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Efectos de la fragmentación sobre la dispersión de semillas y la regeneración del bosque tropical Centroamericano

TESIS

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PRESENTA

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Director General de Administración Escolar, UNAM
Presente

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día 1º. de Septiembre de 2008, se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del alumno **FELIPE PIMENTEL LOPES DE MELO** con número de cuenta **505451048** con la tesis titulada: **"Efectos de la fragmentación sobre la dispersión de semillas y la regeneración del bosque tropical Centroamericano"**, realizada bajo la dirección del **DR. GERARDO JORGE CEBALLOS GONZÁLEZ:**

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POR MI RAZA HABLARÁ EL ESPÍRITU.

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RESUMEN

La dispersión de semillas es un proceso clave para la regeneración de poblaciones de plantas y para el mantenimiento de la diversidad de árboles en bosques tropicales. Sin embargo, la fragmentación y la defaunación de los bosques tropicales pueden resultar en alteraciones en la dispersión de semillas con consecuencias extremadamente negativas para los procesos de regeneración del bosque tropical. En el presente trabajo se estudió la fragmentación y sus efectos asociados a la defaunación en las tasas de dispersión de semillas y el reclutamiento de plántulas así como el papel de la fauna remanente en mantener servicios de dispersión de semillas. Específicamente, se evaluaron los patrones espacio-temporales de la lluvia de semillas y el reclutamiento de plántulas de árboles en un paisaje fragmentado del estado de Quintana Roo, México. Además, analizó el papel que juegan los murciélagos, uno de los principales componentes de la fauna remanente en hábitats fragmentados, como dispersores de semillas de semillas grandes comparando fragmentos defaunados y grandes reservas de Costa Rica. Los resultados del seguimiento por dos años de lluvia de semillas sugieren que fragmentos aislados de bosque presentan mayor densidad pero menor riqueza de semillas. Las características de la vegetación tuvieron apenas una moderada influencia en las semillas dispersadas abióticamente y ninguna influencia en las especies dispersadas por animales. En promedio, las especies fallaron en llegar a la mayoría de las trampas (*seed limitation*) en todos los fragmentos y la selva continua estudiados, pero esa limitación fue mayormente determinada por restricciones de dispersión en fragmentos < 3 ha (*dispersal limitation*). Las semillas grandes demostraron ser más limitadas en dispersión en fragmentos < 3 ha probablemente debido a la eliminación de dispersores de gran talla de estos pequeños parches de bosque. Esos patrones se reflejaron en el reclutamiento de plántulas que se mostró seriamente afectado por la fragmentación al sufrir cambios en la composición de especies y de grupos funcionales. Los resultados sugieren que los patrones de reclutamiento en pequeños fragmentos defaunados tienden a reducir gradualmente la representatividad de especies de plántulas con semillas grandes. Además, el papel de los murciélagos como dispersores de semillas de gran tamaño fue sorprendentemente mayor que lo antes reportado en la literatura. Esos pequeños animales demostraron ser capaces de dispersar una amplia gama de especies mayores que 0.8 cm de largo con un gran potencial para afectar la regeneración del bosque. La fragmentación forestal produce cambios importantes en patrones de dispersión de semillas que se pueden percibir en la regeneración avanzada del bosque. El grupo funcional más afectado son las semillas de tamaño grande cuya fauna dispersora es la más vulnerable a la reducción del área de hábitat disponible. Sin embargo, pudimos demostrar que los murciélagos frugívoros, como parte de la fauna remanente en pequeños fragmentos, tienen el potencial de mantener cierto flujo de semillas de gran porte reduciendo las probabilidades de extinción local de este grupo de plantas. Así, la regeneración de bosques fragmentados y defaunados parece estar fuertemente influenciada por los patrones de dispersión de semillas. Medidas de intervención que favorezcan la conectividad de los parches aislados y posibilite la recomposición de la fauna dispersora puede evitar la erosión de diversidad funcional de árboles y evitar la pérdida de complejidad estructural del bosque Neotropical.

