponde en su mayoría a especies pioneras, mientras que especies tolerantes se encuentran en mayor proporción en fragmentos grandes. En caso de mantenerse este escenario de aislamiento entre los fragmentos y la no inmigración de nuevos individuos a los remanentes de selva se esperaría que eventualmente en los fragmentos chicos (<40 ha) el establecimiento y permanencia de especies tolerantes disminuya, mientras que las especies pioneras estarían dominando estos fragmentos, por otro lado, en los fragmentos grandes se podría mantener la composición florística que hemos detectado, sin embargo, a mediano y/o largo plazo estos fragmentos también podrían presentar efectos negativos sobre su flora. Para el caso particular de Los Tuxtlas, estos hallazgos son importantes ya que la mayor parte de la vegetación original ha desaparecido (Dirzo & García 1992, Castillo-Campos & Laborde 2004, Guevara *et al*. 2004) y en la actualidad el paisaje esta conformado por un gran número de fragmentos de tamaño pequeño (Mendoza *et al.* 2005, Arroyo-Rodríguez *et al.* 2006), así como por vegetación secundaria, de bosque de galería, así como relictos de vegetación en las orillas de caminos, en las "cercas vivas" e inclusive vegetación exótica (*p.e*. varias especies de cítricos) dentro de los potreros (R. Dirzo *coms. pers*).

Para poder entender la dinámica de las poblaciones de plantas en los fragmentos de Los Tuxtlas se requiere de estudios detallados (y a largo plazo) sobre varios procesos biológicos como la polinización y dispersión de semillas o frutos los cuales son fundamentales para mantener el flujo génico entre las poblaciones (Cordeiro & Howe 2003, Ward *et al*. 2005). Para el caso de la polinización teóricamente se ha propuesto que puede haber efectos negativos debido a la fragmentación del hábitat (Harris & Johnson 2004, Ghazoul 2005), ya que más del 90% de las especies de árboles tropicales presentan algún vector biótico para fertilizar sus flores (Bawa 1999). En este sentido es importante también considerar a los sistemas reproductivos de las plantas, ya que la separación espacial y/o temporal de los sexos pueden ser crítica en un ambiente fragmentado y con restricciones en el desplazamiento de los polinizadores en una matriz altamente modificada. En una revisión considerando 14 localidades diferentes alrededor del mundo tropical encontré que en promedio existe un 65.7% de plantas hermafroditas, 20.4% dioicas y 17.7% monoicas (Tabla 1). Estos números parecerían ser alentadores, sin embargo, la mayoría de las especies de árboles que presentan flores bisexuales tienen algún tipo de auto-incompatibilidad (aunque se han encontrado especies donde esta barrera se puede romper y hacer posible la autofecundación) lo que las hace susceptibles a la fragmetación del hábitat (Bawa 1974, Bawa *et al.* 1985, Chan 1981).

Localización	N	% Hermafroditas	% dioicas	% monoicas
Australia, Selva de Monson (Gross, 2005)	84	81	19	-
Australia, Tropico húmedo- zonas altas (Gross, 2005)	145	53.8	20	26.2
Australia, Tropico húmedo- litoral (Gross, 2005)	126	59.5	18.3	22.2
Nueva Caledonia, Selva húmeda (Carpenter *et al.* 2003)	123	84	16	-
Malasia (Ahston, 1969)	711	60	26	14
Brasil, Selva seca (Machado *et al.* 2006) (♣,τ)	147	83	2.7	14.3
Venezuela (Sobrevila & Kalin-Arroyo, 1982)	36	69.4	30.5	-
Colombia (Van Dulman, 2001)	52	54	29	17
Costa Rica, La Selva (Bawa *et al.* 1985)	333	65.5	23.1	11.4
Costa Rica, La Selva (Kang & Bawa, 2003)	294	63.3	13.6	23.1
Costa Rica, Guanacaste (Bawa, 1974; Bawa & Opler, 1975)(τ)	~130	68	22	10
México, Selvas secas (Bullock, 1985) (τ)	188	58	26	16
México, Los Tuxtlas (Ibarra-Manríquez & Oyama 1992)	139	63	9	27
Florida, EUA (Tomlinson, 1974)	116	57	30	13

Tabla 1. Porcentaje de especies hermafroditas, dioicas y monoicas en 14 regiones del mundo tropical. La mayoría de los estudios consideran únicamente especies arbóreas de selvas húmedas, aunque algunos corresponden a selvas secas (τ) y solamente uno considera especies herbáceas y leñosas (♣).

