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EFECTO DE LA FRAGMENTACIÓN DEL BOSQUE SECO EN EL ÉXITO REPRODUCTIVO, LA DEPREDACIÓN Y LA ESTRUCTURA GENÉTICA DE *Ceiba aesculifolia* HBK (BOMBACACEAE)

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Yvonne Herrerías Diego

DIRECTOR DE TESIS**:** Dr. Mauricio Quesada A.

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Contenido

Anexo I.

Resumen General

La fragmentación y la consecuente reducción de los bosques naturales, debido a la deforestación, es uno de los principales problemas que enfrentan los bosques tropicales. La destrucción de los bosques tropicales y su respectiva sustitución por zonas de cultivo y áreas de pastoreo, entre otros, ha ocasionado la formación de parches de bosques sucesionales y remanentes de bosques maduros. Las modificaciones antrópicas tienen diferentes efectos en la biodiversidad de los bosques tropicales, incluyendo la alteración de regímenes de competencia entre las especies de plantas, cambios en los patrones de dispersión del polen y semillas por vectores bióticos y la reducción del tamaño efectivo de las poblaciones de plantas y animales.

Este proyecto propone utilizar a *Ceiba aesculifolia* (Bombacaceae) como un modelo para estudiar los efectos de la fragmentación del bosque tropical seco sobre el éxito reproductivo, la estructura genética, el flujo de polen y la depredación de frutos y semillas. La tesis esta estructurada en tres capítulos: 1) Efectos de la fragmentación del bosque sobre los patrones fenológicos y éxito reproductivo; 2) Efectos de la fragmentación en la correlación de paternidad y tasa de exocruzamiento; 3) Efecto de la fragmentación en la depredación de frutos y semillas.

El proyecto fue desarrollado en el bosque tropical seco de Chamela, estado de Jalisco, México. Las condiciones de aislamiento espacial a evaluar son las siguientes: 1) árboles en sitios perturbados (cuatro poblaciones en fragmentos de bosque, incluyendo individuos en corredores o fragmentos de bosque alterados rodeados por una matriz de campos agrícolas y pastizales, en donde su densidad no exceda tres individuos reproductivos por hectárea) y 2) árboles en sitios no perturbados (tres poblaciones ubicadas en bosques continuos con una densidad de seis individuos reproductivos por hectárea).

Capítulo 1

Durante cuatro años, se determinaron los efectos de la fragmentación del bosque y el aislamiento espacial en la fenología floral y el éxito reproductivo del árbol tropical *Ceiba aesculifolia.* Se compararon las siguientes variables entre las poblaciones de las dos condiciones de hábitat (hábitat no perturbado y hábitat perturbado) en cada uno de los años de muestreo: 1) sobrelapamiento de floración, 2) proporción de individuos con flores y frutos, 3) producción total de flores y frutos por individuo, 4) proporción de flores que producen frutos, 5) producción de semillas y 7) semillas abortadas. Se observó un desfase en los periodos de floración de las poblaciones de sitios perturbados comparadas con las poblaciones de sitios no perturbados. El periodo de floración de los árboles en poblaciones perturbados inició entre 15 a 20 días antes del periodo de floración de árboles en poblaciones no perturbadas durante los 4 años de estudio. La proporción de árboles que florecieron fue mayor en poblaciones de sitios no perturbados, sin embargo, la producción total de flores por árbol fue mayor en las poblaciones de sitios perturbados y esta diferencia se mantuvo a lo largo de 3 años de estudio. La proporción de individuos que produjeron frutos fue similar entre las condiciones del hábitat aunque varió a través de los años. La producción total de frutos fue mayor en las poblaciones de hábitats perturbados, pero tanto la proporción de flores que llegaron a producir frutos (fruit set) como la producción de semillas fueron similares entre las dos condiciones de hábitat, patrón que se repitió a través del tiempo. Se encontró variación en el número de semillas abortadas entre condiciones de hábitat y a lo largo del tiempo. En consecuencia, la fragmentación del hábitat afectaría el patrón fenológico de los árboles en las poblaciones en sitios perturbados pero no el éxito reproductivo de *C. aesculifolia.* Esto posiblemente sea consecuencia de que los murciélagos polinizadores pueden volar largas distancias moviendo suficiente polen entre los árboles de sitios perturbados, lo que mantiene la conectividad reproductiva.

Capítulo 2

En los cuatro años de estudio, se determinó el efecto de la fragmentación del bosque en la estructura genética y en la correlación de paternidad de *C. aesculifolia*. Durante el periodo de estudio, la tasa de exocruzamiento no fue afectada por la fragmentación del bosque. Todas las poblaciones de *C. aesculifolia* estudiadas fueron 100 % exocruzadas y presentaron frutos con uno donador de polen, de la misma manera, todas las semillas de un fruto fueron hermanas completas. La estructura genética fue mayor en las poblaciones del hábitat perturbado que en las poblaciones de hábitat no perturbado. El porcentaje de paternidad calculado indicó que en el 70 % de las progenies analizadas provenientes de poblaciones de hábitats perturbados, el padre potencial provino de afuera de la población. Por el contrario entre el 10% a 20% de las progenies de poblaciones en sitios no perturbados, los padres potenciales provinieron de una población diferente. Los resultados de este capítulo resaltan la importancia de los árboles de sitios perturbados como corredores de polen entre los árboles de sitios perturbado de *C. aesculifolia* entre las diferentes poblaciones.

Capítulo 3

Una de las interacciones bióticas que puede ser afectada por la fragmentación y que ha sido poco estudiada es la depredación de frutos y semillas. En este capítulo se determinó el efecto de la fragmentación en la depredación de frutos y semillas de *C. aesculifolia.* Para esto se midió la frecuencia de depredación de frutos así como la frecuencia de aparición del principal insecto depredador de semillas (*Dysdercus* sp) en cada uno de los árboles. Por otro lado se realizó un experimento de laboratorio para determinar la viabilidad de la semilla tras la exposición a tres diferentes tratamientos de depredación (estado ninfal, pre-adulto y adulto). La depredación de frutos fue del 40% en árboles de sitios no perturbados y sólo del 6% en árboles de hábitat perturbado. *Dysdercus sp* se encontró presente en el 27% de los árboles de sitios no perturbados y únicamente en el 1% de los árboles en sitios perturbados. Los resultados del experimento de laboratorio indicaron que los individuos adultos y pre-adultos de *Dysdercus* sp. depredaron semillas de mayor tamaño que los individuos de estadio ninfal. De manera similar, las semillas atacadas perdieron más peso que las semillas no atacadas. La proporción de semillas germinadas así como en el tiempo de germinación fue negativa y significativamente afectada por la depredación. La intensidad en los niveles de depredación de semillas entre sitios perturbados y no perturbados puede tener un efecto en la regeneración de los bosques y en la estructura demográfica de las poblaciones de plantas.

Abstract

The reduction of natural forests and the formation of forest fragments caused by anthropogenic activity are the main causes of biodiversity loss in tropical forests. Several studies have shown that tropical trees are particularly vulnerable to the effects of habitat disturbance because they occur at low density, have complex self-incompatible mechanisms, high outcrossing rates, and specific specialized interactions with pollinators and seed dispersers.

We conducted our study in the dry forest of Mexico and compared populations in two habitat conditions based on density and environmental conditions: (1) disturbed habitat (four populations of three or less reproductive individuals/ha surrounded by agricultural fields or pastures) and (2) undisturbed habitat (three populations of groups of six or more reproductive individuals/ha surrounded by undisturbed mature forest).

Chapter I

Spatial isolation caused by forest fragmentation and temporal isolation caused by asynchronous flowering of plants have been proposed as important factors that affect the reproduction of plant populations. In a 4-year study, we determined the effects of forest fragmentation and spatial isolation on flowering phenology and reproductive success of the tropical bombacaceous tree *Ceiba aesculifolia*. We compared the following variables within these populations over 4 years: flowering overlap, proportion of individuals with flowers and fruit, total flower production, total fruit production, fruit set, seed production, and seed abortion. Little overlap in flowering occurred between the populations in the two habitat conditions. The flowering period of trees in the disturbed habitat initiated between 15 to 20 days before the flowering period of trees from the undisturbed habitat during 3 years. Flowering of trees from the undisturbed habitat peaked at the end of the flowering period of the trees from the disturbed habitat. The proportion of trees that flowered was greater in the undisturbed habitat. Nevertheless, total flower production was greater in the disturbed habitat and these differences were maintained across 3 years. The proportion of individuals that produced fruit did not differ across habitat conditions but did differ across years. Total fruit production was greater in the disturbed habitat, but fruit set and seed

production were the same across years and between habitat conditions. Seed abortion varied over years between habitats. We concluded that forest fragmentation does not negatively affect the reproductive success of *C. aesculifolia*. It appears that the highly mobile bat pollinators maintain reproductive connectivity between trees in both habitats.

Chapter II.

The reduction of the natural population causes isolation of remnant populations, this isolation have negative consequences to the genetic structure of plant species. In a four year study, we determined the effect of habitat fragmentation on the genetic structure and paternity correlation of the tropical tree *Ceiba aesculifolia.* We estimate the following variables within these populations over 4 years: outcrossing rate, paternity correlation, mean relatedness, genetic structure (Φ_{FT}) and paternity. All trees of *C. aesculifolia* were 100% outcrossing and each fruit have one pollen donor and all the seeds in a fruit were full sibs. Contrary of the expected, the populations in both habitat conditions presented a high genetic structure. But, the genetic structure was greater in disturbed populations than undisturbed populations. In undisturbed populations presented more effective pollen donors than the disturbed populations. The distance between donors was shorter in disturbed habitat. Paternity analysis showed that, between 50-90% of the paternities assigned in undisturbed forest was sired from fathers within the undisturbed habitat condition. In disturbed habitat conditions only between 20-50% of the paternities assigned were sired from within the population, the pattern was maintained for both habitat conditions over years. The fragmentation can increase the levels of gene flow between the fragments and maintain genetic diversity inside the populations. From a conservation perspective, this study provides important elements. Because most of the total genetic variation detected in *C. aesculifolia* resides within populations.

Chapter III

Fragmentation of tropical forests reduces the density of natural plant populations forming patches of the remaining populations. One of the biotic interactions that can be affected by forest

fragmentation and is poorly studied is seed predation. We compared the following variables: a) frequency of fruit predation by the squirrel *Sciurus colliaei* in each habitat; b) frequency of the insect seed predator *Dysdercus* sp. (principal seed predator) in each habitat; and c) the effect of predation on germination frequency and time; and d) the effect of different life stages of *Dysdercus* sp.(nymph, pre-adult and adult) on the viability of seeds. In undisturbed habitat 100% of the trees analyzed presented fruits with squirrel predation while only 34% of trees in disturbed habitats presented fruit predation. In undisturbed forest, 27% of the trees contained fruits with the seed predator *Dysdercus* sp,, while only 2% of the trees in disturbed forest presented *Dysdercus* sp. Damaged seeds weighed more than seeds that were not damaged. Predated seeds lost significantly more weight than seeds that were not predated. The frequency of seed germination was significantly affected by different life stages. Seed predation also had a significant effect on the time of germination. The study about the effect of the forest fragmentation in levels of depredation of fruits and seeds is determinant for regeneration of disturbed forests.

INTRODUCCIÓN GENERAL

Fragmentación del bosque tropical seco

La fragmentación del hábitat puede definirse como un proceso en el cual una gran extensión del hábitat es transformado en parches pequeños aislados unos de otros por una matriz de hábitat diferente a la original (Wilcove et al. 1986; Saunder et al. 1991; Murcia 1996; Fahrig 2003). La pérdida de la biodiversidad, la reducción del área cubierta por bosques naturales ocasionada por la deforestación y la formación de fragmentos remanentes rodeados de pastizales, zonas agrícolas o desarrollos urbanos, constituyen uno de los principales problemas que han enfrentado los bosques tropicales en los últimos siglos (Janzen 1988; Maass 1995; Quesada & Stoner 2004). Las especies vegetales de los ecosistemas tropicales presentan características particulares que las hacen susceptibles a la fragmentación del hábitat puesto que ocurren en baja densidad, tienen tasas de crecimiento y regeneración lenta , presentan una capacidad fotosintética reducida, tienen periodos reproductivos adaptados a una marcada estacionalidad, son polinizadas por animales y presentan tasas de exocruzamiento altas (Bawa 1974;Frankie 1976; Murphy & Lugo 1986; Hamrick & Murawski 1990; Janzen & Vázquez-Yañes 1990; Frankie et al. 1990; Bullock 1995; Murcia 1996; Quesada et al. 2001; Cascante et al. 2002; Fuchs et al. 2003; Quesada et al. 2003, 2004).

Uno de los ecosistemas tropicales que se encuentra en mayor peligro es el bosque tropical seco. En Mesoamérica, se calcula que sólo el 0.09% del área original de este ecosistema se encuentra bajo algún tipo de protección (Janzen 1988), el resto ha sido sustituido por pastizales utilizados para la ganadería extensiva y tierras de cultivo (Maass 1995). En México se considera que únicamente el 27% de la cobertura original del bosque tropical seco permanece intacto. Datos para 1990 indican que cerca del 60% de la vegetación original se ha perdido, por lo que actualmente sólo queda el 19% en condición de bosque restringido en árreas con grandes pendientes (Trejo & Dirzo 2000). La deforestación ha ocasionado una fragmentación de los bosques disminuyendo la densidad de las poblaciones naturales y formando parches de bosques con poblaciones remanentes distantes de las poblaciones en bosque continuos.

Efecto de la fragmentación en el éxito reproductivo y estructura genética de árboles tropicales

La fragmentación del bosque, el aislamiento espacial y la reducción de poblaciones naturales, pueden afectar el éxito reproductivo (Aizen & Feinsinger 1994a, b; Cascante et al. 2002; Fuchs et al. 2003; Quesada et al. 2004), la estructura genética (Aldrich & Hamrick 1998, Hall et al. 1996; Young et al. 1996, Dick 2001) y la regeneración de las especies de plantas (Benitez-Malvido 1998; Cascante et al. 2002). El éxito reproductivo en las poblaciones de plantas está determinado por varios procesos como la producción de flores, frutos y semillas (Murcia 1996). Una reducción en el número de individuos que componen la población, se relaciona con una disminución en la intensidad de floración por unidad de área. Asimismo, al incrementarse la distancia entre árboles reproductivos, disminuye la disponibilidad de polen y el número de visitas de polinizadores se reduce, por lo que la eficiencia de polinización se ve alterada. (Aizen & Feinsinger 1994 a, b; Cunningham 2000a, b; Cascante et al. 2002).

La reducción en la riqueza y abundancia de los polinizadores o de la eficiencia en la polinización, producto de la fragmentación, también pueden reducir la cantidad y calidad del polen que reciben las flores con consecuencias negativas para la progenie que se produce. Se ha visto que el tamaño de las cargas de polen que reciben las flores después de la polinización es un factor importante en el éxito reproductivo de las plantas (Quesada et al. 2001). La competencia entre el polen se pueden alterar al reducir la eficiencia en la polinización, permitiendo que genotipos con una menor viabilidad fertilicen los óvulos y resulten en el desarrollo de frutos con progenies poco viables o inclusive en abortos (Quesada et al, 1993; Niessenbaum, 1999). Existe evidencia empírica que demuestra que la fragmentación provoca una disminución en el número de donadores de polen (Cascante et al. 2002, Fuchs et al. 2003; Quesada et al. 2003, 2004) y una reducción en el flujo génico dentro de las poblaciones. Este fenómeno puede ocasionar una frecuencia mayor de apareamientos entre individuos de la misma población o emparentados, incrementando los niveles de endogamia dentro de poblaciones y el grado de diferenciación entre poblaciones remanentes (Hamrick 1987; Sork et al. 1999). Pero no todos los resultados obtenidos en los trabajos empíricos han obtenido los mismos resultados; también en algunas especies de árboles tropicales se ha encontrado un incremento en el flujo de polen después de la fragmentación (White et al. 2002, Dick 2001, Dick et al. 2003).

A largo plazo, el aislamiento espacial entre los árboles adultos puede generar tanto “depresión endogámica” como "depresión exogámica". El primer caso se produce cuando la disminución en la densidad de árboles promueve el apareamiento entre individuos con alto grado de parentesco, produciendo así progenie menos vigorosa y afectando la regeneración de las poblaciones. En el segundo, el apareamiento se lleva a cabo entre individuos distantes que quedan aislados como producto de la fragmentación, de tal manera que existe una ruptura de complejos génicos coadaptados al ambiente local, disminuyendo así la capacidad de respuesta de la progenie a cambios ambientales y a diferentes presiones selectivas (Charlesworth & Charlesworth 1987; Ellstrand 1992; Waser 1993; Lowe 2005). Lo anterior podría ocasionar que en generaciones sucesivas la aptitud de los individuos disminuya haciéndolos más susceptibles a los cambios que se producen en su entorno biótico y abiótico, aumentando así la probabilidad de extinción de estas poblaciones (Ellstrand & Elam 1993, Murcia 1996, Young et al. 1996, Lowe et al. 2005).

Otro aspecto que puede afectar el éxito reproductivo de las plantas es la asincronía de floración de individuos en la población. En los árboles tropicales la duración del período reproductivo de individuos de una misma especie es variable (Gentry 1974, Frankie et al. 1974; Newstrom et al. 1994 a, b). En los bosques fragmentados, el aislamiento espacial que existe entre los árboles reproductivos puede aumentar con la asincronia fenológica floral; de tal manera que individuos que tengan flores al inicio y al final de la temporada podrían tener una menor probabilidad de ser polinizados y esto se verá reflejado en la producción de frutos y semillas. El efecto de este tipo de aislamiento fenológico depende del grado de sincronía en el período de floración entre árboles de una población o entre flores del mismo árbol, así como del tipo de polinizadores. Por ejemplo, Murawski y Hamrick (1992a, b) señalan que algunas especies de Bombacaceae (*Ceiba pentandra* y *Cavanillesia plataniflora*) que presentan marcados picos de floración se promueve la geitonogamia, mientras que otras especies con periodos de floración prolongados presentan principalmente exocruzas. La sincronía en la fenología floral determina directamente el número efectivo de donadores y la densidad de individuos con flores, ambos factores tienen efecto sobre el flujo de polen entre los árboles (Stephenson 1982; Murawski & Hamrick 1992b). En *Pachira quinata*, por ejemplo, árboles que se sobrelaparon en los periodos de floración recibieron polen de un mayor número de donadores en comparación con los árboles que no se sobrelaparon en su pico de floración (Fuchs et al. 2003). Es por esta razón que resulta importante incluir el análisis de los patrones fenológicos en los estudios de fragmentación de hábitat y relacionar esto con el éxito reproductivo de las plantas.

Estudios en la familia Bombacacea

Los trabajos sobre los efectos de fragmentación de hábitat en la reproducción y variación genética en árboles de la familia Bombacaceae se limitan a 5 especies: *Quararibea asterolepis* (Murawski y Hamrick 1991), *Cavanillesia platanifolia* (Murawski et al. 1990, Murawski y Hamrick 1992a), *Ceiba pentandra* (Murawski y Hamrick 1992b, Lobo et al. 2005), *Ceiba grandiflora* (Quesada et al. 2003) y *Pachira quinata* (Fuchs et al. 2003) y el presente trabajo con *Ceiba aesculifolia* (Herrerías-Diego et al. 2006).

Las características reproductivas de las especies estudiadas son diversas y la variación genética depende de la especie. Por ejemplo, Murawski et al. (1990) determinaron para *Cavanillesia platanifolia* una tasa de exocruzamiento que varía entre 0.569 y 0.347, dependiendo de la población y del año de estudio. Esta variación se debió, principalmente, a que la tasa de exocruzamiento y la frecuencia génica del polen recibido se relacionaron directamente con la densidad de floración y denotan una estrategia mixta de apareamiento. Una estrategia mixta de apareamiento ha sido también inferida para *Ceiba pentandra* asociada a la frecuencia de visita de los polinizadores, siendo las poblaciones con mayor frecuencia de visita predominantemente exocruzadas y conforme la frecuencia de visita se reduce estas poblaciones tienden a ser mas endocruzadas (Murawski y Hamrick 1991, 1992b; Lobo et al. 2005).

Un estudio realizado en *Pachira quinata* (Fuchs et al. 2003) revela que la progenie de árboles en poblaciones de bosque continuo experimenta menores niveles de parentesco, una tendencia a mayores niveles de exogamia y/o más padres que los árboles que se encuentran en sitios fragmentados. Este resultado sugiere que la fragmentación de bosques puede tener un efecto sobre los patrones de apareamiento de *P. quinata*, reduciendo el número de padres en la progenie de árboles en sitios fragmentados. Por otro lado, en un estudio con la especie de *C. grandiflora* en diferentes condiciones de fragmentación, se encontró que no hubo variación en la tasa de exocruzamiento pero si hubo una reducción en el éxito reproductivo. Estos trabajos han demostrado la variabilidad en los parámetros reproductivos y el efecto que sobre ellos puede tener la fragmentación, por lo que especies de la familia Bombacaceae son un buen modelo para analizar los efectos de la fragmentación en la estructura génica y el éxito reproductivo.