ABSTRACT

Among the mechanisms proposed to explain high tree diversity in tropics, seed dispersal plays a major role. However, both forest fragmentation and elimination of fauna due to hunting and loss habitat may put in risk this key ecological process for maintenance of tree diversity thus affecting the regeneration pathways of fragmented forests. To assess how disruptions in seed dispersal may affect future successional trajectories in fragmented and defaunated landscapes is crucial for conservation purposes. This study assessed the combined effects of forest fragmentation and defaunation on the dispersal rates and seedling recruitment in a community wide level in a disturbed landscape in the Quintana Roo State, Southern Mexico. A third hypothesis regarding the role of the remaining fauna, specifically small fruit-bats, in the dispersal of large-seeded seeds was tested in the lowland rain forest of Costa Rica. Number of medium- to large-bodied seed dispersers (> 1 kg) decreased with forest patch area in Southern Mexico. As a consequence, our results suggest that seed rain is more variable both spatially and temporally in small forest fragments (< 30 ha) than in larger forest patches (> 640 ha). Representation of immigrant seeds was higher in fragments < 3 ha but dispersed seeds were more abiotically-dispersed and clumped distributed in than in continuous forest. Yet, influence of vegetation structure on seed rain density was almost negligible but number of seeds was positive correlated with importance value of adults in all fragments. Finally, large-seeded species were more dispersal limited in small defaunated fragments and overall seed limitation in this forest patch size was mainly due to dispersal than to source limitation. Our results highlight that functional attributes of seed species together with composition of adult stands may help to predict different responses of seed deposition patterns to forest fragmentation that may be valuable for understand forest succession in fragmented landscapes. This was reflected in the seedling assemblage. Although adult tree communities did not vary significantly among forest patches in terms of both taxonomic and functional composition, large-seeded seedlings tended to be low-represented within the smallest forest patches (< 30 ha). We conclude that forest fragmentation and defaunation may seriously reduce dispersal rates of large-seeded tree species (> 1.4 cm length), negatively affecting regeneration pathways of small defaunated forest patches. However, remaining fauna in small disturbed areas such as small fruit bats may have an important role in the maintenance of some level of dispersal service. Samples collected beneath bat feeding roosts had, on average, 10 times more seeds and species than nearby samples away from bat feeding-roosts but this difference tended to be reduced in small, disturbed forest patches. Species-specific abundance of seeds found beneath bat-roosts was positively correlated with respective abundance of seedlings suggesting that these bats may influence seedling recruitment of large-seeded plants. Our study demonstrates a greater role of small frugivorous bats as seed dispersers than previously thought that may assume an invaluable role in the dispersal of large-seeded plants actually threatened by extirpation of large-bodied seed dispersers. Therefore, to prevent the loss of ecological services such as seed dispersal and the re-establishment of lost services may be key to raise conservation value of disturbed landscapes as important sites for the conservation of the biodiversity in the Tropics.

INTRODUCCIÓN GENERAL

Entre las interacciones planta-animal, la dispersión de semillas es un proceso que ha suscitado gran atención de la comunidad científica desde la década de los 70, cuando Daniel Janzen (1970) y Joseph Connell (1971) propusieron un mecanismo que le atribuía un papel fundamental en la dinámica de comunidades vegetales y el mantenimiento de la diversidad de plantas en bosques tropicales. A partir de entonces un gran número de trabajos ha identificado y definido las consecuencias de la dispersión de semillas para las plantas. Entre las más importantes se encuentran la posibilidad de colonización de nuevos sitios, del mantenimiento de su estructura poblacional y el aumento de la adecuación mediante reclutamiento de nuevos propágulos (Harper 1977, Howe y Smallwood 1982, Howe y Miriti 2000). La mayoría de las angiospermas ha evolucionado hacia la atracción de dispersores vertebrados mediante la producción de frutos carnosos (Foster 1986, Sussman 1991). Son abundantes los ejemplos en la literatura en donde se establece un claro vínculo entre patrones de dispersión de semillas y otros atributos de la dinámica poblacional de las plantas como colonización de sitios adecuados, distribución espacial de plántulas, probabilidades de reclutamiento, etc (e.g. Howe 1981, Peres y Baider 1997, Pimentel y Tabarelli 2004).