La gran mayoría de especies arbóreas tropicales requieren polen exógeno para su polinización, debido a que presentan algún mecanismo de auto-incompatibilidad o bien a través de la dioecia. Asimismo muchas especies monoicas son predominantemente de entrecruzamiento obligado a través de la separación temporal de las flores femeninas y masculinas en la misma planta, o bien por la separación espacial de las estructuras reproductivas dentro de la misma flor (Bawa 1977, 1992, Beach 1982, 1984, Barret 2003). Bajo este escenario la disminución en la riqueza y abundancia de especies árboreas debido a la fragmentación podrían traer consecuencias negativas en el mantenimiento de la biodiversidad en paisajes altamente modificados.

Por otro lado, en lo que respecta a la dispersión, en Tanzania se encontró que en fragmentos chicos la dispersión de semillas por aves para el árbol *Leptonychia usambarensis* (Sterculiaceae) fué afectada negativamente por la fragmentación (Cordeiro & Howe 2003). En Argentina la fragmentación afectó la abundancia de un marsupial (*Dromiciops gliroides*) que se desempeña como un dispersor especializado del árbol (*Tristerix corymbosus*) con consecuencias directas negativas sobre la remoción de frutos, dispersión y reclutamiento de semillas de ese árbol (Rodríguez-Cabal *et al.* 2007). Ibarra-Manríquez *et al.* (1997) analizando 364 especies de árboles y lianas de Los Tuxtlas encontraron que el 71.7% de las especies presentan dispersión por animales, mientras que el 18.7% restante presenta dispersión por viento, y un porcentaje menor por balocoria y barocoria (9.6%), lo cual las hace susceptibles a la fragmentación del hábitat. Teóricamente se ha planteado la hipótesis de que plantas con semillas grandes son mas susceptibles a la fragmentación que las plantas con semillas chicas (Fortuna & Bascompte 2006). Sin embargo existe evidencia que muestra efectos diferenciales dependiendo del tamaño de las semillas y del tipo de dispersor (Lopes de Melo *et al*. 2006, Cramer *et al*. 2007, Dirzo *et al.* 2007), con lo cual se requiere de más investigaciones en está área. Por otro lado, recientemente se ha comenzado a estudiar los efectos de la fragmentación sobre interacciones “negativas” como la depredación de semillas (Chacoff *et al.* 2004, Fleury & Galetti 2006; Herrerías-Diego *et al.* 2008) y la herbivoría (Arnold & Asquith 2002, Benítez-Malvido & Lemus-Albor 2005, Valladares *et al*. 2006) procesos que pueden afectar también la permenencia de plantas en los fragmentos de selva. Se requiere de nuevas líneas de investigación sobre varios de los procesos antes señalados en la zona de Los Tuxtlas, con la finalidad de implementar estrategias de manejo, conservación y restauración en una zona altamente impactada por la presencia humana.

En el segundo capitulo utilizamos como base los resultados obtenidos sobre la caracterización florística en seis fragmentos de selva y ahora incluimos un área más grande dentro de la misma zona de Los Tuxtlas, utilizando tres tipos de paisajes caracterizados por presentar distinto estado de conservación (cantidad de cubierta forestal, tamaño de los fragmentos, forma del fragmento y aislamiento) y escogimos como modelo de estudio una especie típica de selva madura: *Astrocaryum mexicanum* (Arecaceae). Las palmas pueden ser un buen modelo para evaluar los efectos de la fragmentación al ser especies típicas de selva madura y un componente muy importante en los diferentes estratos de la selva (Henderson 1986, Khan & Granville 1992). Para la región de Los Tuxtlas en los alrededores de la Estación de Biología Tropical de la UNAM se tiene registros de ~13 especies de palmas (Tabla 2). De las cuales 8 corresponden al género *Chamaedorea* y 5 a otras especies de palmas.