Objetivo general

Esta tesis se propone evaluar los efectos de fragmentación del hábitat en la reproducción, diversidad génica y depredación de frutos y semillas de *Ceiba aesculifolia* (Bombacaceae).

Objetivos particulares

Esta tesis se encuentra dividida en tres capítulos:

Capítulo I. Caracterizar las variaciones en los patrones fenológicos y el éxito reproductivo de árboles de diferentes poblaciones en sitios perturbados y en sitios no perturbados a través de cuatro años de observaciones.

Capítulo II. Estudiar la estructura genética, las tasas de exocruzamiento y las correlaciones de paternidad de las poblaciones remanentes en sitios perturbados en comparación con las poblaciones que se encuentran en poblaciones no perturbadas durante cuatro años.

Capítulo III. Evaluar, el efecto de la depredación de frutos y semillas de *Ceiba aesculifolia* entre árboles en sitios perturbados y árboles en sitios no perturbados. Evaluar el efecto de la depredación de semillas en la germinación de *Ceiba aesculifolia.*

Predicciones

Capítulo I. La producción de frutos y semillas será mayor en árboles de sitios no perturbados que en árboles de sitios perturbados dado que se espera que la polinización sea más eficiente en el hábitat natural de los polinizadores y su capacidad de desplazamiento entre zonas perturbadas se vea disminuida.

El flujo de polen puede ser modificado en los fragmentos de bosque o en los árboles aislados (Bawa, 1990). Janzen (1974), menciona que los sistemas especializados entre planta–polinizador son muy sensibles a cualquier tipo de perturbación. Varios estudios han demostrado que en los hábitats fragmentados la abundancia de polinizadores disminuye y ocasiona una reducción en la producción total de frutos y en el “fruit set” (Aizen & Feinsinger, 1994 a).

Capítulo II. El número de donadores de polen y la tasa de exocruzamiento se espera que sea menor para árboles en sitios perturbados.

Al haber una reducción en el número de individuos de una población, como ocurre en sitios perturbados, existen más probabilidades que la progenie producida provenga de un número menor de donadores de polen que la progenie producida en los sitios no perturbados.

Un incremento en el aislamiento espacial puede afectar negativamente la atracción de los polinizadores, por lo que su principal efecto podría ser una disminución en el número de visitas del polinizador (en este caso murciélagos) y por lo tanto una reducción en el flujo de polen. Además en sitios aislados aumenta la probabilidad de que las visitas de los polinizadores que el flujo de polen se presente sólo entre individuos cercanos, reduciendo la posibilidad de cruzas entre individuos de diferentes poblaciones.

Capítulo III. La depredación de frutos y semillas será mayor en los árboles de sitios no perturbados que en árboles de sitios perturbados, debido a factores denso-dependientes.

La producción de frutos varía año con año así como entre individuos y se espera que la fragmentación del hábitat sea un factor que incremente la variación en el éxito reproductivo de los individuos remanentes. Se espera que la disponibilidad de frutos y semillas para los depredadores, sea menor en árboles de sitios perturbados. En árboles de sitios no perturbados se espera que por lo menos un individuo fructifique dentro de la población cada año y mantenga la disponibilidad del recurso a través del tiempo.

Independientemente de la fragmentación del hábitat planteamos la siguiente predicción relacionada con los estadios de desarrollo de los insectos depredadores.

La depredación de semillas por parte de *Dysdercus* sp. variará dependiendo del estadio de desarrollo del insecto, puesto que los requerimientos nutricionales son mas altos en estadios inmaduros.

De acuerdo a los requerimientos nutricionales de los insectos, en los estadios de desarrollo inmaduros, se requieren de mayores cantidades de alimento debido al desgaste energético que representa el paso de un estadio a otro; adicionalmente, los estadios ninfales y pre-adultos tienen una conducta de depredación en grupo, por lo tanto, se espera que los mayores niveles de depredación se presenten en los primeros estadios de desarrollo de *Dysdercus* sp.

Sitio de Estudio

El tipo de vegetación predominante en la región es clasificado como bosque tropical caducifolio (Rzedowski 1978) o selva baja caducifolia (Miranda & Hernández X. 1963), aunque también se presentan algunas áreas de Selva Mediana Subcaducifolia y en menor grado zonas de matorral mediano espinoso (Solís 1980). La selva baja se localiza en los lomeríos con suelos más o menos someros mientras que la selva mediana ocurre a lo largo de los arroyos y en lugares protegidos sobre suelos profundos (Lott et al. 1987). La selva baja es marcadamente estacional, caracterizándose por la pérdida total del follaje durante la temporada seca. En esta época quedan con follaje solamente algunas especies que habitan cerca de arroyos o en cañadas, los cuales son lugares con una mayor humedad, donde se encuentran los parches de selva mediana. La riqueza florística de Chamela es alta, ya que se conocen alrededor de 779 especies que se agrupan en 107 familias de plantas vasculares (Lott, 1985). El número de especies asciende a 1120, agrupadas en 124 familias, al incluirse el área de la bahía de Chamela (Lott, 1993). Las familias más diversas son Leguminosae y Euphorbiaceae, seguidas por Asteraceae, Convolvulaceae, Rubiaceae, Bromeliaceae, Malvaceae y Acanthaceae.

La orografía consta de lomeríos de 0 a 200 msnm. El suelo se deriva de basaltos o riolitas y es esencialmente neutro (pH 6.8+-15). El clima es del tipo Aw O (x´) según Köppen modificado por García (1964) con una temperatura poco estacional, la cual va desde 15.9 ºC a 32.2 ºC. Las lluvias se presentan en períodos cortos (Julio a Octubre), en tanto que los periodos de seca son más largos (de Noviembre a Mayo). La precipitación promedio anual de 748mm (Bullock, 1986).

Las poblaciones en ambientes no perturbados se ubicaron dentro de la reserva de la Biosfera Chamela-Cuixmala, la cual abarca 16 000 ha y esta ubicada en el municipio de la Huerta, Jalisco. La reserva limita al norte con el Río Chamela y al sur con el Río Cuixmala, al oeste con la carretera federal 200 y al este con el Arroyo Caimán. Las poblaciones en sitios perturbados se encuentran sobre la carretera federal no. 200 (Fig. 2). Las condiciones de aislamiento espacial que se evaluaran en el estudio son las siguientes: 1) árboles en sitios perturbados (cuatro poblaciones en fragmentos de bosque, incluyendo individuos en corredores o fragmentos de bosque alterados rodeados por una matriz de campos agrícolas y pastizales, en donde su densidad no exceda tres individuos reproductivos por hectárea) y 2) árboles en sitios no perturbados (tres poblaciones ubicadas en bosques continuos con una densidad de seis individuos reproductivos por hectárea).

Figura 2. Reserva de la Biosfera Chamela Cuixmala y zonas aledañas. a) Cauce del arroyo Colorado en la temporada seca. b) Zona de humedales, Río Cuixmala. c) Reserva de la Biosfera Chamela- Cuixmala temporada Seca. d) Reserva de Biosfera Chamela –Cuixmal temporada lluviosa. e) Zona quemada ceca de los límites de la Reserva. f) Zona de Cultivo al Norte de la Reserva, sobre la carretera federal 200. g)

CAPÍTULO I

Running head**.-Forest fragmentation and reproductive success**

Word count: 6651 words

Effects of forest fragmentation on phenological patterns and reproductive success of the tropical dry forest tree *Ceiba aesculifolia*

YVONNE HERRERÍAS-DIEGO[1], MAURICIO QUESADA[1], KATHRYN E. STONER[1] JORGE A. LOBO[2]

[1]Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México, Campus Morelia, and [2]Universidad de Costa Rica, Escuela de Biología, San Pedro, Costa Rica; Apartado Postal 27-3 (Xangari), Morelia, Michoacán, México 58089

Correspondence: Mauricio Quesada (e-mail: mquesada@oikos.unam.mx)

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Abstract

Spatial isolation caused by forest fragmentation and temporal isolation caused by asynchronous flowering of plants have been proposed as important factors that affect the reproduction of plant populations. In a 4-year study, we determined the effects of forest fragmentation and spatial isolation on flowering phenology and reproductive success of the tropical bombacaceous tree *Ceiba aesculifolia* ([Kunth]) Britton and Rose). We conducted our study in the dry forest of Mexico and compared populations in two habitat conditions based on density and environmental conditions: (1) disturbed habitat (four populations of three or less reproductive individuals/ha surrounded by agricultural fields or pastures) and (2) undisturbed habitat (three populations of groups of six or more reproductive individuals/ha surrounded by undisturbed mature forest). We compared the following variables within these populations over 4 years: flowering overlap, proportion of individuals with flowers and fruit, total flower production, total fruit production, fruit set, seed production, and seed abortion. Little overlap in flowering occurred between the populations in the two habitat conditions. The flowering period of trees in the disturbed habitat initiated between 15 to 20 days before the flowering period of trees from the undisturbed habitat during 3 years. Flowering of trees from the undisturbed habitat peaked at the end of the flowering period of the trees from the disturbed habitat. The proportion of trees that flowered was greater in the undisturbed habitat. Nevertheless, total flower production was greater in the disturbed habitat and these differences were maintained across 3 years. The proportion of individuals that produced fruit did not differ across habitat conditions but did differ across years. Total fruit production was greater in the disturbed habitat, but fruit set and seed production were the same across years and between habitat conditions. Seed abortion varied over years between habitats. We concluded that forest fragmentation does not negatively affect the reproductive success of *C. aesculifolia*. It appears that the highly mobile bat pollinators maintain reproductive connectivity between trees in both habitats.

Introduction

The reduction of natural forests and the formation of forest fragments caused by anthropogenic activity are the main causes of biodiversity loss in tropical forests (Janzen 1988; Quesada & Stoner 2004). One of the most threatened ecosystems in tropical areas is tropical dry forest, which represents nearly 42% of tropical forests around the world (Murphy & Lugo 1986). In the Neotropics, the tropical dry forests that once formed an undisturbed habitat are now found in fragmented patches, and in Mexico only 27% of the original tropical dry forest cover remained as intact forest in 1990 (Trejo & Dirzo 2000).

Deforestation causes the formation of patches of forest habitat and diminishes the density of tree populations. This spatial isolation and reduction of natural populations negatively affects the reproductive success of many tropical plants (e.g., Aizen & Feinsinger 1994a; Fuchs et al. 2003; Quesada et al. 2003, 2004; but see Costin et al. 2001 & Quesada et al. 2004). A reduction in the number of individuals in a population decreases the number of flowers per unit area and may affect the efficiency and activity of pollinators. Results of several studies show that forest fragmentation negatively affects plant reproductive success by reducing pollinator activity (e.g., Aizen & Feinsinger 1994b; Quesada et al. 2003, 2004); pollen deposition (e.g., Cunningham 2000a; Cascante et al. 2002; Quesada et al. 2003); fruit and seed set (e.g., Ghazoul et al. 1998; Fuchs et al. 2003; Quesada et al. 2004; but see Cunningham 2000b and Cascante et al. 2002); and the regeneration of many plant species (Benitez-Malvido 1998; Cascante et al. 2002; Benitez-Malvido & Martínez Ramos 2003). Nevertheless, results of other studies show a positive effect of forest fragmentation on pollen flow (e.g., Dick 2001; White et al. 2002; Dick et al. 2003) and no effect on total fruit and seed production (Cascante et al. 2002; Fuchs et al.2003). These results indicate that tropical trees have different responses to forest fragmentation and suggest that individual trees in fragmented landscapes may have an especially important conservation value for some species that are not affected negatively by forest fragmentation.

Forest fragmentation and disturbance can also change the reproductive success of plants by affecting their flowering period and frequency of reproduction over time. Results of some studies indicate that forest fragmentation changes several environmental conditions that may regulate the phenological and reproductive patterns of plants (Kapos 1989; Saunders et al*.* 1991; Kapos et al*.* 1997). In tropical trees the duration of reproductive events is highly variable among species (e.g., Gentry 1974; Frankie et al. 1974, 1990); however, only a few researchers have evaluated the variation in floral phenology of particular species over long periods of time (e.g., Opler et al*.* 1980; Stiles 1978; Newstrom et al. 1994). These studies that cover a span of several years have documented great yearly variation in flowering frequency and reproductive success in natural populations in undisturbed continuous forest. Nevertheless, no one has evaluated the long-term response of phenological expression and reproduction of long-lived perennial plants over years in different habitat conditions. In addition, several studies have shown that, in natural mature undisturbed habitats, trees are predominantly outcrossing and have animal vectors for pollen dispersal (e.g., Bawa 1974; Hamrick and Murawski 1990; Bullock 1995). We expect forest fragmentation to affect flowering phenology, reproductive success and mating patterns of plants because human disturbance will negatively affect pollinator behavior, tree density and habitat conditions. A few studies have evaluated the effects of spatial and temporal isolation due to forest fragmentation on plant reproduction, but they only analyzed a single reproductive event in long-lived plants (Fuchs et al*.* 2003; Quesada et al*.* 2003, 2004). In our 4-year study, we determined the effects of forest fragmentation on flowering phenology and the reproductive success of the tropical tree *Ceiba aesculifolia* (pochote, [Kunth]) Britton and Rose) by comparing reproductive parameters between tree populations in disturbed and undisturbed habitats.

Methods

Study species

Ceiba aesculifolia (Bombacaceae) is a Neotropical species distributed from Mexico to northern Costa Rica (Cascante-Marin 1997). Adult trees grow up to 20 m tall and have diameter at breast height (dbh) of 20 to 50 cm. *Ceiba aesculifolia* has large (10 - 16 cm) flowers with five brown pubescent petals. Styles are on average 15 cm long and surpass the stamens by two centimeters. In the tropical dry forest of Mexico and Costa Rica, *Ceiba aesculifolia* is the last species of the family to flower at the end of the dry season and all the fruit mature during the following dry season

(Lobo et al. 2003; Quesada et al. 2004). *Ceiba aesculifolia* has a predominantly outcrossing mating system and has two bat pollen vectors, *Glossophaga soricina* and *Leptonycteris curasoae* (Quesada et al. 2004).

Study area

The study was conducted in the central Pacific coast of Mexico within and surrounding the Chamela-Cuixmala Biosphere Reserve (ca. 19°30'N, 105°03"W.). This reserve is between Puerto Vallarta, Jalisco, and Manzanillo, Colima, and covers 13,200 ha. The predominant vegetation type is tropical dry forest, which is characterized by a rainy season from the middle of June through October and an extended dry season from November through May. Two main habitats occur in this area, the upland dry forest and "arroyo" forest which are found along the seasonally wet riverbeds (Lott 1993). Average annual rainfall is 750 mm, and average temperature is 25°C.

Selection of trees

To examine the effects of forest fragmentation on the reproductive success of *C. aesculifolia*, we compared trees from two habitat conditions: disturbed and undisturbed. All trees selected were reproductive adults. Trees were considered to be in disturbed habitats if there were three or fewer reproductive individuals per hectare in small forest fragments and surrounded by agricultural fields or pastures. Trees in disturbed habitats were systematically selected along Federal Road 200 (Barra de Navidad to Puerto Vallarta) near the Chamela-Cuixmala Biosphere Reserve. We selected four populations in disturbed habitats that were separated by more than 10 km from each other. Undisturbed habitats consisted of groups of six or more reproductive individuals per hectare occurring in an area surrounded by mature forest within the Chamela-Cuixmala Biosphere Reserve. To include the largest area possible within the reserve, we selected three populations from three different watersheds within the reserve that were separated from each other by more than 8 km. The number of individuals that flowered and produced matured fruits of *C. aesculifolia* varied depending on the year. In total we studied 36 trees from disturbed habitats and 56 trees from undisturbed (Table 1).

Phenological patterns

To determine the flowering and fruiting patterns of *C. aesculifolia,* we recorded the phenology of each marked individual for each population every 2 weeks from May to August 2000, 2001, 2002, and 2003 (Table 1). We determined the flowering peak for each individual in Julian days by counting the total number of flowers produced every 15 days during the reproductive season and then estimated the average peak flowering date for the population within disturbed and undisturbed habitats.

To compare the flowering phenology between trees in undisturbed and disturbed habitats, we determined the difference between flowering dates of these habitat conditions over 4 years. To do this we used the unimodal flowering phenology model proposed by Malo (2002). This model uses an exponential sine function based on data obtained from a sample of the number of flowers produced by individuals in a population over a period of time to fit a curve. The curve generated by the model estimates the following parameters: maximum number of flowers produced by a tree at the peak flowering date of the population (hereafter flower production); date at which flowering started (flowering commencement);length of time of flower production (flower production time); symmetry of the curve; and tails of the curve (Malo 2002). We simplified the model by assuming that curve symmetry and tail length equal 1 (i.e., symmetrical distribution and kurtosis = 0). We compared flower production, flowering commencement, and flower production time between trees in disturbed and undisturbed habitats to determine the degree of separation of flowering dates caused by forest fragmentation.

We determined the variation in the intensity and duration of the phenological patterns in *C. aesculifolia* during 4 consecutive years. Flowering overlap was estimated by pairwise comparisons of flowering intensity between each population for each year. Flowering intensity for each year was the percentage of trees flowering at each sampling date. To compare the flowering intensity between disturbed and undisturbed populations, we calculated an overlap index (Pianka 1973) for each year. To determine whether flowering overlap indexes differed statistically from random expectations (i.e., Pianka's index differed statistically from zero), we used a null model analysis to compare the mean overlap index with 1000 randomly simulated values (Lobo et al. 2003). Flowering overlap was considered to occur when the observed index was over 95% of the 1000 simulated values. All calculations were performed in the EcoSim 7.0 computer program for null model analysis in community ecology (Gotelli & Entsminger 2001).

To compare the frequency of reproductive individuals of each population under different habitat conditions and across years, we determined the proportion of trees that produced flowers and fruit each year in each population in disturbed and undisturbed habitat conditions (Table 1). We used a generalized linear model applying the GENMOD procedure (SAS, 2000) for repeated measurements with tree as the repeated factor in the model. The model used population nested within habitat condition, habitat condition, year, and the interaction between year and habitat condition as the categorical independent variables. The proportion of trees that produced either flowers or fruits were dependent variables and were calculated as the number of trees with flowers or fruits divided by the total number of trees respectively. The analysis used a binomial distribution and a logit link function. To control for variation associated with tree size, we used diameter at breast height (dbh) as a covariate in the model. Because *C. aesculifolia* is predominantly outcrossing and requires external donors to reproduce (Quesada et al. 2004), distance to the nearest neighbor and distance to forest were used as additional covariates in the analysis for the trees that produced fruit.

Reproductive success

To evaluate the effect of forest fragmentation on the reproductive success of *C. aesculifolia*, we determined total flower and fruit production and fruit set (i.e., number of fruits per flower) for each tree for 3 years (Table 1). Because we counted the number of flowers produced by each individual every 15 days, we estimated total flower production of each tree as the area under the distribution obtained by the number of flowers versus time, following the procedure of Fuchs et al. (2003). We estimated the production of fruits of each individual tree by counting the total number of fruits produced every 15 days during the fruiting period. The total number of fruits produced by each individual was estimated as the maximum number of fruits counted. Fruit set was estimated as the proportion of the total number of fruits over the total number of flowers produced by each individual.

To determine whether habitat condition affected flower and fruit production and fruit set for each year, we used generalized linear models applying the GENMOD procedure (SAS 2000) for repeated measurements with tree as the repeated factor in the model. The model used population nested within habitat condition, habitat condition, year, and the interaction between year and habitat condition as the categorical independent variables. The dependent variable for each of the three analyses, respectively, was flower production, fruit production, and fruit set. Because flower production and fruit production do not follow a normal distribution, we used a Poisson distribution for these two analyses. These models use a logarithmic link function. A binomial distribution and a logit link function were used for the analysis of fruit set. To control for the variation associated with tree size, we used dbh as a covariate in the model. Distance to the nearest neighbor and distance to forest were used as additional covariates in the analysis of fruit production and fruit set.

To determine whether habitat condition affected seed production, we collected a sample of five fruits from each maternal tree and counted seeds from each fruit, and classified seeds as aborted or potentially viable. We considered seeds that were wrinkled and brownish with a dry endosperm aborted, whereas potentially viable seeds were filled, well-rounded and black. We collected fruits from trees from disturbed and undisturbed populations for 2 years, 2000 and 2001 (Table 1). We used a multivariate analysis of variance for repeated measurements over time (GLM, SAS 1999) to analyze the effects of habitat on the number of potentially viable seeds, aborted seeds, and total seeds, where tree was the repeated factor in the model. The model used population nested within habitat condition and habitat condition as categorical independent variables. A separate analysis using the previous model was conducted for each one of the following response variables: number of aborted seeds, potentially viable seeds, and total seeds produced per fruit. These variables followed a normal distribution. To control for the variation associated with tree size, we used dbh as a covariate in the model. Distance to the nearest neighbor and distance to forest were used as additional covariates in the analysis.