Especie	Sistema reproductivo
Astrocaryum mexicanum Liebm.	Monoico
Bactris mexicana Mart.	Monoico
Geonoma oxycarpa Mart.	Monoico
Reinhardtia gracilis H. Wendtl.	Monoico
Desmoncus orthacanthos Mart.	Monoico
Chamaedorea oblongata Mart.	Dioico
Chamaedorea concolor Mart.	Dioico
Chamaedorea ernesti-augusti H. Wendtl.	Dioico
Chamaedorea tepejilote Liebm.	Dioico
Chamaedorea alternas H. Wendtl.	Dioico
Chamaedorea elatior Mart.	Dioico
Chamaedorea pinnatifrons Jacq.	Dioico
Chamaedorea tuerckheimii Burret.	Dioico

Tabla 2. Especies de palmas de Los Tuxtlas y su sistema reproductivo. Las palmas con un sistema reproductivo monoico presentan separación temporal de las fases sexuales.

Uno de los aspectos que hace de las palmas un grupo potencialmente susceptible a la fragmentación es su sistema reproductivo, que para el caso de las especies de Los Tuxtlas es dioico en las especies del género *Chamaedorea* y monoico en el resto de las palmas (Tabla 2). En las especies de palmas con un sistema reproductivo monioco estas presentan separación temporal de las fases sexuales dentro de la misma inflorescencia (dicogamia), para lo cual requieren de polen de otro individuo en el cual sus flores estén en la fase sexual opuesta para poder ser fertilizadas (Baicon & Bailey 2006, Búrquez *et al.* 1987, Oyama 1990, Ibarra-Manríquez 1992, Quero 1994, Ibarra-Manríquez & Sinaca-Colín 1997) (Tabla 2).

Existen pocos estudios que hayan utilizado a las palmas como modelo para evaluar el efecto de la fragmentación. Scariot (1999) en Amazonia Central evaluó el efecto de la fragmentación sobre una comunidad de palmas utilizando diferentes categorias de edad (adultos, juveniles, plántulas y el total de las categorias) y encontro que las plántulas son las mayormente afectadas. Yunh Ho (2007) encontro resultados similares en Costa Rica, utilizando también palmas en sus diferentes estadíos, encontrando una asociación negativa entre la permanencia de palmas jóvenes y la perdida de cubierta forestal. Sin embargo, Baez & Balslev (2007) encontraron resultados contrastantes en Ecuador, mostrando que palmas adultas son más suceptibles al efecto de borde que las palmas en estadíos más jóvenes. Este resultado coincide parcialmente con el nuestro, menor densidad de individuos adultos de *A. mexicanum* en los fragmentos de selva más aislados, más chicos y con formas más irregulares (Fig. 1). Desafortunadamente no contamos con datos que nos permitan evaluar el impacto de la fragmentación sobre los otros estadíos de esta palma, sin embargo, con base en el conocimiento que se tiene de esta especie podemos hacer algunas especulaciones sobre los factores que pudieran afectar la permanencia de *A. mexicanum* en los fragmentos de selva.

Uno de los procesos que puede ser afectado por la fragmentación es la depredación de semillas. *A. mexicanum* produce en promedio 20 frutos por infructescencia ricos en lípidos los cuales son alimento para varias especies de animales (Sarukhán 1980, Navarro-López 1982, Coates-Estrada & Estrada 1986, Martínez-Gallardo 1988), dentro de los cuales existen dos especies de ardillas (*Sciurus depeii* y *S. Aureogaster*) que son un factor importante en la depredación de las semillas inclusive antes de que ser dispersados (~50% de los frutos son depredados al caer al suelo) (Martínez-Gallardo 1988). Además en estadíos más jóvenes los frutos son depredados, muy probablemente por escarabajos, tal como se ha documentado en otras especies de palmas (Smythe 1989, Terborg *et al.* 1993, Forget *et al.* 1994, Fragoso 1997, Fragoso *et al.* 2003, Wrigth & Duber 2001, Alves-Acosta & Knogge 2005). En un estudio reciente (2007) en Los Tuxtlas evaluamos el efecto de la fragmentación sobre la depredación pre-dispersión de frutos de *A. mexicanum,* encontrando una tendencia a mayor depredación de semillas por infrutescencia en fragmentos chicos (9.42±2.86) (promedio±error estandar) que en fragmentos grandes (3.61±0.44) (*t*-student= 2.0, gl= 4, *P*=0.11) (R. Dirzo & A. Aguirre, *datos no publicados*), en otras palabras, cerca del 50% de los frutos que en promedio tiene una palma son depredados en los fragmentos chicos, mientras que en los fragmentos grandes es aproximadamente un 25%, lo cual podría influir negativamente en el establecimiento de plántulas de esta especie. Asimismo otro factor importante a considerar es que la dispersión de semillas de *A. mexicanum* es prácticamente nula quedando las semillas al pie de la planta madre y dispersadas de manera secundaria por algunos depredadores de éstas (Martínez-Ramos 1997). Una vez que las semillas están en el suelo son fuertemente depredadas y en promedio solo el 5% de las semillas dan lugar al nacimiento de plántulas (Alvárez-Buylla & Martínez-Ramos 1992). Las tasas de mortalidad de las plántulas varían de acuerdo al a la edad de las palmas y a la fase regenerativa de la selva (Piñero *et al.* 1984, Martínez-Ramos *et al.* 1988). Existe una mayor tasa de mortalidad en los primeros 15 años de vida de la palma y disminuye considerablemente al alcanzar la edad reproductiva (Pinero *et al.* 1984). Con estos dos antecedentes esperaríamos que la probabilidad de muerte de *A. mexicanum* en los fragmentos chicos sea aún mayor. Asimismo esta especie tiene un ciclo de vida adaptado a condiciones de sombra (Martínez-Ramos y Samper 1996), con lo cual las condiciones lumínicias contrastantes en los fragmentos *vs* selva continua pudieran tener un efecto negativo en el establecimiento y permanencia de *A. mexicanum*, por ejemplo, palmas expuestas por periodos cortos a la luz solar directa (abundancia de los recursos lumínicos presente en los claros) aumenta la velocidad de crecimiento y la actividad reproductiva (Martínez-Ramos *et al*. 1988). De tal forma que la apertura y cierre del dosel (dinámica típica en la selva de Los Tuxtlas) produce cambios en las tasas de natalidad, crecimiento y mortalidad de ésta especie. Como consecuencia se generan diferencias en la abundancia y distribución de las palmas en distintas categorias de edad entre las fases regenerativas de la selva. De esta manera el ambiente en los claros de la selva aumenta el número de individuos reproductivos pero disminuye el de plantas jóvenes, escenario que podría estar sucediendo en los fragmentos de selva, mientras tanto en los sitios cerrados de selva se genera un efecto demográfico opuesto (Martínez-Ramos e*t al*. 1988, Enríquez 1991). Estos argumentos podrían sustentar el hecho de que especies con carácterísticas típicas de selva madura, como *A. mexicanum*, presenten bajas probabilidades de permanencia en sitios fragmentados. Afortunadamente para *A. mexicanum* se cuenta con una basta información que nos permite hacer estas hipótesis, sin embargo, es necesario llevar a cabo investigaciones en cada uno de los aspectos discutidos anteriormente para hacer inferencias más precisas sobre las consecuencias reales que podrían presentar las poblaciones de esta palma, así mismo se requiere de más estudios involucrando el mayor número de especies posibles y hacer inferencias ahora ya no solo a nivel de poblaciones sino a un nivel más amplio, como podría ser las consecuencias de la fragmentación sobre las comunidades vegetales en Los Tuxtlas.

Otro proceso biológico que pudiera ser modificado con la fragmentación del hábitat es la polinización, y de éste me ocupo en el tercer capitulo de ésta tesis en el cuál analizo el impacto de la fragmentación sobre la polinización y sus consecuencias sobre el éxito reproductivo de *A. mexicanum*. La polinización puede ser afectada negativamente por la fragmentación del hábitat, debido a que involucra una amplia gama de animales que pueden ser sensibles a los cambios en la configuración espacial del hábitat, además de la especialización que puedan tener con las plantas que polinizan (*p.e*. orquídeas y abejas euglossinas) (Murcia 1996). La fragmentación tambien puede disminuir la abundancia de individuos (plantas) sexualmente compatibles existentes en los fragmentos de selva, lo cual puede a su vez afectar el éxito reproductivo y provocar erosión genética debido a la modificación de flujo génico (vía polen o semillas) (Alvarez-Buylla *et al.* 1996, Young *et al*. 1996, Aizen *et al.* 2002), lo cual teóricamente puede exacerbarse en el caso de interacciones con polinizadores que presentan una limitada capacidad de desplazamiento entre fragmentos (Didham *et al.* 1996, Kearns *et al.* 1998).