Results

Phenological patterns

The unimodal sine exponential model used to estimate the flowering phenology patterns of disturbed and undisturbed populations showed differences between them (Table 2, Fig. 1). Maximum flower production was greater in the disturbed habitat condition for 3 consecutive years. Flowering period of trees from disturbed populations began between 15 to 20 days before the flowering period of trees from undisturbed populations for the years 2000, 2002, and 2003. No difference was observed for 2001. Length of time for the flowering of trees between habitat conditions was similar.

The flowering overlap index showed significant differences in the flowering period between disturbed and undisturbed populations for the years 2000, 2002, and 2003, with populations in disturbed areas flowering first (Table 3). In 2001 only two pairwise comparisons showed significant differences between flowering periods.

The proportion of individuals of *C. aesculifolia* that flowered varied depending on the year (χ^2=16.32, df = 3, *p*=0.0010, Fig. 2a). No significant effects were observed for population nested within habitat condition (χ^2 =8.47, df=5, *p*=0.1321), habitat condition (χ^2 =0.28, df=1, *p*=0.0598), interaction of habitat condition by year (χ^2=5.16, df=3, *p*=0.1601), or dbh (χ^2 =2.40, df=1, *p*=0.1210).

The proportion of individuals that set fruit varied depending on the year (χ^2=34.22, df=3, *p*<0.0001, Fig. 3b), habitat condition (χ^2=7.38, df=1, *p*=0.0066, Fig. 2b), and interaction of year by habitat condition (χ^2=15.56, df=3, *p*=0.0014, Fig. 2b); however, no effect of habitat population nested within habitat condition was observed (χ^2=8.70, df=5, *p*=0.1217). Diameter at breast height (χ^2=1.94, df=1, *p*=0.16), distance to nearest neighbor (χ^2=0.13, df=1, *p*=0.71), and distance to the forest (χ^2=2.40, df=1, *p*=0.1212) had no significant effects.

Reproductive success

Total flower production over 3 years was significantly different between habitat conditions, with trees in disturbed habitats producing more flowers per individual (mean = 971 flowers/tree

[1.16]) than trees from undisturbed populations (mean= 625 [1.14], χ^2=6.11 df= 1, *p*=0.013, Fig. 3a). This difference was maintained across years (χ^2= 18.05, df= 2, *p* <.0001) with no significant effect of population nested within habitat condition (χ^2= 4.05, df= 5, *p* = 0.5425) or the interaction of habitat condition by year (χ^2= 3.22, df= 2, *p*= 0.2). Total flower production was significantly affected by tree dbh (χ^2= 4.06, df=1, *p*=0.04), with more flowers produced by larger trees.

Similar to total flower production, total fruit production was significantly different between habitat conditions. Total fruit production was greater in trees from disturbed habitats (mean =17 [1.18]) than trees from undisturbed populations (mean =5, SE= 1.33, χ^2=9.06, df=1, *p*=0.0026, Fig. 3b). This difference was maintained across the 3 years (χ^2=41.27, df= 2, *p* < 0.0001). There was also a marginal interaction between habitat condition and year (χ^2= 5.59, df= 2, *p*=0.06) and population nested within habitat condition (χ^2= 9.86, df= 5, *p*=0.07). The dbh of trees (χ^2= 7.95, df= 1, *p*=0.0048) and distance to nearest neighbor (χ^2= 3.92, df= 1, *p*=0.04) significantly affected total fruit production, but there was no significant effect of distance to the forest (χ^2=0.77, df=1, *p*=0.3788).

Similar to total flower production and fruit production, fruit set was significantly different between habitat conditions (χ^2= 4.58, df= 1, *p*= 0.0324, Fig. 3c), and this difference was maintained across years (χ^2 = 24.63, df=2, *p*= 0.0001). Population nested within habitat condition (χ^2=9.46, df=5, *p*= 0.09) and interaction of habitat condition by year (χ^2=5.04, df=2, *p*= 0.08) did not differ significantly between populations. The dbh (χ^2=1.03, df=1, *p*= 0.31) and distance to the forest (χ^2=0.37, df=1=, *p*=0.54) were not related to fruit set, but there was a significant effect of distance to nearest neighbor (χ^2=5.31, df=1, *p*=0.021). The overall average of total seed production per fruit in *C. aesculifolia* was 106 seeds (SE=7.67), of which an average of 97 (10) were potentially viable and 12 (5.4) were aborted seeds. Population nested within habitat condition significantly affected total seed production (*F*=2.84, df=5, *p*=0.042), but habitat condition, distance to the forest, distance to nearest neighbor, and dbh did not significantly affect seed production per fruit (*F*=0.12, df=1, *p*=0.7341; *F*=1.44, df= 1, *p*=0.24; *F*=0.02, df=1, *p*=0.88 and *F*=0.45, df= 1, *p*=0.51, respectively). A multivariate repeated measures analysis of variance (MANOVA) showed there was not a significant year effect on total seed production (Wilk's λ =0.99, *F*=0.03, df=1, 20 *p*=0.87); population nested within habitat condition (Wilk's λ =0.67, *F*=1.96, df= 5, 20 *p*=0.12); or habitat condition by year interaction (Wilk's λ =0.95, *F*=0.89, df=1, 20 *p*=0.36). The dbh, distance to the forest, and distance to the nearest neighbor were not related to total seed production over the 2 years (Wilk's λ =0.96, *F*=0.64, df= 1, 20 *p*=0.43; Wilk's λ =0.99, *F*=0.04, df= 1, 20 *p*=0.84; Wilk's λ =0.98, *F*=0.26, df= 1, 20 *p*=0.61 respectively).

Habitat condition, distance to the forest, distance to nearest neighbor, and dbh did not significantly affect the production of potentially viable seeds (*F*=0.38, df=1, *p*=0.54; *F*=0.26, df=1, *p*= 0.61; *F*=0.73, df=1, *p*=0.40; *F*=0.60, df=1, *p*=0.44, respectively). Population nested within habitat condition significantly affected the production of viable seeds (*F*=3.07, df=5, *p*=0.03). A MANOVA showed no significant year effect on the production of potentially viable seeds (Wilk's λ =0.87, *F*=2.85, df=1, 20 *p*=0.1071) and no significant interaction of population nested within habitat condition with year effect (Wilk's λ =0.79, *F*=1.00, df=5, 20 *p*=0.4410). There was a significant habitat condition by year interaction (Wilk's λ =0.76, *F*=6.14, df= 1, 20 *p*=0.022). In 2000 the potentially viable seeds of undisturbed populations were significantly greater than the potentially viable seeds of undisturbed populations for 2001. The dbh, distance to nearest neighbor, and distance to the forest did not affect the production of potentially viable seeds over the 2 years (Wilk's λ =0.92, *F*=1.54, df= 1, 20 *p*=0.22; Wilk's λ =0.91, *F*=1.67, df= 1, 20 *p*=0.21; Wilk's λ =0.99, *F*=0.09, df= 1, 20 *p*=0.76 respectively).

Habitat condition, population nested within habitat condition, dbh, distance to nearest neighbor, and distance to the forest had no effect on seed abortion (*F*=3.54, df=1, *p*=0.07; *F*=0.97, df=5, *p*=0.45; *F*=0.02, df=1, *p*=0.87; *F*=1.33, df=1, *p*=0.26 and *F*=1.69, df=1, *p*= 0.21 respectively). There was a marginal year effect on the number of aborted seeds (Wilk's λ =0.85, *F*=3.53, df=1, 20 *p*=0.07) and a significant habitat condition by year interaction (Wilk's λ =0.76, *F*=6.3, df= 1, 20 *p*=0.02). There was no effect of year and population nested within habitat condition (Wilk's λ =0.81, *F*=0.92, df= 5, 20 *p*=0.48). In 2000 aborted seeds from fragmented populations were significantly greater than aborted seeds from fragmented populations in 2001. The dbh, distance to nearest neighbor, and distance to the forest were not related to the number of aborted seeds over time

(Wilk's λ =0.96, *F*=0.72, df= 1, 20 *p*=0.41; Wilk's λ =0.87, *F*=2.56, df= 1, 20 *p*=0.12; Wilk's λ =0.98, *F*=0.24, df= 1, 20 *p*=0.63 respectively).

Discussion

Our results indicated that the frequency of flowering was similar between populations in disturbed and undisturbed conditions, but the flowering peak of *C. aesculifolia* in disturbed populations occurred between 2 weeks to 1 month ahead of the trees from undisturbed habitats. The flowering period of trees from disturbed populations commenced between 15 to 20 days before trees from undisturbed populations during 3 years, but the length of flowering was similar for trees in both habitat conditions. Undisturbed populations presented their flowering peak at the end of the flowering period of disturbed populations. Some environmental factors have been invoked to explain variations in phenological patterns in some plant species (Opler et al. 1976; Rathcke & Lacey 1985; Van Schaik et al. 1993). For example, a certain threshold level of drought may trigger flowering in some species of plants (Alvim 1960; Wright et al. 1999). In addition, forest fragmentation may increase solar radiation and wind speed and decrease soil water availability at the edge of the forest and in forest fragments (e.g., Kapos 1989; Saunders et al. 1991; Kapos et al. 1997). In Chamela soil water availability in agriculture fields and pastures differs from that in forest (Maass et al. 1988). *Ceiba aesculifolia* flowers during the driest period of the dry season in Chamela (Lobo et al. 2003). In our study, disturbed populations may be experiencing drier soil conditions and greater temperatures, thereby triggering their flowering period earlier than trees in undisturbed populations.

The results of the unimodal sine exponential model that we used to estimate flowering phenology patterns showed that 20% of the total flower production of disturbed populations in 2000 occurred before the beginning of flower production in undisturbed populations. Furthermore, 25% of the total flower production of undisturbed populations occurred after the end of the flower production of disturbed populations. In 2002 these parameters were 16% and 18 % respectively and in 2003 30% and 23%. No difference was observed in 2001. These observations suggest that as many as half of the individuals that flower in each habitat condition each year experience reproductive isolation from trees found within the other habitat. Similarly, according to Pianka's overlap index analysis, there was no flowering overlap period between disturbed populations and tree populations in undisturbed during 3 of the 4 years (the exception was 2001).

Similar numbers of trees flowered in both habitat conditions, but more trees set fruit in disturbed populations. In addition, total flower production was different between habitat conditions. Disturbed populations produced more flowers per individual than trees from undisturbed populations, and this difference was maintained across 3 consecutive years. Similarly, total fruit production was greater in disturbed populations, where individuals tended to develop wider tree crowns with more reproductive branches than undisturbed populations. This architecture is most likely a consequence of being located in open areas, where there was no competition from neighboring conspecifics or other species. This in turn, possibly leads to a greater total fruit production in disturbed habitats. Fruit set also was different between habitat conditions. Each flower in disturbed populations had a greater probability to produce a fruit. It is possible that pollinators in disturbed populations are responsible for maintaining a greater fruit set because disturbed populations receive more pollinator visits than trees in undisturbed populations (Quesada et al. 2004). Another possible explanation for higher fruit set in disturbed populations is that they may experience less competition and thus have more resources that result in an increase in fecundity by producing more flowers, either by flowering more often or by increasing flower number in each episode. This prediction is supported by findings that the quantity of flowers produced responds to variation in some important limiting resource, such as light (Chazdon 1991; Niesenbaum 1993; Cunningham 1997).

Although the effects of habitat fragmentation on the reproductive success of particular plant species have been investigated, contrasting results have been reported. In some cases habitat fragmentation negatively affects the reproductive success of grassland species (Oostermeijer et al. 1994; Ågren 1996, Kery et al. 2000) or tree species (Ghazoul et al. 1998; Fuchs et al. 2003, Quesada et al. 2003, Aguilar & Galetto 2004); whereas in other cases there is no effect on plant reproductive success (e.g., Dick 2001; Cascante et al. 2002, Cunningham 2000b). In particular, fruit set may be modified due to the reduction in the rate of pollinator visits (e.g., Aizen & Feinsinger

1994b; Cunningham 2000a; Quesada et al. 2004) and the subsequent decrease in pollen deposition (Aizen & Feinsinger 1994a; Ghazoul et al. 1998; Cunningham 2000a). One of the reasons the effects of forest fragmentation may be so variable between different studies is likely due to differences in responses of different species of plants during different portions of their life history. For *C. aesculifolia* we evaluated the effect of forest fragmentation on reproductive success in only one small portion of the life of this long-lived perennial species. Reproductive success in perennial species is only accurately reflected by their cumulative success over many years (Piñero & Sarukán 1982; Clark & Clark 1987).

Another possible explanation for the variable results of forest fragmentation on plant populations is the breeding system of each species. The level of isolation is particularly important for obligate outcrossing plants because small populations may be less likely to attract pollinators than large ones (e.g., Aizen & Feinsinger 1994b; Stefan-Dewinter & Tscharntke 2001; Quesada et al. 2003). *Ceiba aesculifolia* is an obligate outcrossing species (Quesada et al. 2004); therefore, this tree depends on pollinators for successful pollen removal and fruit production. The two main pollinators of *C. aesculifolia* are the nectarivorous bats *Glossophaga soricina* and *Leptonycteris curasoae* (Quesada et al. 2004). Contrary to expectations, these two species of pollinators visit more flowers in disturbed habitats than in undisturbed habitats (Quesada et al. 2004). One individual of *C. aesculifolia* may produce 14 flowers/night (10-135) in undisturbed populations and 21 flowers/night (10-232) in disturbed populations so the more frequent visits of bats to flowers from disturbed populations may occur because flowers are more abundant and conspicuous in disturbed populations. Therefore, more flower visitation by pollinators may result in greater fruit production. Although we did not study gene flow via pollen or the relatedness of the progeny produced by trees, it is possible that in disturbed populations bats are forced to travel longer distances, favoring more compatible crosses between unrelated trees and greater fruit set (Quesada et al. 2001; Fuchs et al. 2003; Lobo et al.2005).

In self-incompatible species, pollinator limitation can result in reduced levels of seed set (Ågren 1996; Steffan-Dewenter & Tscharntke1999; Hendrix & Kyhl 2000), but in other species isolation does not seem to reduce the production of seeds (e.g., Dick 2001; Cascante et al. 2002;

Fuchs *et al*. 2003). In addition to pollinator limitation, habitat fragmentation is likely to negatively affect the reproductive success of trees due to a possible reduction in the number of compatible pollen donors within populations (Fuchs et al. 2003). According to our results, forest fragmentation did not affect total seed production. The number of potentially viable and aborted seeds changed across years but was independent of forest fragmentation.

Our results showed that trees in undisturbed populations present their peak of flower production at the end of the flowering period of trees in fragmented habitats, but this difference depends on the habitat condition and the year. Disturbed populations produced more flowers, and total fruit production and fruit set were greater for trees in disturbed populations over time. This is the first study to show long-term effects of forest fragmentation on the floral phenological patterns and reproductive success of trees.

Forest fragmentation did not negatively affect the reproductive success of *C. aesculifolia*. It appears that at least some of the bat pollinators of this species are traveling long distances and moving sufficient pollen to remote trees to maintain reproductive connectivity. Our results and the results of Cascante (2002) identify the importance of disturbed populations as possible stepping stones for pollen flow between forest fragments and undisturbed habitats.

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Table 1. Number of individuals of *C. aesculifolia* analyzed for each year.

		Year			
Habitat condition	Population	2000	2001	2002	2003
Disturbed	Arroyo Seco	8	12	14	14
	Boca de Iguanas	4	11	15	17
	Programa	4	4	3	3
	Tecuán	4	6	5	6
Total individuals	**Disturbed**	**20**	**33**	**37**	**40**
Undisturbed	Arroyo Cajones	2	23	19	21
	Chamela	21	23	19	19
	Arroyo Limbo	No data	10	4	4
Total individuals	**Undisturbed**	**23**	**56**	**42**	**44**

Table 2. Parameters that describe the unimodal flower phenology model with exponential sine equations for trees of *C. aesculifolia* in disturbed and undisturbed habitats over 4 years.

		Flowering	(SE)	
Year	Habitat	No. produced[a]	Date[b]	Production time[c]
2000	Disturbed	560.6 (114.2)	1.4 (5.8) -10.2 - 13.03	71.0 (X)
	Undisturbed	117.0 (15.9)	21.3 (5.5) 10.4 - 32.25	75.8 (9.2)
2001	Disturbed	1229.5 (133.8)	5.9 (2.5) 0.9 - 10.9	66.0 (X)
	Undisturbed	1009.1 (102.0)	6.0 (2.3) 1.4 - 10.6	66.0 (X)
2002	Disturbed	276.3 (48.0)	13.7 (3.5) 6.7 - 20.7	52.5 (6.5)
	Undisturbed	176.8 (15.5)	26.8 (2.0) 22.8 - 30.9	54.8 (3.7)
2003	Disturbed	X	26.0 (X)	X
	Undisturbed	X	46.0 (X)	X

[a] Maximum number of flowers produced by a tree with SE in parentheses. X indicates the parameter could not be estimated.

[b] Date flowering started with SE in parentheses and confidence interval below. X indicates the parameter could not be estimated.

[c] The length of time flowers are produced with SE in parenthesis; X indicates the parameter could not be estimated.

Table 3. Observed pair-wise phenological overlap between disturbed and undisturbed populations for 4 years calculated with Pianka´s (1973) overlap index. The p-value given in parentheses indicates the probability that the null hypothesis of no flowering overlap is correct.

			Disturbed	Populations	
	Year		Pianka index	(*p*)	
	2000	Arroyo Seco	Boca de Iguanas	Tecuan	Programa
	Cajones	0.59 (0.41)	0.52 (0.48)	0.51 (0.31)	0.66 (0.18)
	Limbo	No data	No data	No data	No data
	Chamela	0.137 (0.71)	0.13 (0.71)	0.12 (0.70)	0.16 (0.71)
	2001				
Undisturbed	Cajones	0.59 (0.31)	0.89 (0.02)	0.97 (0.01)	0.89(0.89)
Populations	Limbo	0.97 (0.00)	0.95 (0.01)	0.96 (0.00)	0.97 (0.01)
	Chamela	0.89 (0.02)	0.89 (0.02)	0.89 (0.01)	0.88 (0.03)
	2002				
	Cajones	0.27 (0.62)	0.48 (0.45)	0.66 (0.16)	0.029 (0.09)
	Limbo	0.61 (0.17)	0.41 (0.59)	0.59 (0.23)	0.08 (0.08)
	Chamela	0.50 (0.33)	0.32 (0.66)	0.46 (0.28)	0.07 (0.76)
	2003				
	Cajones	0.20 (0.77)	0.07 (0.42)	0.068 (0.44)	0.07 (0.73)
	Limbo	0.10 (0.10)	0.16 (1.00)	0.17 (1.00)	0.21 (1.00)
	Chamela	0.081 (0.63)	0.01 (0.42)	0.01 (0.44)	0.01 (0.09)

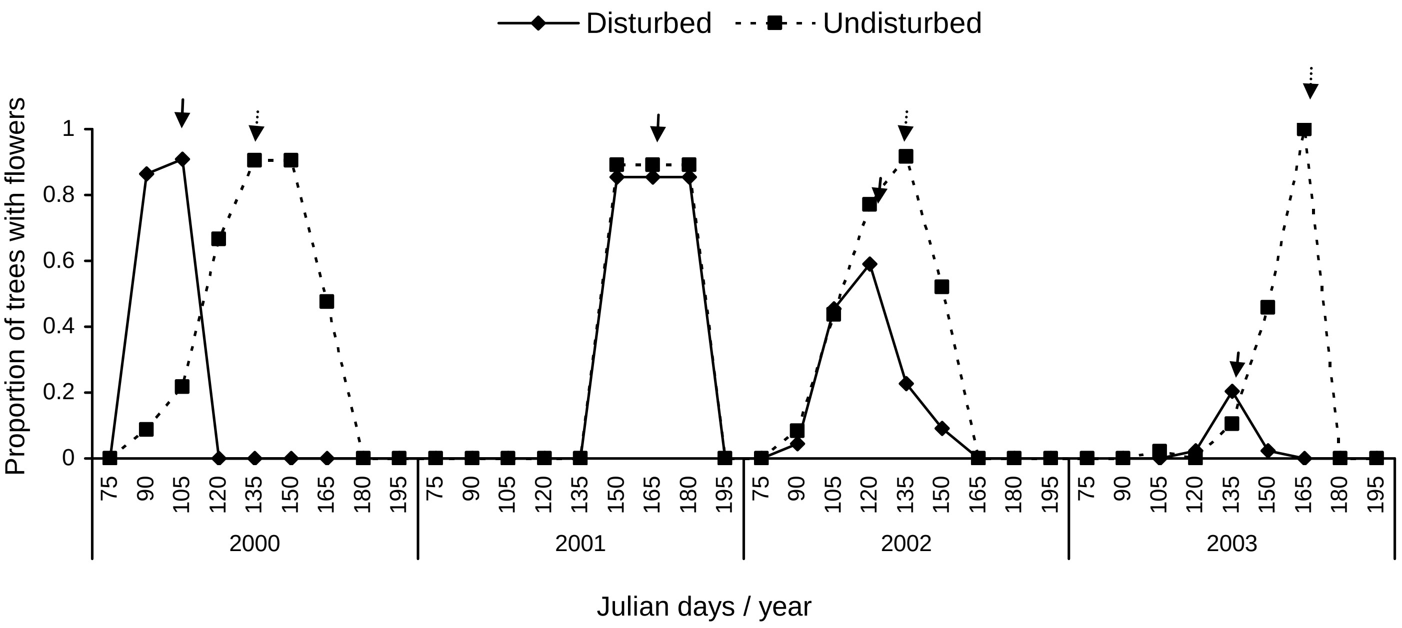
Figure Legends

Figure 1. Phenological patterns of the proportion of *C. aesculifolia* trees that produced flowers for the 4 years in disturbed and undisturbed habitats (in Julian days). Arrows indicate peak flowering for each habitat condition and year.

Figure 2. Proportion of *C. aesculifolia* trees that produced a) flowers and b) fruits during 4 four years in disturbed and undisturbed habitats. Bars represent confidence limits to 95%.

Figure. 3. Reproductive success of *C. aesculifolia* trees. (a) Least-square means (LSM) for total number of flowers produced by tree, (b) LSM for total fruit production by tree, and (c) LSM for fruit set by tree for 3 years in disturbed and undisturbed habitats. Bars represent confidence limits to 95%.

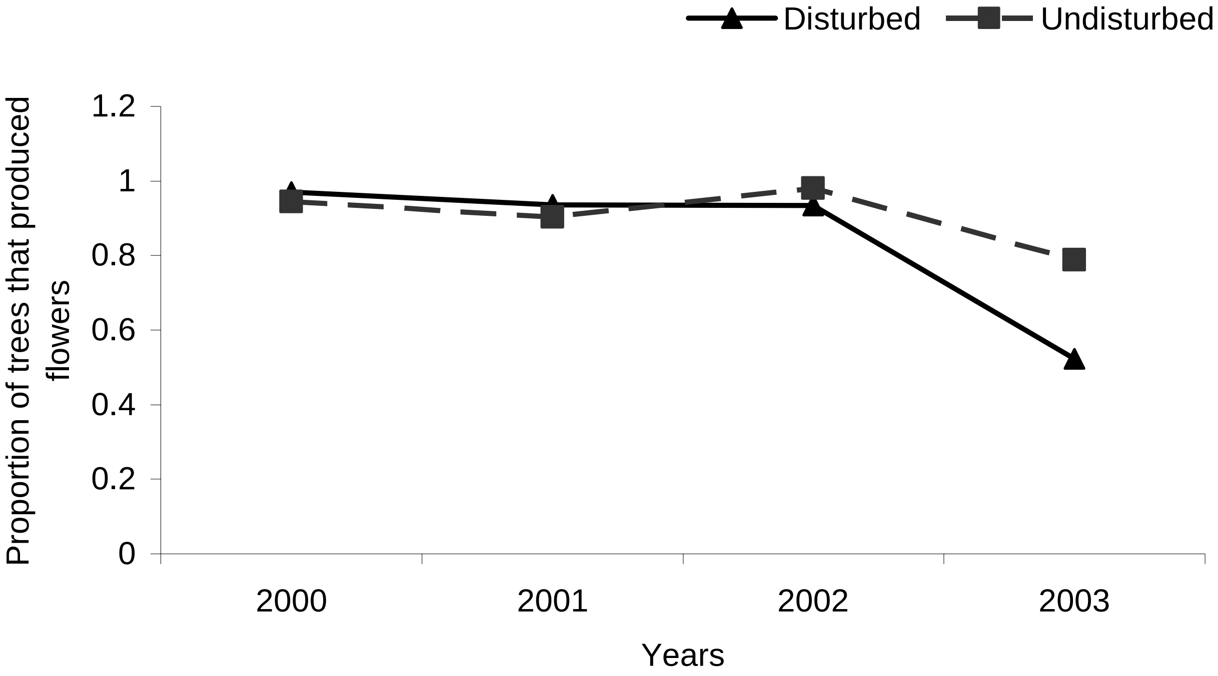
Fig. 1



Disturbed
Undisturbed
Proportion of trees with flowers
0
0.2
0.4
0.6
0.8
1
75
90
105
120
135
150
165
180
195
2000
2001
2002
2003
Julian days / year

Fig. 2

a)


Disturbed
Undisturbed
Proportion of trees that produced flowers
1.2
1
0.8
0.6
0.4
0.2
0
2000
2001
2002
2003
Years

b)

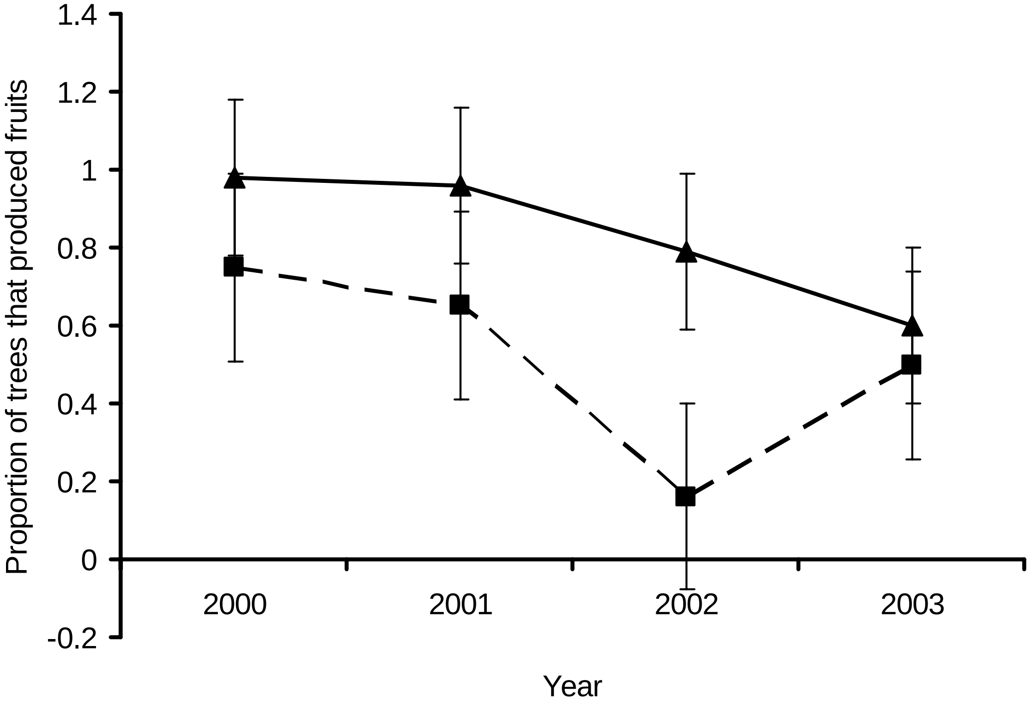
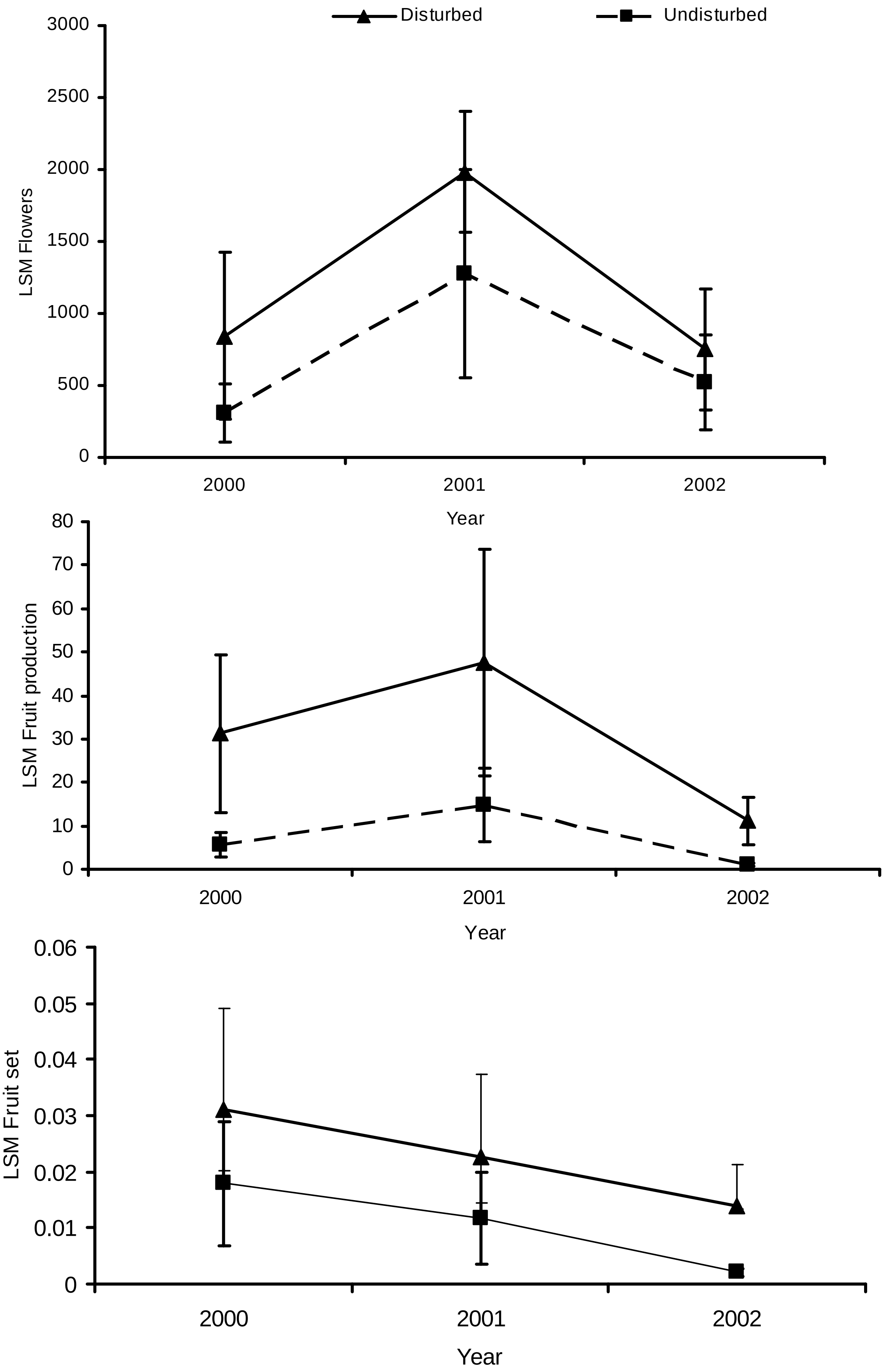

Proportion of trees that produced fruits
1.4
1.2
1
0.8
0.6
0.4
0.2
0
-0.2
2000
2001
2002
2003
Year

Fig. 3


Disturbed
Undisturbed
a)
LSM Flowers
3000
2500
2000
1500
1000
500
0
2000
2001
2002
Year
b)
LSM Fruit production
80
70
60
50
40
30
20
10
0
2000
2001
2002
Year
c)
LSM Fruit set
0.06
0.05
0.04
0.03
0.02
0.01
0
2000
2001
2002
Year

CAPÍTULO II

Running head**.-Forest fragmentation and genetic structure**

Long term effect of habitat fragmentation on the genetic structure of *Ceiba aesculifolia*

YVONNE HERRERÍAS-DIEGO[1], MAURICIO QUESADA[1], JORGE A. LOBO[2],
KATHRYN E. STONER[1] AND GUMERSINDO SÁNCHEZ-MONTOYA

[1]Centro de Investigación en Ecosistema, Universidad Nacional Autónoma de México, Campus Morelia, and [2]Universidad de Costa Rica, Escuela de Biología, San Pedro, Costa Rica; Apartado Postal 27-3 (Xangari), Morelia, Michoacán, México 58089

Correspondence: Mauricio Quesada (e-mail: mquesada@oikos.unam.mx)

Key words: Bombacaceae, forest fragmentation, genetic structure, outbreeding rate,

Abstract

The reduction of the natural population causes isolation of remnant populations, this isolation have negative consequences to the genetic structure of plant species. In a four year study, we determined the effect of habitat fragmentation on the genetic structure and paternity correlation of the tropical Bombacaceae tree *Ceiba aesculifolia* in a Mexican tropical dry forest. We conducted our study in the dry forest of Mexico. We compared trees in populations in two habitat conditions based on density and environmental conditions: (1) disturbed tree populations in disturbed areas consisted of 1 to 2 reproductive individuals per hectare and were surrounded by agricultural fields or pastures and (2) undisturbed tree populations consisted of groups of 5 or more reproductive individuals per hectare surrounded by undisturbed mature forest. We estimate the following variables within these populations over 4 years: outcrossing rate, paternity correlation, mean relatedness, genetic structure (Φ_{FT}) and paternity. In a four year study, the outcrossing rate was not affected by the forest fragmentation. All trees of *C. aesculifolia* were 100% outcrossing and each fruit have one pollen donor and all the seeds in a fruit were full sibs. Contrary to expected, the populations in both habitat conditions presented a high genetic structure. But, the genetic structure was greater in disturbed populations than undisturbed populations. Undisturbed populations trees had more effective pollen donors than the disturbed populations. The distance between donors was shorter in disturbed habitat. Paternity analysis showed that, between 50-90% of the paternities assigned in undisturbed forest was sired from fathers within the undisturbed habitat condition. In disturbed habitat conditions only between 20-50% of the paternities assigned were sired from within the population, the pattern was maintained for both habitat conditions over years. Forest fragmentation can increase the levels of gene flow between the fragments and maintain genetic diversity inside the populations. From a conservation perspective, this study provides important elements. Because most of the total genetic variation detected in *C. aesculifolia* resides within populations.

Introduction

Tropical dry forests are one of the most endangered ecosystems on the planet largely due to increasing deforestation caused by the cattle industry (Trejo and Dirzo, 2000). This reduction and fragmentation of forests are the main causes reasons for the extinction of natural populations in the tropics (Janzen 1988; Heywood et al. 1994; Trejo and Dirzo 2000; Quesada and Stoner 2004).

Several studies have shown that tropical trees are particularly vulnerable to the effects of habitat disturbance because they occur at low density, have complex self-incompatible mechanisms, high outcrossing rates (Hamrick and Murawski 1991; Murawski et al. 1994; Hall et al. 1996; Cascante et al. 2002; Fuchs et al. 2003), and specific specialized interactions with pollinators and seed dispersers (Didham et al, 1996; Dick et al, 2003; Ward et al, 2005). In the short term, habitat reduction and disturbance cause the isolation of remnant natural populations, resulting in potential negative consequences on the genetic structure and gene flow of plant species (Templeton et al. 1990; Young et al. 1993; McCauley 1995; Nason et al. 1997; Sork et al. 1999; Lowe et al. 2005). Additionally, disturbed habitat reduces the density of reproductive individuals thereby increasing the negative effects on offspring by producing more self crosses, especially in the case of obligate outcrossing plants (Charlesworth and Charlesworth 1987; Ellstrand 1992; Ellstrand and Ellam 1993). In the long-term, disturbed habitat can cause the loss of genetic variability of remnant tree populations from factors related to inbreeding depression, genetic drift, and/or changes in the population responses to selection pressures (Barret and Kohn 1991; Menges 1991; Ellstrand and Ellam 1993; Young et al. 1996, Lowe et al. 2005).

It also has been shown that forest fragmentation can increase both the levels of gene flow between fragments, and the genetic diversity within and between populations (Hamrick et al. 1992; Young et al, 1996, White and Boshier 2000; Dick 2001; White et al. 2002; Dick et al. 2003). In such cases, an increase in gene flow maintains the connectivity between fragmented populations, thus reducing their genetic differentiation (Foré et al. 1992). High levels of gene flow may help reduce the loss of genetic diversity in the long-term (Lowe et al. 2005). In this context, the maintenance of forest fragments and isolated trees may be important in acting as stepping stones for gene flow between fragmented populations.

Due to the increased destruction of tropical forests in recent years, it is imperative to study the consequences of forest fragmentation and habitat disturbance for the preservation of tropical tree species. Few studies have evaluated the effects of spatial and temporal isolation due to disturbed habitat on paternity correlation and mating patterns (e.g. Cascante et al. 2002; Fuchs et al. 2003; Quesada et al. 2003, 2004) and these studies only have analyzed a single reproductive event in long-living plants. In this paper, we evaluate the effects of disturbed habitat on the genetic variability of the progeny of a tropical tree, *Ceiba aesculifolia,* over a 4 year period. Specifically, we compare the following variables between undisturbed and disturbed populations: 1) outcrossing rate; 2) paternity correlation; 3) mean relatedness of seeds within and between fruits; 4) genetic pollen structure (Φ_{FT}); and 5) paternity analysis

Materials and Methods

Study species

Ceiba aesculifolia (Bombacaceae) is a Neotropical tree species distributed from Mexico to northern Costa Rica (Cascante-Marin 1997). Adult trees grow up to 20 m tall and have diameter at breast height (dbh) of 20 to 50 cm. *Ceiba aesculifolia* has large (10 - 16 cm) hermaphroditic flowers with five brown pubescent petals. Styles are on average 15 cm long and surpass the stamens by two centimeters. In the tropical dry forest of Mexico and Costa Rica, *Ceiba aesculifolia* flowers from June to July and all the fruits mature during the following dry season (Lobo et al. 2003; Quesada et al. 2004). *Ceiba aesculifolia* has a predominantly outcrossing mating system and it is effectively pollinated by two bat species, *Glossophaga soricina* and *Leptonycteris curasoae* (Quesada et al. 2004).

Selection of trees

To examine the effects of forest fragmentation on the outbreeding rate, paternity correlation and relatedness of seeds in *C. aesculifolia*, we compared trees in disturbed and undisturbed habitat conditions. All trees selected in each population were reproductive adults. A tree was considered in disturbed habitat if four or fewer reproductive trees per hectare were found surrounded by agricultural fields or pastures. Trees in disturbed habitat were systematically selected in sites along the Federal Road no. 200 (Barra de Navidad to Puerto Vallarta), near the Chamela-Cuixmala Biosphere Reserve. Trees located in disturbed habitat were grouped in four populations to control for the variation within sites (Arroyo Seco, Tecuán, Programa and Boca de Iguanas). Undisturbed populations consisted of groups of six or more reproductive individuals per hectare surrounded by mature forest and were located within the Chamela-Cuixmala Biosphere Reserve. To include the largest possible area within the reserve, we selected three populations from three different watersheds within the reserve that were separated from each other by more than 8 km (Chamela, Cuixmala and Arroyo Limbo). The number of individuals of *C. aesculifolia* sampled varied depending on the year (Table 1).

Genetic Data

To determine the effects of forest fragmentation on the genetic parameters of the progeny, we conducted an allozyme analysis with starch gel electrophoresis. We collected five to ten fruits from each of the undisturbed and disturbed tree populations (Table 1) and randomly selected five seeds from each fruit. Enzyme extraction, gel buffers, and staining protocols followed Alfenas *et al* (1989) and Soltis and Soltis (1991). We analyzed five polymorphic enzyme systems: shikimate dehydrogenase (SKDH, 1.1.1.25), phosphoglucoisomerase (PGI, 5.3.1.9), aspartate aminotransferase (AAT, 2.6.1.1.), esterase (EST, 3.1.1.1.) and isositrate dehydrogenase (IDH: 1.1.1.41). The AAT enzyme system showed two polymorphic loci; therefore, we used six polymorphic loci to determine the outcrossing rate and genetic relatedness within *C. aesculifolia* progenies.

We estimated multilocus outcrossing rate (tm) and paternity correlation (rp) for the progeny of trees from populations in undisturbed vs. disturbed populations. These genetic parameters were calculated using the models proposed by Ritland (1989) and Lynch and Ritland (1999) and with the MLTR computer program (Ritland 1996). The standard error of the estimates was calculated by bootstrapping with 1000 repetitions (Ritland 1996). We used a nested ANOVA model (SAS, 1995) to compare genetic parameters among the populations of trees in undisturbed and disturbed populations for each year. The model used habitat condition, population nested within habitat condition, year, and the interaction between year and habitat condition as independent variables. The response variables analyzed were multilocus outcrossing rate (tm) and paternity correlation (rp). These variables followed a normal distribution. We used the same procedure to compare the paternity correlation of the progeny from trees in undisturbed and disturbed populations for each of the four years.

We calculated two coefficients of mean progeny relatedness for each fruit: (1) the mean relatedness of seed pairs within fruits and (2) the mean relatedness of seed pairs between fruits, which consisted of seeds from one fruit and seeds from different fruits within the same tree. Estimates of relatedness were calculated with the computer program RELATEDNESS 5.0 (Goodnight and Queller 1990; Queller and Goodnight 1989). Standard errors of these estimates were calculated using Jacknife statistical procedure with 1000 repetitions.