Los resultados mostraron que la fragmentación afectó negativamente tanto a los visitantes florales en global como a los principales polinizadores en particular, sin embargo, el éxito reproductivo no mostró diferencias entre fragmentos (Fig. 1). Los efectos de la fragmentación sobre la polinización son ideosincráticos, desde los que muestran muestran efectos negativos (Powell & Powell 1987, Jennersten 1988, Aizen *et al.* 1994), positivos (mayor riqueza y frecuencia de visitantes florales en sitios fragmentados) (Lopes & Buzato 2007), nulos (Yates *et al.* 2007), o bien los que muestran como la ausencia de un polinizador nativo puede beneficiar a la planta con la llegada de un polinizador exótico (Dick 2001). Existe información sobre polinización en otras especies del género *Astrocaryum* y en otras especies de palmas mostrando la gran diversidad de fauna asociada a las inflorescencias de estas plantas (Búrquez *et al.* 1987, Consiglio & Bourne 2001, Listabarth 2001, Otero-Arnaíz & Oyama 2001, Padilha de Oliveira *et al.* 2003, Nuñez *et al.* 2005). Si embargo, no existen estudios que hayan evaluado el efecto de la fragmentación utilizando como modelo a las palmas, con lo cual los datos obtenidos en *A. mexicanum* son pioneros en la obtención de esta información. La polinización en esta especie es entomofila, mediante escarabajos de la familia *Nitidulidae* (Coleoptera) la cual para los trópicos se ha sugerido que es altamente especializada junto con otros grupos de animales como son murcielagos, polillas, avispas polinizadoras de higos y abejas euglossinas (Búrquez *et al.* 1987, Bawa 1990, Jonhson & Steiner 2000). En este sentido se ha planteado la hipótesis de que las interacciones especializadas pueden ser más susceptibles a la fragmentación que las generalistas y si esto se traduce en efectos negativos sobre el éxito reproductivo de las plantas (Johnson & Steiner 2000, Aizen *et al.* 2002). En los últimos años ha habido un creciente interés por explicar los efectos de la fragmentación sobre la polinización y sus efectos sobre el éxito reproductivo incluyendo además aspectos sobre su sistema reproductivo. Aizen *et al.* (2002) analizaron 46 especies de plantas de diferente grupo taxónico, formas de vida y distribución geográfica para detectar posibles efectos de la fragmentación sobre el éxito reproductivo. Los resultados mostraron que la fragmentación del hábitat tuvo efectos negativos sobre el éxito reproductivo, y que esta respuesta no fue diferente dependiendo del sistema de compatibilidad de las plantas (auto-compatibles y auto-incompatibles) y concluyen que no se pueden hacer generalizaciones sobre la susceptibilidad de las plantas a la fragmentación basándose solamente su sistema de compatibilidad o de polinización. De igual manera Ghazoul

(2005) revisó de que manera la distribución espacial de las plantas (tamaño poblacional, densidad y distancia entre conespecíficos, afectan la polinización y el éxito reproductivo. Los resultados llevaron a la misma conclusión que la de Aizen *et al.* (2002): la susceptibilidad reproductiva de las plantas a la fragmentación del hábitat es indistinta entre plantas con sistemas in-compatibles y auto-compatibles. Por último Aguilar *et al.* (2006) encontraron que la fragmentación tiene efectos negativos sobre la reproducción y polinización de las plantas, y que los sistemas de compatibilidad son importantes en explicar estos resultados ya que expresan el grado de dependencia sobre el mutualismo. Con base en estos estudios resalta la necesidad de continuar haciendo investigación sobre las consecuencias de la fragmentación en la polinización y el éxito reproductivo, más aún, enfocados sobre aquellos síndromes de polinización menos estudiados, como el que presenta *A. mexicanum* (entomófilo) y sus consecuencias sobre el éxito reproductivo.

Los resultados obtenidos en esta investigación mostraron que la fragmentación disminuye la cantidad de polinizadores y visitantes en global, sin embargo, el éxito reproducitvo no cambia entre fragmentos, esto nos podría indicar que con la cantidad tan grande de polinizadores por inflorescencia es suficiente para fertilizar las flores, sin embargo, es necesario evaluar las posibles consecuencias genéticas que esto pudiera tener, ya que el polen muy probablemente sea de palmas dentro del mismo fragmento, con lo cual la probabilidad de disminuir la diversidad y estructura genética se incrementaría, asimismo se favorecería la endogamia al suponer restricciones en el flujo de genes a los fragmentos mas chicos y aislados, de tal forma que se requiere llevar a cabo investigaciones encaminadas a conocer los efectos de la fragmentación sobre la variabilidad genética de las poblaciones de *A. mexicanum* en la zona de Los Tuxtlas.