The distribution and abundance of local pollen donors can influence the genetic structure of pollen pools. The genetic structure characterization of the pollen pool of the populations was conducted with the software “2Gener” (Dyer 2005). This analysis produces a statistic, Φ_{FT} that is identical to the Φ_{ST} statistic in AMOVA (Excoffier et al., 1992) except that the focus of the analysis is on populations of pollen donors instead of adults. For this reason, the subscripts have been changed from Φ_{ST} to Φ_{FT} to emphasize the focus on families rather than subpopulations. (Smouse et al. 2001; Sork et al. 2002). Based on the pollen structure (Φ_{FT}) we calculated the following parameters: 1) the effective number of pollen donors, $N_{ep} = (2\Phi_{FT})^{-1}$ and 2) the average distance between mother trees following the model suggested by Austerlitz and Smouse (2001). We calculated the Φ_{FT}, number of pollen donors and the distance between mother trees for each population in both habitat conditions and for each year. The parameter Φ_{FT} can take values between 0 and 1. High values of Φ_{FT} indicate the population is highly selfing, contains few pollen donors, and/or little pollen movement. Low values of Φ_{FT} indicate the population is highly outcrossing, contains many pollen donors, and/or great pollen movement.

The most direct approach for examining pollen flow is provided by paternity analysis. We used a simulation of paternity inference to determine the most likely pollen donors involved in siring seeds in each population for each habitat condition. We used the procedure CERVUS 2.0 (Marshall et al. 1998) for paternity assignment for maximum likelihood and calculated the proportion of seeds sired in the same and in different habitat conditions in each population each year.

Results

Allele frequencies of trees' progeny from the populations of undisturbed and disturbed habitats were calculated from three alleles of each of four loci Aat 1, Icd, Fe, and Skdh, two alleles from locus Aat2, and six alleles for locus Pgi. We found similar high levels of expected heterozygosity for the progeny of both undisturbed (He = 0.436, SD=0.26) and disturbed populations (He = 0.377, SD=0.21) throughout the four years.

The multilocus outcrossing rate (t_m) obtained for the trees in the different populations for both habitat conditions over the four years was high (Figure 1) indicating that *Ceiba aesculifolia* presents a predominantly outcrossing breeding system. There were no significant differences in t_m values of trees in different habitat conditions (F=0.26, df =1, p=0.607). Similarly, population nested within habitat condition, year, and the interaction between year by habitat condition did not show significant differences in t_m values (F=1.82, df=4, p=0.1; F=1.57, df=3, p=0.1 and F=1.7, df=4, p=0.1, respectively, Figure 1).

Paternity correlation estimates (r_p) between trees varied from 0.132 to 0.224 indicating that more than one outcross pollen donor sired the progeny of trees in both habitat conditions. Progeny relatedness between fruits indicated few sires in both habitat condition (Table 2). Similarly, the progeny relatedness within fruits indicated few pollen donors per fruit (Table 2). This trend held throughout the years. This trend was maintained in all the populations in both habitat conditions for the four years. There were no significant differences in r_p values between the two habitat conditions, population nested within habitat condition, year, and interaction between year by habitat condition (F=1.37, df=1, p=0.607; F=1.2, df=4, p=0.1; F=1.67, df=3, p=0.1 and F=3.55, df=4, p=0.2, respectively, Figure 1b). Progeny relatedness between fruits indicated few sires in both habitat conditions (Table 2, Figure 2a). Similarly, the progeny relatedness within fruits indicated one pollen donors per fruit (Table 2, Figure 2b).

High genetic structure (Φ_{FT}) was estimated throughout the four years of the study in populations from both habitat conditions indicating local pollen movement between and within all the populations (Table 3). Nevertheless, populations in disturbed habitats presented greater Φ_{FT} than undisturbed populations (Table 3), and this difference was maintained throughout the four years. Based on the pollen structure (Φ_{FT}) we calculated the effective number of pollen donors, and the average distance between mother trees. The number of sires per tree was lower in populations in undisturbed habitats than populations in disturbed habitats (Table 3). Additionally, the mean distance of pollen movement was greater in populations in disturbed habitats (Table 3).

Paternity analysis showed that, depending on the population, between 50-90% of the paternities assigned in undisturbed forest was sired from fathers within the undisturbed habitat condition. In contrast, in disturbed habitat conditions only between 20-50% of the paternities assigned were sired from within the population (Figure 3a, b). This same pattern was observed for both habitat conditions over years.

Discussion

Deforestation and habitat destruction can alter tree population density and phenology (Herrerías-Diego et al. in press), as well as the abundance, diversity and behavior of pollinator communities (Dick 2001; Quesada et al. 2003; Lowe et al. 2005; Ward et al. 2005). For example, a significant increase in self-fertilization rates has been reported for the emergent legume *Dinizia excelsa* in disturbed forests in Brazil (Dick et al. 2003). In the particular case of species of the Bombacaceae family, outcrossing rates can be influenced by different habitat conditions (Gribel et al. 1999; Murawski and Hamrick 1992a, b; Fuchs et al. 2003; Quesada et al. 2004), as well as pollinator activity (Lobo et al.2005).

The current study shows that outcrossing rates in *C. aesculifolia* were maintained in disturbed and undisturbed habitat conditions across 4 years suggesting that this is a strictly self-incompatible species. Furthermore, the consistencies of outcrossing over time suggest that the pollen vectors of this species are particularly efficient. The two main pollinators of *C. aesculifolia* at our study site are the nectarivorous bats *Glossophaga soricina* and *Leptonycteris curasoae* (Quesada et al*.* 2004) and *C. aesculifolia* comprises the principal part of the diet of *L. curasoae* in April and May (Stoner et al 2003). A previous study reports that these two species of pollinators visit more flowers of trees in disturbed sites than in undisturbed forest (Quesada et al. 2004). This observation was explained because *C. aesculifolia* trees in disturbed habitats produce more flowers per night than trees in undisturbed habitat and bloom from May to June when few other chiropterophilic trees are available, thus making these trees valuable food sources.

Bats are known to transfer pollen between trees over several kilometers and between forest patches in fragmented landscapes (Law and Lean 1999). For example, Nassar et al. (2003) found low genetic differentiation in three bat-pollinated columnar cacti species, suggesting substantial gene flow among populations. Our results support the hypothesis that bat-mediated gene dispersal via pollen movement confers high levels of genetic exchange among populations, a process that enhances high levels of genetic diversity within populations. Several elements of pollinator foraging behavior are relevant to plant reproduction and spatial isolation including ability to cross open areas, home range size, and distances traveled to arrive at foraging sites (Ghazoul 2005). In the case of *L. curasoae*, the main pollinator of *C. aesculifolia* at our study site, previous studies have documented that this speices can cross open areas, have large home ranges, and may travel up to 50 km to arrive at a foraging area (Horner et al. 1998, Quesada et al. 2004).

Our study found that populations of *C. aesculifolia* presented a high genetic structure (Φ_{FT}) in both habitat conditions. Additionally, trees in undisturbed populations presented more effective pollen donors, demonstrated by the greater number of sires per tree, than disturbed tree populations and distance between donors was shorter in undisturbed than disturbed populations. Theoretical and experimental studies predict that at low plant density pollinators will visit a higher proportion of flowers on each plant before moving to neighboring plants (Kunin 1993; Bosch and Blas1994; Kunin 1997; Ghazoul et al. 1998; Bosch and Waser, 1999; Schulke and Waser, 2001). Furthermore, the paternities calculated for the offspring in disturbed tree populations indicate that 70% of the sires were from other populations (Figure 3b). In undisturbed tree populations, only 10% to 20% of the potential sires belonged to other populations (Figure 3a). The greater number of sires per tree, greater distance between donors, and difference in paternity between these two habitat conditions may be a result of the visitation rates and foraging patterns of the two bat species. Quesada et al. (2004) reported that although both pollinators had the same rate of visitation frequency to flowers in undisturbed forest, *L. curasoae* visited significantly more flowers of disturbed tree populations. The small nectarivore, *Glossophaga soricina (*weight: 8-11 g, forearm 36-38 mm, Nowak 1994) has a relatively small foraging range and is territorial (Heithaus et al. 1975, Lemke 1984, 1985), this could result in restricting the number of pollen donors transferred between and within habitats. In contrast, the large nectarivore *L. curasaoe* (weight: 20-30 g, forearm 46-57 mm, Nowak 1994) has a large foraging range and is a “trap-liner” that goes from plant to plant (Howell 1979, Horner et al. 1998), that could result in moving pollen large distances between and within habitats. It appears as if the intrinsic foraging characteristics of each pollinator affect pollen movement and ultimately the genetic structure of the plant populations they visit.

Our results showed that the outcrossing rate of trees in both habitat conditions was not affected by habitat disturbance and that all the populations presented high genetic structure. Trees in undisturbed habitat presented more effective pollen donors than disturbed tree populations and distance between donors was shorter in disturbed habitat. The paternity calculated for the offspring in disturbed populations indicate more sires were contributing to the gene pool than populations in undisturbed habitat. This is the first study to evaluate the long-term consequences of forest fragmentation on the outcrossing rate, paternity correlation, mean relatedness, genetic structure, and paternity of tropical trees. Forest fragmentation did not negatively affect the genetic parameter estimates of *C. aesculifolia*. It appears that at least some of the bat pollinators of this species are traveling long distances and moving sufficient pollen to remote trees to maintain reproductive connectivity. Other studies have proposed the importance of forest fragments, as well disturbed trees in pastures, as stepping stones for gene flow among patches which contribute to the genetic diversity of undisturbed forest (Cascante et al. 2002; Chase et al. 1996). Our study identifies the importance of trees found in disturbed habitat as possible stepping-stones for pollen flow between trees connecting forest fragments with undisturbed populations. From a conservation perspective, this study provides important elements. Because most of the total genetic variation detected in *C.*

aesculifolia resides within populations, the risk of negatively affecting the species' gene pool by localized population extinctions is relatively high and this factor should be taken into consideration in designing conservation areas for the tropical dry forest.

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Table 1. Number of individuals and offspring analyzed for each population in disturbed and undisturbed habitat conditions.

Habitat condition	Population	No. of trees				Number of offspring			
		2000	2001	2002	2003	2000	2001	2002	2003
Undisturbed	Chamela	15	10	4	5	325	270	85	100
	Cuixmala	20	10	5	6	475	225	100	100
	Limbo	5	6	ND	ND	135	180	ND	ND
Disturbed	Arroyo Seco	11	8	4	5	265	180	75	100
	Tecuan	5	4	ND	ND	105	100	ND	ND
	Programa	6	3	4	4	160	75	100	105
	Boca de Iguanas	12	9	4	4	230	230	100	60
	Total	74	50	21	24	1695	1098	460	465

ND: no data

Table 2. Estimate value of paternity correlation (r_p), and relatedness (R) between and within fruit for each year in both habitat conditions. The number in parenthesis indicates the standard error.

Habitat condition	year	r_p	R (between fruit)	R (within fruit)
Disturbed	2000	0.220 (0.081)	0.310 (0.028)	0.500 (0.006)
	2001	0.181 (0.084)	0.303 (0.005)	0.493 (0.002)
	2002	0.137 (0.028)	0.235 (0.016)	0.465 (0.001)
	2003	0.128 (0.0549	0.354 (0.012)	0.513 (0.01)
Undisturbed	2000	0.224 (0.112)	0.198 (0.029)	0.512 (0.006)
	2001	0.183 (0.047)	0.223 (0.006)	0.45 (0.002)
	2002	0.185 (0.037)	0.200 (0.016)	0.536 (0.001
	2003	0.132(0.034)	0.307 (0.012)	0.473 (0.01)

Table 3. Estimated values of genetic structure (Φ_{FT}) number of sires per tree, and mean pollen distance.

Year	Population	Habitat condition	Φ_{FT}	p	Mean pollen distance (km)	Efective number of sires per tree
2000	Chamela	Undisturbed	0.28855	0.0001	2.89	3.47
	Cajones		0.20765	0.0001	3.40	4.82
	Limbo		0.18297	0.0001	3.62	5.47
	Arroyo Seco	Disturbed	0.37992	0.0001	4.06	2.63
	Tecuán		0.19679	0.0001	5.64	5.08
	Programa		0.44988	0.0001	3.73	2.22
	Boca de iguanas		0.3761	0.0001	4.08	2.66
2001	Chamela	Undisturbed	0.2121	0.0001	3.37	4.71
	Cajones		0.17178	0.0001	3.74	5.82
	Limbo		0.18062	0.0001	3.65	5.54
	Arroyo Seco	Disturbed	0.28769	0.0001	4.66	3.48
	Tecuán		0.34989	0.0001	4.23	2.86
	Programa		0.31476	0.0001	4.46	3.18
	Boca de iguanas		0.29576	0.0001	4.60	3.38
2002	Chamela	Undisturbed	0.37236	0.0001	2.54	2.69
	Cajones		0.45929	0.0001	2.29	2.18
	Limbo		ND		ND	ND
	Arroyo Seco	Disturbed	0.18124	0.0001	5.87	5.52
	Tecuán		ND		ND	ND
	Programa		0.30685	0.0001	4.51	3.26
	Boca de iguanas		0.33956	0.0001	4.29	2.94
2003	Chamela	Undisturbed	0.42367	0.0001	2.38	2.36
	Cajones		0.19738	0.0001	3.49	5.07
	Limbo		ND		ND	ND
	Arroyo Seco	Disturbed	0.30037	0.0001	4.56	3.33
	Tecuán		ND		ND	ND
	Programa		0.2136	0.0001	5.41	4.68
	Boca de iguanas		0.41074	0.0001	3.90	2.43

Figure Legends

Figure 1. Multilocus outcrossing rate (t_m) for each population in both habitat conditions by year. Bars represent standard error.

Figure 2. (a) Coefficients of mean relatedness(R) between fruits and (b) within fruits for each population in both habitats by year. Bars represent standard error.

Figure 3. Percentage of offspring with sires from the same or different populations for each year for (a) undisturbed and (b) disturbed habitats.

Fig. 1

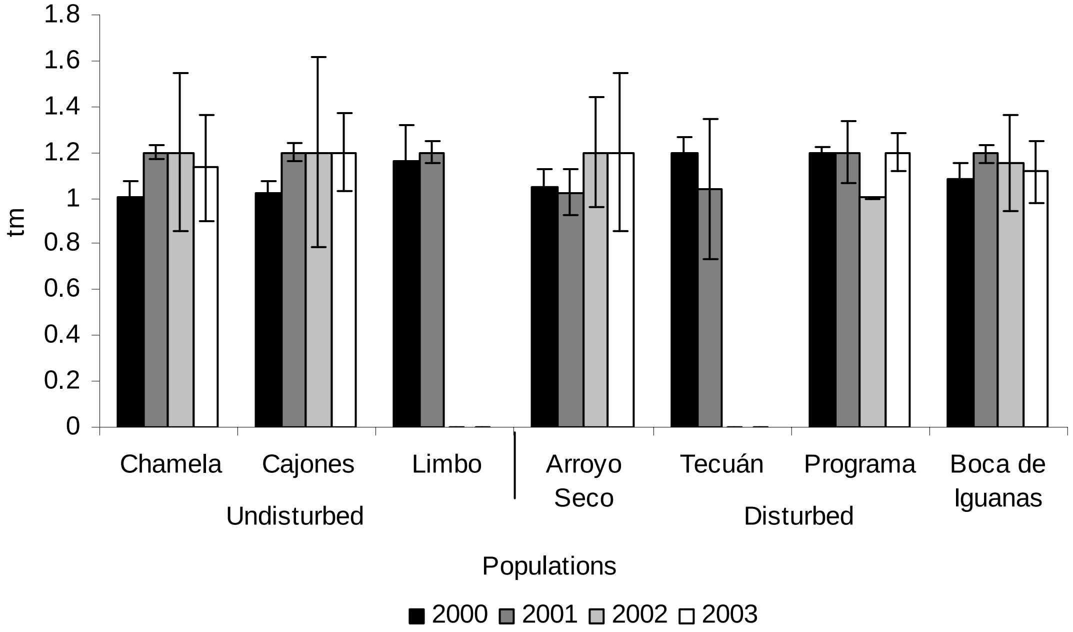
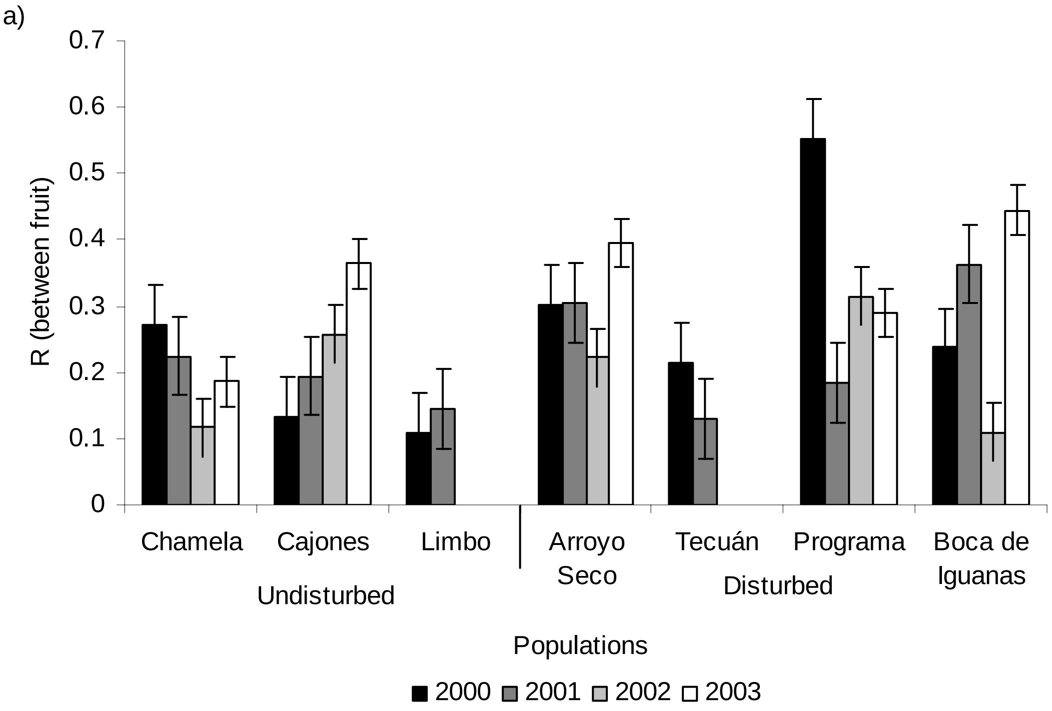

1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
tm
Chamela
Cajones
Limbo
Arroyo Seco
Tecuán
Programa
Boca de Iguanas
Undisturbed
Disturbed
Populations
■ 2000
■ 2001
■ 2002
□ 2003

Fig. 2


a)
R (between fruit)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Chamela
Cajones
Limbo
Arroyo Seco
Tecuán
Programa
Boca de Iguanas
Undisturbed
Disturbed
Populations
■ 2000 ■ 2001 ■ 2002 □ 2003