A continuación presento algunas ideas sobre las posibles consecuencias de la fragmentación sobre la estructura genética de *A. mexicanum*, con base en el conocimiento previo que se tiene de la especie así como con la información disponible para otras especies de palmas. El impacto que puede tener la fragmentación sobre la estructura y flujo génico en plantas tropicales es todavía pobremente entendido, y con respuestas contrastantes (Ward *et al.* 2005). Las consideraciones teóricas sugieren que las poblaciones pequeñas pueden ser particularmente susceptibles a la extinción, debido a un empobrecimiento o deterioro genético por deriva génica, y/o como consecuencia de estocasticidad ambiental y demográfica (Soulé & Wilcox 1980, Shaffer 1981, Lande 1988, Simberloff 1988, Ellstram & Ellam 1993). Además, el flujo génico puede ser modificado o limitado por las distancias existentes entre los remanentes de vegetación (White *et al.* 2002), lo cual puede generar efectos de *cuello de botella genético*, incrementar la deriva génica y la endogamia, teniendo como consecuencia pérdida de variabilidad genética, e incrementar la diferenciación genética entre fragmentos (Young *et al.* 1996, Honnay & Jacquemyn 2007) y eventualmente la perdida de poblaciones y/o especies (Fig. 1).

Las principales variables que se han utilizado para evaluar los efectos de la fragmentación en plantas tropicales son la endogamia, diferenciación genética y flujo génico (utilizando principalmente árboles aislados del continuo de selva) (Hall *et al*. 1996, Quesada *et al*. 2003, Rocha & Aguilar 2001, Nason 2002, Ward *et al.* 2005). La información disponible muestra que las respuestas son contrastantes y no se detecta un patrón definido y consistente (Lowe *et al.* 2003, ver Dunphy & Hamrick 2005, González-Astorga 2006). De los escasos trabajos sobre especies tropicales, una proporción considerable se ha centrado en especies arbóreas y una fracción aún más pequeña en las palmas (Ward *et al.* 2005, Shapcott 1999, 2000; Cardoso *et al.* 2000, Luna *et al.* 2005, 2007) a pesar de que estas últimas son un componente muy importante de los diferentes estratos de la selva tropical (Henderson 1986, Scariot 1999, Vormisto 2002).

En general las palmas presentan altas tasas de entrecruzamiento (aproximadamente el 58% de las especies de palmas conocidas presentan un sistema reproductivo de entrecruzamiento obligado y 45% son dioicas) (Murcia 1996, Eguiarte *et al.* 1993, Quero 1994). Además la mayoría son polinizadas por una gran variedad de insectos pequeños (*p. e.* escarabajos) siendo la polinización cantarófila la predominante en palmas del sotobosque tropical y una menor proporción por viento así como por otros insectos insectos pequeños como dípteros (Henderson 1986, Búrquez *et al.* 1987, Listabarth 1996, Bernal & Ervik 1996, Listabarth 2001). Con base en estos atributos se esperarían consecuencias genéticas negativas al menos en las palmas con polinización biótica.

Algunos estudios muestran aparentemente un efecto nulo de la fragmentación sobre la estructura genética de plantas tropicales, por ejemplo en *Carpentaria acuminat*a (Shapcott 1998), *Symphonia globulifera* (Aldrich *et al.* 1998), *Brongniartia vazquezzi* (González-Astorga & Nuñez-Farfán 2001), *Samanea saman* (Cascante *et al*. 2002), *Picea glauca* (O'Connell *et al*. 2006), así como en *Dieffenbachya seguinae* (Cuartas & Nuñez-Farfán 2006). Por el contrario, se han encontrado efectos negativos de la fragmentación sobre la diversidad genética en *Phitecellobium elegans* (Hall *et al*. 1996), *Swietenia humilis* (White *et al.* 1999), *Terminalia amazonica* (Pither *et al.* 2003), *Caesalpinia echinata* (Sodre-Cardoso *et al*. 2005), plántulas de *Embothrium coccineum* (Mathiasen *et al*. 2007), así como en *Quercus humboltii* (Fernández-M & Sork 2007).