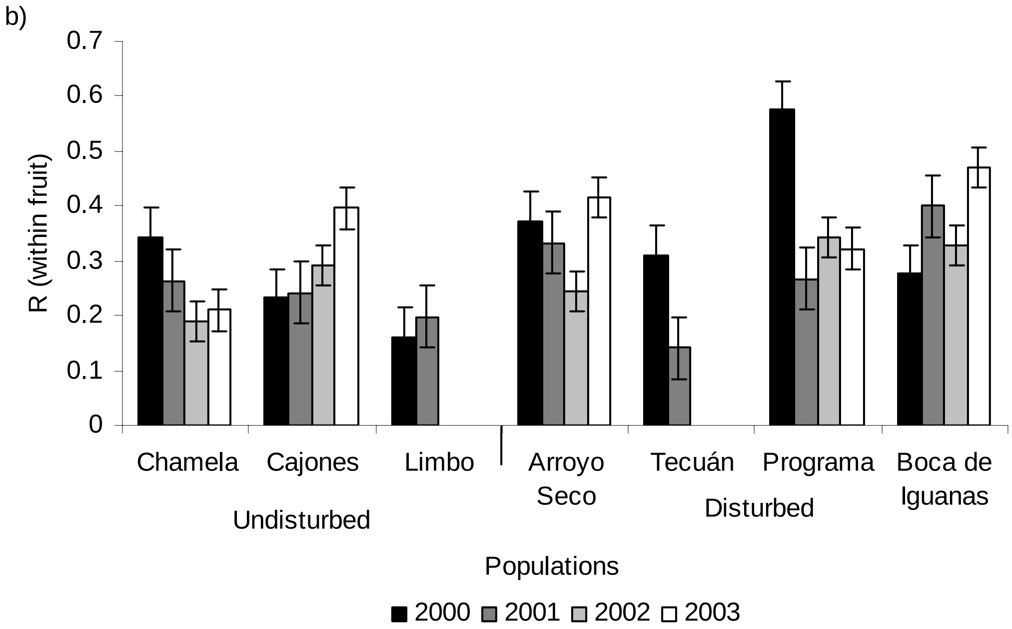
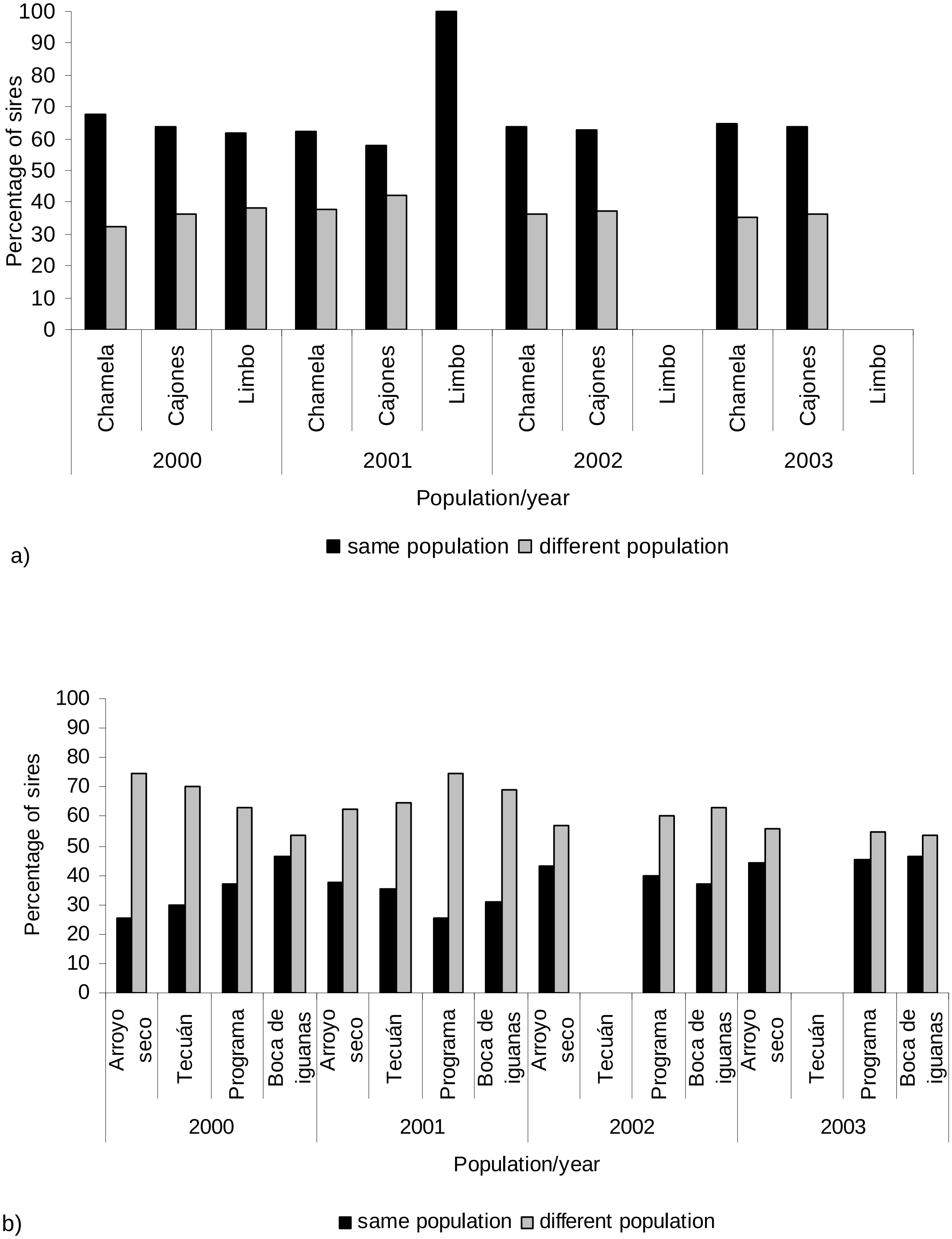

b)
R (within fruit)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Chamela
Cajones
Limbo
Arroyo Seco
Tecuán
Programa
Boca de Iguanas
Undisturbed
Disturbed
Populations
■ 2000 ■ 2001 ■ 2002 □ 2003

Fig. 3


a)
Percentage of sires
0
10
20
30
40
50
60
70
80
90
100
Chamela
Cajones
Limbo
Chamela
Cajones
Limbo
Chamela
Cajones
Limbo
Chamela
Cajones
Limbo
2000
2001
2002
2003
Population/year
■ same population
▨ different population
b)
Percentage of sires
0
10
20
30
40
50
60
70
80
90
100
Arroyo seco
Tecuán
Programa
Boca de iguanas
Arroyo seco
Tecuán
Programa
Boca de iguanas
Arroyo seco
Tecuán
Programa
Boca de iguanas
Arroyo seco
Tecuán
Programa
Boca de iguanas
2000
2001
2002
2003
Population/year
■ same population
▨ different population

CAPÍTULO III

Effect of forest fragmentation on fruit and seed predation of the tropical dry forest tree *Ceiba aesculifolia* [1]

YVONNE HERRERÍAS-DIEGO, MAURICIO QUESADA[2], KATHRYN E. STONER, YARED HERNADEZ-FLORES

Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México, Campus Morelia.

[2]Corresponding autor: e-mail: mquesada@oikos.unam.mx

[1] Received ____; revision accepted ___

Abstract

Fragmentation of tropical forests reduces the density of natural plant populations forming patches of the remaining populations. One of the biotic interactions that can be affected by forest fragmentation and is poorly studied is seed predation. We determine the effects of forest fragmentation on seed and fruit predation in *Ceiba aesculifolia* by comparing trees in undisturbed forest with trees in disturbed forest. We conducted our study in the dry forest of Mexico. We compared the following variables: a) frequency of fruit predation by the squirrel *Sciurus colliaei* in each habitat; b) frequency of the insect seed predator *Dysdercus* sp. (principal seed predator) in each habitat; and c) the effect of predation on germination frequency and timing; and d) the effect of different life stages of *Dysdercus* sp.(nymph, pre-adult and adult) on the viability of seeds. In undisturbed habitat 100% of the trees analyzed presented fruits with squirrel predation while only 34% of trees in disturbed habitats presented fruit predation. In undisturbed forest, 27% of the trees contained fruits with the seed predator *Dysdercus* sp,, while only 2% of the trees in disturbed forest presented *Dysdercus* sp. Damaged seeds weighed more than seeds that were not damaged. Predated seeds lost significantly more weight than seeds that were not predated. The frequency of seed germination was significantly affected by different life stages. Seed predation also had a significant effect on the time of germination. The regeneration of disturbed forest depends on the levels of seed and fruit predation among other factors.

Key words: plant-animal interaction, fruit predation, seed predation, forest fragmentation, tropical trees, dry forest.

Resumen

La fragmentación de los bosques tropicales reduce la densidad natural de las poblaciones de plantas formando parches de poblaciones remanentes. Una de las interacciones bióticas que puede ser afectada por la fragmentación del bosque y es pobremente estudiada es la depredación de semillas. Determinamos los efectos de la fragmentación del bosque en la depredación de frutos y semillas de *Ceiba aesculifolia* comparando árboles en bosque no perturbado con árboles en bosque perturbado. Realizamos el estudio en el bosque tropical seco de México. Comparamos las siguientes variables: a) frecuencia de depredación de frutos por la ardilla *Sciurus colliaei* en cada hábitat; b) frecuencia de depredación del insecto *Dysdercus* sp. (principal depredador de semillas) en cada hábitat; y c) el efecto de la depredación en la germinación y tiempo; y d) el efecto de los diferentes estadios de *Dysdercus* sp.(ninfa, pre-adulto y adulto) en la viabilidad de semillas. En hábitat no perturbado el 100% de los árboles analizados presentan frutos con depredación por ardillas y únicamente el 34% de árboles en hábitat perturbados presentan depredación de frutos. En el bosque no perturbado el 27% de los árboles presentaron depredadores de semillas *Dysdercus* sp,, y únicamente el 2% de los árboles enbosque perturbado presentan *Dysdercus* sp. Las semillas dañadas pesan menos que las semillas no dañadas. Las semillas dañadas pierden significativamente más peso que las semillas que no fueron depredadas. La frecuencia de germinación fue signifactivamente afectada por los diferentes estadios de vida. La depredación de semillas tiene un efecto significativo en el tiempo de germinación. La regeneración de los sitios perturbados depende de los niveles de depredación de frutos y semillas entre otros factores.

Forest fragmentation affects many species of flora and fauna not only by eliminating their habitat but also by disrupting biotic interactions (Didham *et al*. 1996, 1998, Benitez-Malvido and Lemus-Albor 2005). The effect of forest fragmentation on biotic interactions has been mainly studied in pollination systems (Aizen and Feinsinger 1994a, b, Cunninham 2000a, Dick *et al*. 2003, Quesada *et al*. 2003, 2004, Ghazoul 2004, 2005). Less well studied has been effect of forest fragmentation on other biotic systems such as plant herbivory (Benitez-Malvido and Lemus-Alvor 2005, Valladeres *et al*. 2006), plant-pathogen interactions (Gilber and Hubbell 1996, Benitez-Malvido *et. al*. 1999, Benitez-Malvido and Lemus-Alvor 2005), decomposition of dung or litter (Eggleton *et la*. 1996) mutualistic mycorrhizal associations (Matthies et al. 1995, Didham *et al*. 1996), seed dispersal (Hamilton 1999, Restrepo *et al*. 1999, Ghazoul 2005), and fruit and seed predation (Janzen 1978, Sork 1983, Adler 1994, Cascante *et al*. 2002).

Seed dispersal and predation interactions in the tropics are particularly likely to be affected by forest fragmentation because many plant species are subject to animal dispersal and /or predation, and habitat disturbance tends to eliminate these vectors (Janzen 1978, Cascante *et al*. 2002). In addition, density dependent factors related to the availability and fluctuation of food resources will maintain dispersers and predators in undisturbed habitats. Therefore, habitat fragmentation may change the population dynamics of predators and dispersers affecting the spatial heterogeneity and/or survivorship of plants in disturbed habitats (Didham *et al.* 1996, Crawley 2000). Few studies have evaluated the effects of forest fragmentation on fruit and seed predation. The trophic rank hypothesis suggests that increased susceptibility to habitat fragmentation should be found at higher trophic levels (Kruess & Tscharntke 1994, Holt *et al.* 1999). The empiric evidence shows a reduction of seed predation in forest fragments (Janzen 1978, Sork 1983, Burckey 1993, Wright and Douber 2001, Cascante *et al.* 2002).

In this study we determine the effects of forest fragmentation on seed and fruit predation of *Ceiba aesculifolia* by comparing trees in undisturbed forest with trees in disturbed forest. *Ceiba aesculifolia* (Bombacaceae) is a tropical tree that presents high levels of seed and fruit predation by squirrels, *Sciurus colliaei*, and hemipterans, *Dysdercus* sp. (Pyrrhocoridae). Squirrels predate on the fruits by opening the valves of the green fruits one or two months before maturation and then eat the immature seeds. *Dysdercus* sp. get enter newly open dry fruits by introducing their proboscis through the seminal covering and sucking the seminal content (Janzen, 1976). The adults and nymphs are seed predators of others plant species of the Malvals (Janzen 1972).

MATERIALS AND METHODS

STUDY SPECIES. - *Ceiba aesculifolia* (Bombacaceae) is a Neotropical species distributed from Mexico to northern Costa Rica (Cascante-Marin 1997). Adult trees grow up to 20m in height and have diameters of 20 to 50cm. *Ceiba aesculifolia* has large (10 to 16cm) flowers with five brown pubescent petals. Styles are on average 15 cm long and surpass the stamens by one to two centimeters. In the tropical dry forest of Mexico and Costa Rica, *C. aesculifolia* is the last species of the family to flower at the end of the dry season and all the fruit mature during the following dry season (Lobo *et al.* 2003, Quesada *et al.* 2004). *Ceiba aesculifolia* has a predominantly outcrossing mating system. In the tropical dry forest of Mexico, two bat pollen vectors have been documente for this species, *Glossophaga soricina* and *Leptonycteris curasoae* (Quesada *et al.* 2004).

STUDY AREA. - The study was conducted in the central Pacific coast of Mexico within and surrounding the Chamela-Cuixmala Biosphere Reserve (ca. 19^{o}30'N, 105^{o}03"W.). This reserve is located between Puerto Vallarta, Jalisco and Manzanillo, Colima. The predominant vegetation type is tropical dry forest, which is characterized by a rainy season from the middle of June through October, and an extended dry season from November through May. Two main habitats have been described in this area, the upland dry forest and "arroyo" forest which are found along the seasonally wet riverbeds (Lott 1993). Average annual rainfall is 750 mm and average temperature is 25^{o}C.

SELECTION OF TREES. - To examine the effects of forest fragmentation on fruit and seed predation of *C. aesculifolia*, we compared trees in disturbed areas with trees in undisturbed areas. All trees selected were reproductive adults. A tree was considered disturbed if it consisted of less than two reproductive trees per hectare and was surrounded by agricultural fields or pastures. Trees in disturbed areas were systematically selected in sites along the Federal Road No. 200 (Barra de Navidad to Puerto Vallarta), near the Chamela-Cuixmala Biosphere Reserve. Trees in undisturbed areas consisted of groups of five or more reproductive individuals per hectare that were surrounded by undisturbed mature forest; all trees in undisturbed habitats were located within the Chamela-Cuixmala Biosphere Reserve. Fifty trees of *C. aesculifolia* from disturbed habitats and 50 trees from undisturbed forest were studied.

FRUIT PREDATION.-We determined the frequency of fruit predation in both habitat conditions by conducting weekly censuses during one fruiting season. We systematically checked the 50 trees in each habitat condition to quantify the number of trees that contained fruits with predation marks of squirrels (*Sciurus colliaei*). Fruits that were predated by squirrels had characteristic incisive marks on the fruit husks which allowed them to be identified unequivocally. To evaluate the frequency of fruit predation between habitats we used a generalized linear model applying the GENMOD procedure (SAS, 2000). The model used habitat condition as the categorical independent variable and the proportion of trees whit predated fruits as the dependent variable. The analysis used a binomial distribution and a logit link function. To control for variation associated with tree size, we used diameter at breast height (dbh) as a covariate in the model and distance to the nearest neighbor was used as an additional covariate in the analysis.

SEED PREDATION. - We determined the effect of forest fragmentation on seed predation by using two techniques. First, we evaluated the frequency of *Dysdercus* sp. (principal seed predator) in the fruits of each tree by conducting weekly censuses during the fruiting period. During each census, we quantified the presence and absence of nymphs and/or adults by checking all fruits that were detached below each tree. To evaluate seed predation between habitats we used a generalized linear model applying the GENMOD procedure (SAS, 2000). The model used habitat condition as the categorical independent variable and the proportion of trees with fruit predation as the dependent variable. The analysis used a binomial distribution and a logit link function. To control for variation associated with tree size, we used diameter at breast height (dbh) as a covariate in the model, and distance to nearest neighbor was used as an additional covariate.

The second technique used to evaluate the effect of forest fragmentation on seed predation consisted of an experiment. We conducted a laboratory experiment to determine the effect of *Dysdercus* sp. on seed predation and seed viability of *C. aesculifolia*. Individuals of *Dysdercus* sp were placed in glass terrariums with seeds of *C. aesculifolia* to determine seed predation and germination. We randomly selected seeds from 40 trees, three fruits per tree and one seed per fruit for each predation treatment (120 seeds). Each seed was individually numbered with an indelible ink pen.and weighed. Individuals of *Dysdercus* sp. were grouped into three predation treatments based on age to control for any effects associated with the developmental stage of the predator. These three age categories were: young nymph (body completely red), pre-adult (body red with black spots on back without wings); and adults (red body with black back and wings).

We used three terrariums (50 x 30 cm) for each predation treatment and a control. In each of these 9 terrariums we randomly placed 120 seeds and 120 individuals of *Dysdercus* sp. One hundred and twenty seeds were placed in each of 3 terraniums without *Dysdercus* sp. as the control treatments. Because each developmental stage of *Dysdercus* lasts for one week (Herrerías Diego pers. obs.), seeds were exposed to predators in each treatment for one week in each terrarium. During this week, 24 hrs a day, we conducted systematic observations in each terrarium every two hours for 15 minutes. During each observation, for each seed we registered whether it was fed upon by *Dysdercus* sp. (ie. proboscis was inserted into seminal covering).

After the one-week predation treatment, all seeds were germinated (control and experimental) in germination beds with humid sand. Seeds were checked every day and considered germinated once the hypocothyl emerged. Seeds that did not germinate within 15 days were opened and the status of their embryos was observed under the microscope. Seeds predated by *Dysdercus* sp*.* were either hollow inside or their embryos were destroyed by the effect of the digestive enzymes that *Dysdercus* sp. injects while feeding.

The effects of seed selection by predators by *Dysdercus* sp. was evaluated using a generalized linear model applying the GENMOD procedure (SAS, 2000). The model used tree identity, predation treatment (i.e. age class of seed predator) and the interaction between tree identity and predation treatment as categorical independent variables. Seed weight was used as the dependent variable. We also conducted another analysis to determine the effect predation treatment has on seed weight after predation. We first estimated the difference in seed weight before and after seeds were exposed to predators. The model of the analysis considered tree identity and predation treatment and the interaction between tree identity and predation treatment as the categorical independent variables, and the difference in weight as the response variable.

The frequency of germination after predation was evaluated using a generalized linear model applying the GENMOD procedure (SAS, 2000). The model used predated seeds (yes or no), predation treatment, and the interaction between predation treatment and predated seeds as the categorical independent variables. The proportion of germinated seeds was the dependent variable. The analysis used a binomial distribution and a logit link function. To control for variation associated with seed size, we used seed weight as a covariate in the model.

Seed germination success after predation was evaluated using a generalized linear model applying the GENMOD procedure (SAS, 2000). The model used predated seeds (yes or no), predation treatment and the interaction between predation treatment and seed predation as categorical independent variables. Days to seed germination was the dependent variable. The analysis used a binomial distribution and a logit link function. To control for variation associated with seed size, we used seed weight as a covariate in the model.

RESULTS

The proportion of individuals of *C. aesculifolia* with fruit predation by *Sciurus colliaei* was significantly greater in trees found in undisturbed habitat ($\chi^2 = 16.73$, df = 1, $p < 0.0010$, Figure 1a). No significant effects were observed for dbh or distance to nearest neighbor ($\chi^2 = 2.15$, df = 1, $p = 0.142$, $\chi^2 = 0.20$, DF = 1, $p = 0.653$, respectively). In undisturbed habitats 100% of trees presented fruit predation by *S. colliaei* while only 34% had fruits predated in disturbed habitats. The frequency of the insect predator *Dysdercus* sp. also was dependent on habitat condition (χ^2 = 14.87, d f= 1, *p* = 0.0001, Figure 1b). Simalarly, in undisturbed forest, 27% of the trees contained fruits with depredation by *Dysdercus* sp. while only 2% of the trees in disturbed forest had fruits with insect damage. No significant effects were observed for dbh or distance to nearest neighbor (χ^2 = 0.34, df = 1, *p* = 0.561, χ^2 = 0.02, df = 1, *p* = 0.877, respectively).

The analysis of the relationship between seed weight and the probability of being predated by *Dysdercus* sp. showed a significant difference in weight between attacked and intact seeds (F = 0.13, df =1, *p* = 0.71, Fig. 2a). Attacked seeds had greater weight than intact seeds. The probability of being predated also depended upon tree identity and the interaction between predation treatment and seed predation (F = 99.51, df = 39, $p < 0.0001$, F = 9.38, df = 2, $p<0.0001$, respectively). Adults and pre-adults of *Dysdercus* sp. attacked seeds more than the nymphs.

Similarly, attacked seeds lost significant more weight than intact seeds after seed predation exposure (F = 6.35, df = 1, *p* = 0.019, Fig. 2b). The difference of seed weight before and after seed predation was significantly affected by tree identity and the interaction between predation treatment and seed predation (F=99.51, df =39, $p<0.0001$, F=9.38, df=2, $p<0.0001$, respectively).

The frequency of seed germination was significantly affected by seed predation. The frequency of germination of predated seeds was significantly lower (χ^2 =756, df =1, $p<0.0001$). Predation treatment (χ^2=2.37, df =2, *p*=0.305) had no significant effect on frequency of germination, nor did the interaction between predation treatment and seed predation (χ^2=1.8, df =2, *p*=0.407). Seed weight affected the frequency of seed germination (χ^2=27.68, df =1, p<0.0001) with larger seeds being predated more.

Similarly, seed predation had a significant effect on the timing of germination (χ^2=66.9, df=1, $p<0.0001$, Fig. 3). The timing of germination in non-attacked seeds was less than attacked seeds. Seed weight had an effect on the timing of germination (χ^2=21.33, df =1, $p<0.0001$). Predation treatment and the interaction between predation treatment and seed predation did not significantly affect the timing of germination (χ^2=0.1, df =2, *p*=0.901, $\chi^2$1.61, df =2, *p*=0.199, respectively).

DISCUSSION

The current rates of defaunation and habitat fragmentation are affecting drastically the interactions between animals and plants in tropical forests (Turner 1996, Wright et al., 2000, Silva and Tabarelli 2000, Galetti 2001, Galetti et al. 2003). Our results indicate that fruit predation of *C. aesculifolia* by the squirrel *S. colliaei* decrease in forest fragments. These results indicate that density dependent factors are more likely to maintain vertebrate seed predator interactions in undisturbed forests. Disturbed areas may not provide the appropriate habitat to harbor seed predators in terms of resource availability or possibly the presence of feral animals in disturbed habitats may reduce potential populations of seed predators like the *S. colliaei*

Similarly, the frequency of the insect *Dysdercus* sp. in trees was also dependent on habitat condition. In disturbed habitats, only two percent of the trees presented *Dysdercus* sp., while 27 percent in undisturbed habitats. Some studies have found that the fragmentation of habitats have negative effects on fruit and seed predation (Janzen 1978, Burkey 1993, Wright and Duber 2001, Cascante et al. 2002, Francisco et al. 2002, Chacoff et al. 2004). For the tropical dry forest trees, *Bahuinia pauletia* and *Samanea saman* less seed predation was found in small forest patches than in disturbed areas (Janzen 1978, Cascante et al. 2002, respectively). The populations of *Dysdercus* sp. are likely affected by density-dependent factors related to the availability of food resources within disturbed areas and the limited capacity to fly between trees that are distantly located in disturbed populations.

We also evaluated the relation between seed predation by *Dysdercus* sp. and seed weight. Damaged seeds had greater weight than undamaged seeds, indicating that seed weight is an important factor in the preference of *Dysdercus sp*. This result is more evident in the experiments where pre-adult and adult predation treatments preferred the largest seeds. Although, seeds of all sizes are subject to predation from a variety of predators while on the soil surface (Abbott and Van Heurck 1985, Thompson *et al.* 1994, Meiners and Stiles 1997, Reader 1997, Leishman et al. 2000), only small seeds (which are consumed by invertebrates) can usually escape predation by incorporating themselves into the seed bank (Leishman et al. 2000).

Damaged seeds lost significantly more weight than undamaged seeds. Pre-adult and adult *Dysdercus* sp. reduced the biomass of seeds more than the nymphs. In *Sterculia apetala, Dysdercus* predated ¼ to ¾ of the seed weight and these seeds failed to germinate (Janzen 1972). Seed predation can have repercussions on survival, distribution patterns, and composition of plant communities (Sallabanks and Courney 1992, Hammond 1995, Benitez-Malvido 1998, Cascante et al. 2002, Fleury and Galetti 2004). Predation by insects reduces seed germination either by damaging the embryonic axis or by consuming the cotyledon (Schelin et al. 2004). Our results indicate that the frequency of seed germination was significantly reduced by seed predation. Similarly, seed predation significantly increased the timing of germination. Few studies have shown that plant distribution is affected by seed predation and recruitment along forest fragments (Sork, 1983). Reduction of seed viability can change the spatial heterogeneity and demography of plant species and can affect the regeneration in disturbed forest fragments.

The effect of forest fragmentation on the interaction of predators of fruits and seeds has not been well studied. A high proportion of seed production is lost due to seed predators in every fruiting event and can have significant negative effects on the reproductive success of plants (Janzen 1972, 1981, Howe 1980, Schupp 1988). This biotic interaction is a major ecological and evolutionary force that affects individual plants, populations, and communities (Schupp 1988). A previous study shows that in undisturbed habitats the reproductive success of individual trees may change every year and that forest fragmentation is an additional factor that increases the variation of reproductive success of trees in remnant forest patches (Herrerías-Diego et al. in press). In the current study, we conclude that fruit and seed predation are also important components that affect the reproductive success of trees in different habitats. We found an important reduction in fruit and seed predation in disturbed forests. Additionally, we also found that predation negatively affects seed viability. From a conservation biology perspective, changes in seed predation can alter the density of seeds, seedling establishment and regeneration of plant populations and ultimately have long-term affects on plant communities (Burkey, 1993, Didham et al.1996, Benitez-Malvido 1998, Wright and Duber 2001).

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Figure legend

Figure 1. a) Percentage of tress that had vertebrate fruit predation in undisturbed and disturbed habitats. b) Percentage of trees that had fruits that contained *Dysdercus* sp. in undisturbed and disturbed habitats.

Figure 2. a) The weight of seeds selected for predation by different age classes of *Dysdercus* sp*.* b) The difference in seed weight before and after seed predation by different age-classes of *Dysdercus* sp*.* Bars represent standard error. Different letters represent significant differences ($p < 0.05$).

Figure 3. Time of germination after seed predation test by each predation treatment of *Dysdercus sp.* Bars represent standard error. Different letters represent significant differences.

Fig. 1

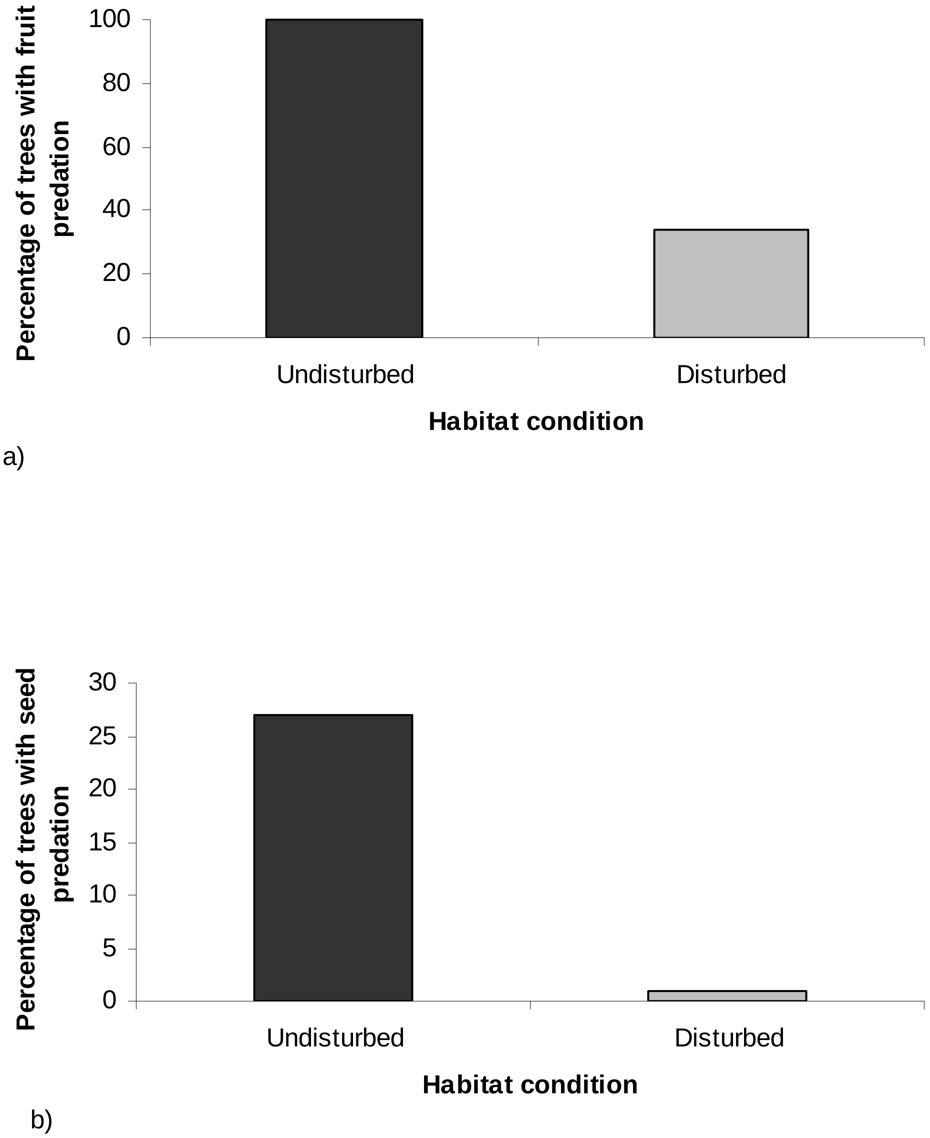
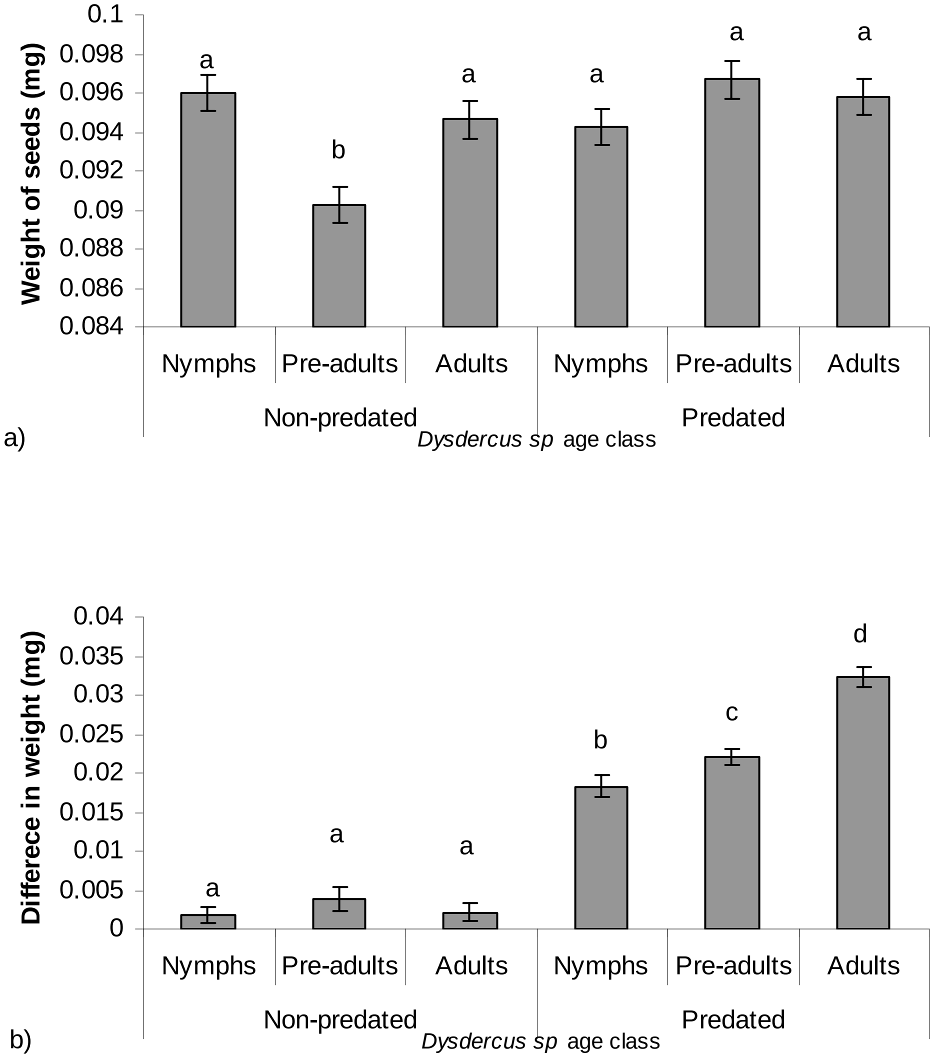
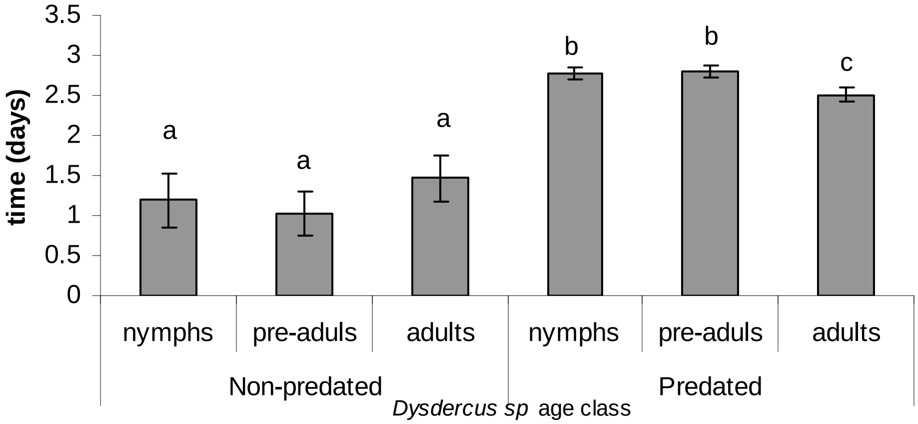

Percentage of trees with fruit predation
100
80
60
40
20
0
Undisturbed
Disturbed
Habitat condition
a)
Percentage of trees with seed predation
30
25
20
15
10
5
0
Undisturbed
Disturbed
Habitat condition
b)

Fig. 2



a)
Weight of seeds (mg)
0.1
0.098
0.096
0.094
0.092
0.09
0.088
0.086
0.084
a
b
a
a
a
a
Nymphs
Pre-adults
Adults
Nymphs
Pre-adults
Adults
Non-predated
Predated
Dysdercus sp age class
b)
Differece in weight (mg)
0.04
0.035
0.03
0.025
0.02
0.015
0.01
0.005
0
a
a
a
b
c
d
Nymphs
Pre-adults
Adults
Nymphs
Pre-adults
Adults
Non-predated
Predated
Dysdercus sp age class

Fig. 3



time (days)
3.5
3
2.5
2
1.5
1
0.5
0
a
a
a
b
b
c
nymphs
pre-aduls
adults
nymphs
pre-aduls
adults
Non-predated
Predated
Dysdercus sp age class

DISCUSIÓN GENERAL

Efecto de la fragmentación del bosque en los patrones fenológicos, éxito reproductivo y estructura genética de *C. aesculifolia*

El más claro efecto del proceso de fragmentación es la remoción del hábitat. Adicionalmente a la pérdida del hábitat, el proceso de fragmentación ocasiona el incremento del número de parches de bosque, la reducción del tamaño del parche de bosque y el incremento del aislamiento entre parches de bosques o individuos remanentes. Asimismo, la fragmentación del hábitat afecta de manera simultánea factores bióticos y abióticos (tales como, la frecuencia de floración, la incidencia de luz, etc.), que de manera directa o indirecta pueden modificar la abundancia y la composición de las especies de plantas, de la fauna de polinizadores y depredadores así como otras interacciones bióticas que pueden influir en el éxito reproductivo y la estructura genética de las poblaciones de plantas. El efecto de la fragmentación en el éxito reproductivo y estructura genética puede depender del grado de aislamiento de los fragmentos y del grado de aislamiento de los individuos remanentes.

En esta Tesis se evaluaron los efectos de la fragmentación del hábitat en los patrones fenológicos, en el éxito reproductivo y en la estructura genética de *Ceiba aesculifolia* por cuatro años. De manera adicional se evaluó el efecto de la fragmentación sobre la depredación de frutos y semillas puesto que la depredación puede ser un factor de gran importancia al disminuir la cantidad de progenie producida y en consecuencia el éxito reproductivo.

La evidencia empírica que existe hasta el momento acerca de los efectos de fragmentación del bosque sobre el éxito reproductivo de las plantas muestra patrones diferentes. Existen casos en donde se ha observado que el éxito reproductivo ha sido negativamente afectado como consecuencia de cambios en la composición y/o abundancia de polinizadores que afectan la cantidad y calidad de la polinización (Aizen & Feinsinger 1994*b*; Cunningham 2000*a*; Cascante et al. 2002; Quesada et al. 2003, 2004), otros donde no se ha observado ningún efecto (Cunningham 2000*b;* Cascante et al. 2002) y finalmente casos donde la fragmentación ha afectado positivamente el éxito reproductivo (Quesada et al. 2004; Herrerías-Diego et al. 2006).

En este estudio se observó que la fragmentación del hábitat no tuvo ningún efecto sobre el éxito reproductivo de *C. aesculifolia.* De acuerdo a los resultados obtenidos en este trabajo, la frecuencia de floración (más individuos con flores) fue mayor en las poblaciones no perturbadas. Sin embargo, el número de flores y frutos por árbol fue mayor en los árboles de sitios perturbados no obstante, la proporción de frutos producidos (fruit- set) fue la misma en ambas condiciones (Capítulo I). Este incremento en la producción de flores y frutos puede deberse a un aumento en el recurso luz que permite un mayor desarrollo en biomasa en los árboles en sitios perturbados. Debido a que los árboles se localizan en áreas abiertas donde no hay competencia por luz o por otros recursos con árboles de la misma o de diferentes especies, desarrollan copas más amplias con un mayor número de ramas secundarias y es precisamente ahí donde se producen las flores y por lo tanto se desarrollan los frutos. El fruit-set posiblemente fue mantenido por los polinizadores que pueden viajar entre los árboles y atravesar las zonas perturbadas. Otro estudio evaluó la frecuencia de visita de los polinizadores a *C. aesculifolia* en ambas condiciones de hábitat y encontró que las flores de los árboles que se encontraban en sitios perturbados recibieron una mayor cantidad de visitas de ambos polinizadores (*Glossophaga soricina* y *Leptonycteris curasoae*) que las flores de árboles en bosque no perturbado (Quesada et al. 2004).

Además del aislamiento espacial causado por la fragmentación del bosque, el aislamiento temporal causado por la asincronía en los periodos de floración puede ser otro factor importante que afecta la reproducción y la estructura genética de las poblaciones de plantas en ambientes alterados (Murawski et al. 1990; Murawski & Hamrick 1991; Murawski & Hamrick 1992b; Chase et al. 1996; Doligez & Joly 1997; Nason 1997; Nason et al. 1997). Los niveles de sincronía en la fenología floral permiten determinar el número de árboles reproductivos simultáneos y estimar el número de donadores y receptores de polen. Modificaciones en la sincronía de floración pueden modificar los patrones de flujo de polen de las plantas (Stephenson 1982; Murawski & Hamrick 1992b). Los individuos que florecen en el pico del periodo de floración poblacional son los que tienen la mayor probabilidad de recibir polen de un mayor número de donadores comparado con los individuos que florecen de manera asincrónica. En el caso particular de *C. aesculifolia*, se encontró que la floración es sincrónica dentro de las poblaciones pero el pico de floración varía dependiendo de la condición del hábitat en la que se encuentren los individuos (Capítulo I). En los árboles ubicados en sitios perturbados el pico de floración se produce entre dos semanas y un mes antes del pico de floración de los árboles en sitios no perturbados, este desfase se mantuvo a través de los cuatro años de estudio. A pesar que los picos de floración variaron en el tiempo, la longitud de los periodos de floración fue la misma entre las poblaciones de ambas condiciones y para cada uno de los años. La anticipación en los picos de floración puede deberse a las variaciones ambientales ocasionadas por la pérdida de la cobertura vegetal. Algunos estudios han demostrado que la fragmentación del bosque puede ocasionar un incremento en la radiación solar y en la velocidad del viento y una disminución en la disponibilidad de agua en el suelo (Kapos 1989; Saunders et al. 1991; Kapos et al. 1997). *Ceiba aesculifolia* florece durante el periodo seco (Lobo et al. 2003), donde el factor limitante es el agua. Las poblaciones de *C. aesculifolia* en los sitios no perturbados se encuentran en pequeñas cuencas o cauces de ríos, rodeadas de vegetación riparia donde se mantiene la humedad. Por el contrario, las poblaciones en sitios perturbados podrían experimentar condiciones de menor disponibilidad de agua en el suelo y mayores temperaturas lo cual puede estar propiciando la floración adelantada de las poblaciones en sitios no perturbados

Es particularmente interesante el estudio de las diferencias en los tiempos de floración dentro de las poblaciones. Un alto grado de sincronía dentro de las poblaciones se puede considerar adaptativo, debido a que promueve el exocruzamiento y la saciedad de los depredadores de semillas (Janzen 1976). La asincronía en los tiempos de floración puede explicarse como una respuesta a la competencia intraespecífica por los polinizadores, para promover el movimiento de los polinizadores entre plantas, incrementar la posibilidad de dispersión de los depredadores de semillas o variar la intensidad y sincronía de la depredación de semillas o una selección diferencial en diferentes años dependiendo de los factores ambientales (Bawa 1983; Frankie & Haber 1983; Primack 1985; Rathcke & Lacey 1985). En *C. aesculifolia,* como se mencionó anteriormente, el desfase de los picos de floración es posiblemente una respuesta a la variación ambiental, pero los resultados a largo plazo sobre la variación genética de las poblaciones que se establezcan es algo que todavía no se ha estudiado y que proporcionaría información acerca del mantenimiento de las poblaciones en el tiempo.

Como parte de este estudio se realizó una evaluación de la tasa de exocruzamiento, la correlación de paternidad y la estructura genética de las progenies producidas en cuatro eventos reproductivos consecutivos (Capítulo II). Los resultados indican que *C. aesculifolia*, presenta una tasa de exocruzamiento de uno (valor máximo para este parámetro), demostrando que es una especie estrictamente autoincompatible. La tasa de exocruzamiento se mantuvo a través de los años de estudio y no fue modificada por la condición del hábitat, ni por la población como se ha reportado para otras especies de árboles de la familia Bombacacea. Por ejemplo, en el caso de *Pachira quinata* se reporta una reducción en la tasa de exocruzamiento en los árboles que se encontraban en sitios perturbados, pasaba de completamente a parcialmente exocruzada (Fuchs et al. 2003). Otra especie del mismo género con tasas de exocruzamiento variable es *Ceiba pentandra*, la cual presenta variaciones en la tasa de exocruzamiento dependiendo de la población, teniendo poblaciones completamente exocruzadas a otras con un sistema mixto de apareamiento (Lobo et al. 2005).