Teóricamente se esperarían consecuencias negativas de la fragmentación sobre la estructura genética de especies que requieren polinización biótica ya que ésta puede ser modificada debido a la incapacidad de los polinizadores para desplazarse entre los fragmentos de bosque modificando con ello el flujo génico (Young *et al.* 1996), sin embargo también existe evidencia que muestra que el polen puede ser dispersado grandes distancias (Gaiotto *et al.* 2003). Los escasos trabajos sobre estructura genética en palmas proporcionan información sobre una alta diversidad genética, con valores relativamente altos tanto de polimorfismo ($\bar{x}$=70.8) como de riqueza alelica ($\bar{x}$=2.6) (Tabla 3). La diferenciación genética es contrastante y va en un ámbito de muy poca diferenciación como en *Astrocaryum mexicanum* (F_{ST}= 0.009) hasta una diferenciación alta como en *Carpentaria acuminata* (F_{ST}=0.37) (Tabla 3). Para el caso de la endogamia de las 14 especies revisadas solo *Astrocaryum mexicanum* mostró un bajo índice de endogamia (F=-0.19), las demás presentan valores relativamente altos con índices de fijación positivos.

ESPECIES	P	A	Ho	He	F	Fis	Fst
Astrocaryum mexicanum[1]	32.0	2.14		0.153	-0.19	-0.188	0.0091
Pinanga aristata[2]	89.0	2.1	0.082	0.379	0.76	0.770	0.21
Pinanga brevipes[2]	89.0	2.8	0.026	0.256	0.856	0.892	0.261
Pinanga dumetosa[2]	100.0	3.2	0.093	0.294	0.64	0.680	0.099
Pinanga tenella[2]	82.0	2.8	0.029	0.133	0.753	0.776	0.148
Pinanga veitchii[2]	89.0	3.0	0.098	0.352	0.674	0.709	0.194
Chamaedorea elatior[3]	82.3	2.93	0.173	0.316	0.79	0.442	0.030
Chamaedorea tepejilote[3]	90.7	3.15	-	0.41	0.74	0.482	0.152
Chamaedorea tuerchheimii[4]	64.1	2.37	-	0.25	-	-	-
Carpentaria acuminata[5]	80.0	2.7	0.052	0.143	0.641	0.640	0.379
Washingtonia filifera[6]	0.1	2.5	0.009	0.008	-	-0.007	0.038
Phoenix canariensis[7]	41.8	1.59	0.179	0.158	-	-0.2	0.287
Phoenix dactyllifera[7]	60.1	1.95	0.259	0.277	-	0.126	0.252
Euterpe edulis[8]	62.5	3.05	0.264	0.416	0.092	-	-
Euterpe edulis[15]	100.0	3.4	0.423	0.445	0.049	-	-

[1] Eguiarte *et al.* 1992
[2] Shapcott 1999
[3] Luna *et al*. 2007
[4] Luna & Oyama, en Luna 1999
[5] Shapcott 2000
[6] McClenaghan & Beauchamp 1986
[7] González-Perez *et al.* 2004
[8] Conte 2004
[9] Reis *et al.* 1998, en Conte *et al*. 2003
Datos no disponibles (-)

Tabla 3. Parámetros genéticos analizados en varias especies de palmas.

Con base en estos antecedentes, así como en el gran conocimiento que existe de *A. mexicanum* tanto de historia natural (Martínez-Ramos 1997), biología reproductiva

(Búrquez *et al.* 1987), demografía (Piñero *et al.* 1984), genética de poblaciones (Eguiarte *et al*. 1992, 1993) y su dinámica en la comunidad (Piñero & Sarukhán 1982, Martínez-Ramos *et al*. 1998), además de los resultados mostrados en los diferentes capitulos de esta tesis hacen de *A. mexicanum* un excelente modelo para explorar las consecuencias de la fragmentación sobre su estructura y flujo génico.

Las posibles consecuencias de la fragmentación del hábitat sobre la estructura y diferenciación genética en *A. mexicanum* podrían ser que los fragmentos más aislados y pequeños presenten menor menor diversidad genética (Figura 5a), mayor endogamia (Figura 5b) así como mayor una diferenciación genética (Figura 5c).