Adicionalmente, las poblaciones evaluadas de *C. aesculifolia* presentaron alta estructura genética dentro de cada una de las poblaciones para ambas condiciones de hábitat. El número de donadores de polen en las poblaciones en sitios no perturbados fue mayor pero la distancia de desplazamiento entre donador y receptor de polen fue menor; esta tendencia se mantuvo durante los cuatro años de estudio (Capítulo II, Tabla 2). El número de donadores y la distancia de desplazamiento del polen puede ser explicada por el patrón fenológico y el comportamiento de los polinizadores que presentó *C. aesculifolia*. Las dos especies principales de polinizadores son los murciélagos nectarivoros *Leptonycteris curasoae* y *Glossophaga soricina* (Quesada et al. 2004). Los murciélagos se conocen como buenos vectores de polen para largas distancias (Law & Lean 1999; Nassar et al. 2003) y entre parches de bosque en ambientes perturbados (Quesada et al. 2003, 2004). Estudios realizados previamente describen que la capacidad de vuelo de *L. curasoae* es alrededor de 100 km en una noche (Horner et al. 1998) de tal manera que este animal puede incrementar el área de búsqueda de flores y así incrementar el número de padres potenciales. En contraste, *G. soricina* tiene un ámbito hogareño más pequeño, de 2 a 4 ha (Heithaus et al. 1975; Lemke 1984) por lo que su restringida área de búsqueda limita la cantidad de padres potenciales.

De esta manera, *G. soricina* podría ser responsable de la alta estructura génica dentro de cada una de las poblaciones, en tanto que *L. curosae* mantendría la conectividad reproductiva entre los individuos que se encuentran aislados (o en diferentes poblaciones) y en bosque continuo. Esta idea es apoyada por el hecho de que en árboles en sitios perturbados la mayoría de la progenie fue originada por polen proveniente de árboles ajenos a la población. Adicionalmente, la frecuencia de floración de *C. aesculifolia* promueve que en las poblaciones en ambientes no perturbados los polinizadores tengan que desplazarse menos dentro de un individuo en flor debido a que hay más individuos floreciendo simultáneamente y la distancia entre ellos es menor. Mientras que en las poblaciones en ambiente perturbado hay menos individuos en floración, una mayor distancia entre árboles, pero con una mayor producción de flores lo que podría promover una alta frecuencia de cruces geitonogámicos. Ambas especies de polinizadores resultan ser eficientes en el movimiento de polen entre los árboles en ambas condiciones.

Numerosos estudios empíricos han demostrado que en las plantas que presenten una baja densidad de individuos, los polinizadores visitan una gran proporción de flores antes de moverse a otro sitio en busca de recursos (Kunin 1993; Bosch & Blas1994; Kunin 1997; Ghazoul et al. 1998; Bosch & Waser 1999; Schulke & Waser 2001). Este comportamiento de los polinizadores de *C. aesculifolia* en sitios perturbados produciría una gran cantidad de cruces geitonogámicos y autogámicos. Sin embargo, debido a que *C. aesculifolia* es una especie autoincompatible, estos cruces no prosperarían y los frutos que maduran y tienen la capacidad de dispersarse son sólo aquellos que fueron producto de polinización cruzada. Más aún, las paternidades asignadas durante el estudio, indican que el 70% de los padres potenciales de las progenies de sitios perturbados provienen de afuera de la población. Mientras que las progenies de los sitios no perturbados únicamente entre 10 % y 20 % de los padres provienen de una población diferente (Capítulo II, Figura 3). Algunos estudios realizados señalan que los árboles tropicales tienen altos niveles de exocruzamiento y la diferenciación genética se incrementa cuando hay un incremento en la distancia geográfica entre los individuos (Hamrick & Murawski, 1991; Murawski et al. 1994; Hall et al. 1996). Adicionalmente el flujo génico entre vecindarios es un factor importante en el mantenimiento de la diversidad genética en metapoblaciones (Boshier et al. 1995). El flujo génico dentro de las poblaciones de plantas se puede dar por tres vías: 1) ambos padres están dentro de la población (flujo vía polen y/o semilla); 2) ambos padres se encuentran fuera de la población (flujo vía semilla) y 3) el árbol madre se encuentra dentro de la población y el árbol padre se encuentra fuera de la población (flujo vía polen).

Las alteraciones en la diversidad genética como resultado de la fragmentación pueden tener un mayor impacto en especies de árboles tropicales debido a que éstas ocurren en bajas densidad y la mayoría requiere de un vector animal para llevar a cabo la polinización. En casi el 50% de las especies de árboles tropicales, se ha descrito una densidad de un individuo o menos por hectárea (Poore 1968; Hubbell & Foster 1983; Whitmore 1984; Gentry & Terborgh 1990). Las bajas densidades de los árboles tropicales sugieren que aún en reservas naturales de cientos de hectáreas, el número de árboles adultos podría ser menor al requerido para el mantenimiento efectivo de las población es a largo plazo. Varios estudios han revelado que la variación genética es alta en los bosques tropicales y la mayoría de la variación reside dentro de la población, por lo que se ha sugerido que en estas especies existe un alto flujo génico (Hamrick & Loveless 1989; Hall et al 1996*;* Nason & Hamrick 1997; Loveless et al 1998).

Importancia de los polinizadores en ambientes fragmentados

Si bien en esta Tesis no se ha abordado el estudio de los polinizadores de *C. aesculifolia*, varios de los resultados que se desprenden del capítulo I (éxito reproductivo) y capítulo II (estructura genética), pueden ser entendidos gracias al conocimiento previo que se tiene de sus polinizadores, de las frecuencias de visita y de sus patrones de forrajeo. Por esta razón se decidió integrar dentro de la discusión general un apartado acerca de los polinizadores en ambientes fragmentados.

La fragmentación del hábitat tiende diversos efectos sobre las poblaciones de plantas y animales. Un factor que ha sido poco estudiado es el efecto de la fragmentación sobre las interacciones bióticas no obstante, una de las más estudiadas es la polinización. La polinización es una de las interacciones bióticas más importantes para las plantas debido a que cerca del 90% de las plantas con flores existentes dependen, en diferentes grados, de animales como vectores de polen para su reproducción sexual (Bawa 1990; Buchmann & Nabhan 1996; Kearns et al. 1998;

Aizen et al. 2002; Aizen & Feinsinger 2003; Aguilar et al. 2006). Desde el punto de vista evolutivo, la adquisición de animales para la transferencia de polen ha resultado en una mayor eficiencia en la polinización de las plantas. No obstante, esta dependencia de las plantas en la interacción mutualista con los polinizadores para reproducirse, puede incrementar la susceptibilidad de las plantas a la fragmentación del hábitat o a cualquier otro tipo de disturbio (Bond 1994; Spira 2001; Aizen & Feinsinger 2003; Ashworth et al. 2004). La disrupción de la interacción planta-polinizador puede ocurrir debido a la susceptibilidad de los animales polinizadores a los cambios en la cantidad y en la calidad del hábitat remanente (Kearns et al. 1998). La degradación de este mutualismo planta-polinizador puede ocasionar una disminución en el número y en la calidad de las semillas producidas y esto podría conducir a una reducción en las poblaciones de plantas a largo plazo (Buchmann & Nabhan 1996; Renner 1998; Cox & Elmqvist 2000; Paton 2000).

En un ambiente fragmentado, la reducción en la densidad de plantas implica que los polinizadores podrían estar llegando con menos frecuencia ya que se incrementa la distancia entre los individuos reproductivos, podría haber una reducción en el despliegue florar y por consiguiente se reduce la atracción por la “recompensa” para los polinizadores (Bosch & Waser 1999). Sin embargo, en un estudio sobre *C. aesculifolia*, llevado a cabo en el mismo sitio (Quesada et al. 2004) que el presente trabajo, se encontró que las flores de árboles en sitios perturbados recibieron mas visitas que en sitios no perturbado; esto estaría indicando que la atracción a los polinizadores no se ve disminuida en los sitios perturbados, sino, por el contrario, se ve incrementada, posiblemente como consecuencia del mayor despliegue floral. Adicionalmente, los servicios de polinización se pueden reducir si el aislamiento entre los fragmentos de bosque es mayor que el rango de forrajeo de los polinizadores, si las poblaciones locales de polinizadores se reducen o si éstos evitan visitar las poblaciones que se encuentren aisladas. Los polinizadores con una limitada capacidad de desplazamiento entre fragmentos pueden ser más afectados si no hay corredores presentes que les permita desplazarse entre los remanentes de bosque (Townsend & Levey 2005). Además, las plantas auto-incompatibles con polinizadores especializados pueden ser particularmente afectadas por limitación de polen después de la fragmentación del hábitat (Bond 1994; Knight et al. 2005; Aguilar et al. 2006). Este proceso puede ocasionar una reducción en la cantidad y en la calidad del polen que llega a los árboles en fragmentos de bosque, reduciendo el éxito reproductivo de los individuos (Aizen & Feinsinger, 1994 a,b, 2003; Aizen et al. 2002; Dick 2001, 2003;Quesada et al. 2003, 2004; Aguilar & Galetto 2004; Ghazoul 2005; Aguilar 2006).

Depredación de frutos y semillas

Una interacción biótica que ha sido muy poco estudiada en el ámbito de la fragmentación de hábitat es la depredación de frutos y semillas. Este tipo de interacción es importante en los bosques tropicales debido a que permite la regulación de las poblaciones de plantas (Sallabanks & Courney 1992; Hammond 1995; Benitez-Malvido 1998; Cascante et al. 2002, Fleury & Galetti 2004). Las actuales tasas deforestación están afectando las poblaciones de depredadores y su presencia en los sitios fragmentados (Turner 1996; Wright et al. 2000; Silva & Tabarelli 2000; Galetti 2001; Galetti et al. 2003). Algunos estudios han evaluado la disminución de los depredadores de semillas en los sitios fragmentados pero el efecto que esto ocasiona en las poblaciones de plantas es algo que aún no ha sido evaluado (Janzen 1978; Burkey 1993; Wright & Duber 2001; Cascante et al. 2002; Francisco et al. 2002; Chacoff et al. 2004).

Los resultados obtenidos en este trabajo indican que la frecuencia de depredadores de frutos (ardilla: *Sciurus colliaei*) y de semillas (Hemíptero: *Dysdercus sp.*) disminuye en las poblaciones de *C. aesculifolia* en sitios perturbados (Capítulo III). Posiblemente la falta de cobertura vegetal esta influyendo para que se obstruya la movilidad entre los árboles en sitios perturbados. Adicionalmente, en el caso de la especie depredadora de frutos, un factor muy importante que podría estar influenciando la ausencia de ardillas en las poblaciones perturbadas es que las áreas de pastizales y urbanas pueden albergar a depredadores potenciales de las ardillas como son los animales ferales (ie. perros y gatos).

Otro factor importante que fue evaluado en este trabajo fue el efecto de la depredación de semillas en la germinación de las semillas depredadas. La depredación de semillas por insectos reduce la germinación y no sólo daña el embrión, sino que consume las reservas de la semilla (Schelin et al. 2004). Los resultados de este trabajo confirman lo anterior debido a que la frecuencia y el tiempo de germinación se vieron negativamente afectados por la exposición de las semillas a la depredación por *Dysdercus sp.* Por otro lado, se realizó un experimento en laboratorio donde se expusieron las semillas a depredación bajo diferentes estadios de desarrollo del principal depredador de semillas de *C. aesculifolia*, *Dysderdcus sp.* Los resultados obtenidos demuestran que las semillas más depredadas son aquellas que tienen un mayor peso. Además, los adultos y pre-adultos son los que consumen una mayor biomasa de las semillas, lo cual hace pensar que el daño al embrión es mayor y podría poner en riesgo la supervivencia de esas semillas. Una alta proporción de semillas se pierde en cada uno de los eventos reproductivos debido a la depredación (Janzen 1972, 1981; Howe 1980; Schupp 1988) y esta mortalidad es considerada una fuerza ecológica y evolutiva que afecta las poblaciones y comunidades de plantas (Schupp 1988). La producción de frutos y semillas es variable en el tiempo (Capítulo I) así como entre individuos y la modificación en la tasa de depredación de frutos y semillas puede ser un factor que altere el reclutamiento de la población en las poblaciones en sitios perturbados.

Relevancia del trabajo

En esta Tesis se han presentado resultados de importancia tanto para la ecología básica como para la ecología aplicada en el ámbito de la conservación biológica, a saber:

a) Es uno de los primeros trabajos donde se evalúa el efecto de la fragmentación sobre los patrones fenológicos, el éxito reproductivo y la estructura genética de la progenie en cuatro eventos reproductivos. Adicionalmente, se evalúo la depredación de frutos y semillas entre sitios perturbados y no perturbados; así como, el efecto de la depredación de semillas en la germinación.

b) Este trabajo identifica la importancia de los árboles en sitios perturbados como corredores biológicos que permitan conectar las poblaciones de sitios perturbados con las poblaciones en bosque no perturbado. Algunos estudios han propuesto que los árboles que se encuentran aislados podrían considerarse como muertos en vida (Janzen & Vázquez-Yañez 1990) dado su escasa capacidad reproductiva. En los años recientes la evidencia empírica ha demostrado la importancia de los fragmentos de bosque y de los individuos aislados en zonas perturbadas como corredores o puentes para el flujo génico y su contribución en el mantenimiento de la diversidad genética tanto en los bosques no perturbados como en los parches donde se encuentran (Cascante et al. 2002; Chase et al. 1996). Es necesaria la realización de más estudios que evalúen la contribución de las poblaciones remanentes como donadores o receptores de polen o fuente de semillas en poblaciones perturbadas y poblaciones en bosque no perturbado.

c) Desde una perspectiva de conservación es importante reconocer la variabilidad de respuestas que tienen las diferentes especies de plantas a la fragmentación. A medida que se entienda como las especies con diferentes características de historia de vida responden a un mismo factor, en este caso la fragmentación del hábitat, será posible predecir el impacto de ese tipo de perturbaciones en el éxito reproductivo, las características genéticas y la regeneración de las poblaciones naturales. Así se podrán tomar medidas para conservar la biodiversidad y la restauración de las poblaciones de plantas en sitios perturbados.

Conclusión General

Capítulo I

- La fragmentación del bosque afecta los patrones de floración de *C. aesculifolia.*
- El pico de floración de los árboles de *C. aesculifolia* en poblaciones aisladas ocurre entre dos semanas y un mes antes de los árboles en poblaciones continuas,
- Florecen un mayor número de árboles cada año en las poblaciones de bosque continuo que en las poblaciones de sitios perturbados
- Las poblaciones en sitios perturbados producen dos veces más flores y mayor cantidad total de frutos que los árboles en poblaciones de bosque continuo. Esta diferencia se mantiene a través de 3 años de análisis
- La proporción de frutos producidos (fruit set) fue similar entre condiciones de hábitat. .
- La fragmentación del bosque no afectó la producción de semillas totales por fruto.
- El número de semillas potencialmente viables y semillas abortadas cambia a través del tiempo pero es independiente de la condición del sitio.
- Aparentemente en nuestro estudio, la fragmentación del bosque no afecta el éxito reproductivo de *Ceiba aesculifolia*. Esto puede deberse a que el principal polinizador *Leptonycteris curasoae* tiene la capacidad de viajar largas distancias y mover el polen de manera eficiente entre los árboles que se encuentran en sitios lejanos. Este comportamiento de forrajeo mantiene una conectividad reproductiva entre los individuos de sitios perturbados.

Capítulo II

- En los cuatro años, la tasa de exocruzamiento no se afectó por la fragmentación.
- Todas las poblaciones de *C. aesculifolia* fueron 100% exocruzadas
- Cada fruto presenta un sólo donador y todas las semillas de un mismo fruto son hermanas completas.
- Las poblaciones en ambos hábitats presentan una alta estructura genética. La estructura genética es consistentemente mayor en las poblaciones en hábitats perturbados.
- En las poblaciones no perturbadas se encuentra un número mayor de donadores de polen.

- La distancia entre donadores es menor en las poblaciones no perturbadas.
- El movimiento de polen es entre pocos donadores en ambas condiciones
- En las poblaciones en sitios perturbados, el porcentaje de paternidad calculado indica que cerca del 70 % de los padres potenciales fueron de otras poblaciones.
- En sitios no perturbados únicamente entre el 10 % al 20 % de los padres potenciales fueron de poblaciones en sitios perturbados.

Capítulo III

- La frecuencia de individuos *C. aesculifolia* con frutos depredados por *S. colliaei* es de 40% en sitios no perturbados y 6% en árboles de sitios perturbados.
- La frecuencia de *Dysdercus* sp. en sitios perturbados es 1% y de 27% en árboles en sitios no perturbados.
- Las semillas de mayor tamaño fueron las más depredadas por *Dysdercus*.
- La depredación de semillas tiene un importante efecto negativo en el tiempo de germinación.
- La depredación de frutos y semillas en bosques remanentes es un factor muy importante para la regeneración de las poblaciones vegetales y ha sido muy poco estudiado.

En sitios perturbados la floración se adelanta, hay menos árboles en floración simultanea y mas flores por árbol, esta situación podría ser la causante de que en dichas poblaciones el polen que origina las semillas provenga mayoritariamente de afuera de la población, que las flores de los árboles reciban mas visitas y que la estructura genética sea mayor. En sitios perturbados no solo se producen en términos absolutos más frutos, sino que además los frutos y semillas sean menos depredados. Entonces en sitios perturbados quedaría mayor cantidad de progenie potencialmente viable. Sin embargo esa progenie esta siendo generada particularmente por polen de otras poblaciones y comparativamente por una menor cantidad de donadores que en bosques no perturbados, lo cual podría contribuir a mantener o incrementar la diversidad genética de la progenie, pero podría tener efectos negativos en la adecuación de esa progenie. Por otro lado hay que considerar que en sitios perturbados las flores recibieron mas visitas que en sitios no perturbados, si mas visitas implica mayor carga de polen y esto mayor competencia polínica, se esperaría que el vigor de la progenie fuera superior en sitios perturbados, si además se agrega el hecho de que las depredación es mayor en sitios no perturbados y las semillas consumidas son las de mayor tamaño seria lógico pensar que la progenie mas vigorosa esta siendo comparativamente mas depredada en los sitios no perturbados. Estas serian ideas interesantes de poner a prueba en trabajos posteriores.

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ANEXO I

TABLAS ANÁLISIS ESTADÍSTICOS

CAPÍTULO I

Proporción de árboles que producen flores

Fuente	gl	χ2	P
Población (condición)	5	8.47	0.13
Condición	1	0.28	0.5980
año	3	16.32	0.0010
Condición*año	3	5.16	0.1601
DAP	1	2.40	0.1210

Proporción de árboles que producen frutos

Fuente	gl	χ2	P
población(condición)	5	8.70	0.1217
condición	1	7.38	0.0066
año	3	34.22	<.0001
condición*ano	3	15.56	0.0014
DAP	1	1.94	0.1641
Dist. Ind. cercano	1	0.13	0.7186

Flores Totales

Fuente	gl	χ2	P
población(condición)	5	4.05	0.5425
Condición	1	6.11	0.0135
Año	2	18.05	0.0001
condición*año	2	3.22	0.2000
DAP	1	4.06	0.0440

Frutos Totales

Fuente	gl	χ2	P
población(condición)	5	9.86	0.0793
condición	1	9.06	0.0026
año	2	41.27	<.0001
condición*año	2	5.59	0.0610
DAP	1	7.95	0.0048
Dist. ind. Cercano	1	3.92	0.0476

Fruit Set

Fuente	gl	χ2	Pr
población(condición)	5	9.46	0.0919
condición	1	4.58	0.05
año	2	24.63	<.0001
condición*año	2	5.04	0.0804
DAP	1	1.03	0.3098

Dist. Ind. cercano	1	5.31	0.0212

Capítulo III

Proporción de depredación de frutos

Fuente	gl	χ2	P
condición	1	16.73	0.001
DAP	1	2.15	0.142
Dist. Ind. cercano	1	0.20	0.653

Proporción de depredación de semillas

Fuente	gl	χ2	P
condición	1	14.87	0.0001
DAP	1	0.34	0.561
Dist. Ind. cercano	1	0.34	0.877

Selección de Tamaño

Fuente	gl	F	P
Depredadas	1	14.87	0.0001
Identidad	39	99.51	0.0001
Tratamiento de Depredación	2	9.38	0.0001

Diferencia en Peso

Fuente	gl	F	P
Depredadas	1	6.37	0.019
Identidad	39	99.51	0.0001

Tratamiento de Depredación	2	9.38	0.0001

Germinación

Fuente	gl	χ2	P
Depredadas	1	756	0.00001
Tratamiento de depredación	2	2.37	0.305
Peso de la semilla	1	27.68	0.0001
Interacción	2	1.8	0.305

Tiempo de Germinación

Fuente	gl	χ2	P
Depredadas	1	66.9	0.00001
Tratamiento de depredación	2	0.1	0.901
Peso de la semilla	1	21.33	0.0001
Interacción	2	1.61	0.199