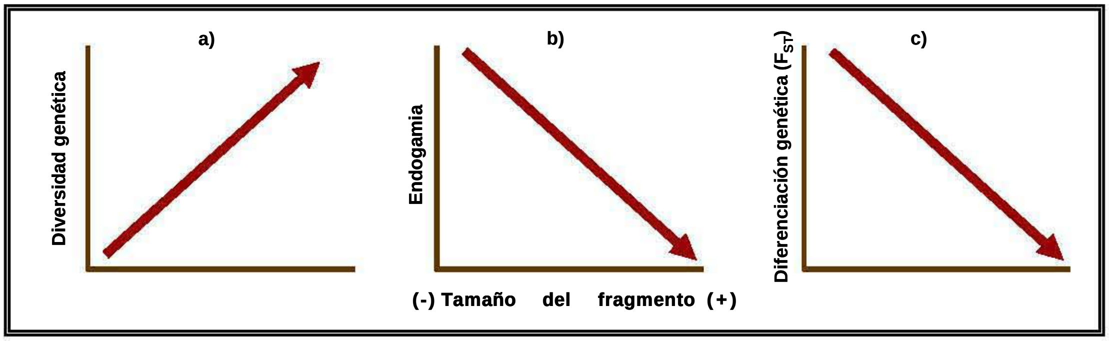

Figura 2. Representación de la hipótesis que propone que la diversidad genética será menor en los fragmentos más pequeños y que al incrementar el tamaño del fragmento ésta se incrementará (a), mientras que la endogamia y la diferenciación genética presentarán una tendencia opuesta: sitios más pequeños presentarán más endogamia y diferenciación, y a medida que se incrementa el tamaño del fragmento éstas tenderán a disminuir (c).

Para concluir puedo decir que la forma de abordar esta investigación, con un marco teórico sólido, y con un énfoque desde nivel del paisaje, de grupos funcionales, de la modificación de un proceso biológico (polinización) y sus consecuencias sobre el éxito reproductivo, hasta llegar a hacer inferencias sobre las posibles consecuencias sobre la variabilidad genética de una especie, es un enfoque integral que muy pocas investigaciones han conseguido. Los resultados de este trabajo, colectivamente demuestran que las consecuencias de la fragmentación tropical son complejas y multivariadas y probablemente con mucha dependencia del tiempo. La dificultad de predicción de las consecuencias de la fragmentación parecería ser idiosincrática y se requiere de estudios que contemplen el efecto temporal (largo plazo) y de estudios con metodologías comparables, que permitan un mejor entendimiento de las consecuencias de la fragmentación del hábitat sobre los ecosistemas tropicales y que pueda ayudarnos a elaborar estrategias de conservación más eficientes en las áreas naturales remanentes.

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APENDICE I

		LOCATION	
N	**LANDSCAPE**	**COORDENATE (X)**	**COORDENATE (Y)**
1	Central	308997.3268	2045322.7849
2	Central	305321.9959	2045120.7992
3	Central	305587.7682	2048814.4466
4	Central	309035.3689	2044874.7990
5	Central	307142.2675	2045425.7136
6	Central	308236.0842	2044005.6936
7	Central	304679.4270	2047802.7977
8	Central	306336.6293	2049558.1685
9	Central	304590.3212	2048034.2336
10	Central	304996.3806	2047316.2440
11	Central	309881.0549	2044661.3685
12	Central	305976.1481	2049895.8902
13	Central	304153.1644	2047809.2469
14	Central	307484.0410	2048513.6262
15	Central	308883.3824	2043146.8194
1	Northern	281467.2593	2058743.4568
2	Northern	282342.1330	2058653.3639
3	Northern	282702.8117	2058142.8240
4	Northern	277451.4691	2060248.5253
5	Northern	280583.7112	2057150.4431
6	Northern	280811.4461	2057717.7261
7	Northern	278204.7415	2058286.2480
8	Northern	277962.8077	2060142.3227
9	Northern	280675.8321	2059078.2628
10	Northern	279854.2867	2062306.0498
11	Northern	282211.6716	2059152.9549
12	Northern	282865.7275	2057117.7311
13	Northern	281864.3859	2055408.2823
14	Northern	278823.9101	2058465.4054
15	Northern	280977.1998	2060112.6921
1	Southern	315043.99472	2031581.64406
2	Southern	315411.24057	2031914.39723
3	Southern	312521.89626	2031429.29390
4	Southern	312280.01286	2029026.47916
5	Southern	314535.88936	2034693.03708
6	Southern	313149.67784	2030214.60276
7	Southern	315089.30187	2033375.60356
8	Southern	316616.93805	2033927.91946
9	Southern	312479.44378	2033800.44934
10	Southern	310290.05631	2032041.12130
11	Southern	311455.82916	2031638.03271
12	Southern	313616.90665	2031130.96513
13	Southern	313243.61167	2032959.18026
14	Southern	312210.62558	2032143.77897
15	Southern	312460.67942	2030975.40158