Diversos modelos teóricos se han propuesto para explicar la generación y el mantenimiento de los patrones de diversidad de árboles, casi todos atribuyendo importantes funciones a la dispersión de semillas como parte de su mecanismo intrínseco (Janzen 1970, Sussman 1991, Thery et al. 1998, Moles et al. 2005a, Moles et al. 2005b). Sin embargo, existe un vacío de conocimiento acerca de los efectos de las actividades antrópicas en la dispersión de semillas. La mayoría de los estudios sobre dispersión de semillas se han llevado a cabo con el objetivo de describir las consecuencias de los patrones de relación planta-animal en ambientes relativamente bien conservados. Los estudios en ecología de dispersión de semillas están apenas empezando a comparar patrones y procesos de dispersión en sitios con distintos niveles de conservación (Ratiarison y Forget 2005, Galetti et al. 2006, Melo et al. 2006, Terborgh et al. 2008). La mayoría de estos estudios ha arrojado importante información que ha permitido empezar a comprender las consecuencias de la alteración en la dispersión de semillas. La pregunta principal todavía por contestar es: ¿cómo se da la dispersión de semillas en hábitats alterados en donde la fauna dispersora es reducida y en donde los atributos demográficos de las plantas se encuentran alterados? Las repuestas a esta pregunta, a pesar de relativamente intuitivas, han demostrado ser variadas, complejas y por veces contrastantes. Indudablemente existen consecuencias serias para las poblaciones de árboles cuyas alteraciones en los patrones de dispersión de semillas resultan, a nivel de comunidad, en amenazas al mantenimiento de la diversidad de árboles. El entendimiento de la dinámica biológica en paisajes perturbados permitirá evaluar su viabilidad a largo plazo como unidades de hábitat y proponer estrategias exitosas de recuperación y manejo (Tabarelli et al. 2005).

Fragmentación y Defaunación

Las plantas tropicales son dispersadas por una infinidad de medios: desde monos (Link y Di Fiore 2006) a hormigas (Mitchell et al. 2002), desde tapires (Fragoso et al. 2003) a murciélagos (Muscarella y Fleming 2007), por el viento (Clark et al. 2005) o por al agua (Sengupta et al. 2005), por peces (Galetti et al. 2008) y por aves (Bleher y Böhning-Gaese 2006). Es razonable esperar que la fragmentación forestal afecte de manera distinta a esos modos de dispersión y que incluso haya peculiaridades en la respuesta de cada relación planta-dispersor específica. Entender cómo se alteran relaciones planta-dispersor en un paisaje fragmentado presume comprender como la fragmentación afecta las poblaciones de distintos dispersores (Chiarello 1999, Cullen et al. 2000), sus tamaños poblacionales (Peres y Palacios 2007), los cambios en su comportamiento (Ghazoul 2005) y los movimientos que pueden realizar en un paisaje fragmentado (Stoner et al. 2007). Todos esos aspectos son importantes para tratar de predecir posibles consecuencias para las semillas que dispersan.

Para los dispersores vertebrados, el efecto más inmediato de la fragmentación de hábitats es la reducción del área disponible (Fahrig 2003). Por una simple relación especie área es probable que muchas especies animales desaparezcan de los fragmentos reproduciendo patrones predichos por MacArthur y Wilson (1963) para las islas oceánicas. Hoy en día se sabe que la repuesta de la fauna a la fragmentación es variada y muchas veces compleja, dependiendo de factores como el efecto de borde, la conectividad entre parches aislados y del grado de alteración de la estructura del hábitat (Dalecky et al. 2002, Sodhi et al. 2004, Vargas y Simonetti 2004, Pires et al. 2005, Cane et al. 2006, Wayne et al. 2006). Aunque hay algunos ejemplos de especies que aumentan su abundancia en fragmentos o áreas perturbadas, la mayoría de las especies, al perder hábitat, tiene drásticamente reducida su población o llega a la extinción local. Esta reducción es especialmente severa en vertebrados de gran talla cuyo hábitat mínimo requerido para mantener una población viable no es comportado dentro de la mayoría de los paisajes fragmentados (Dalecky et al. 2002, Laurance 2005).

Para los mamíferos terrestres un paisaje fragmentado es casi catastrófico. Animales de gran talla como tapires (*Tapirus* sp), venados (*Mazama* sp y *Odecoileus* sp), y puercos (*Tayassu* sp) necesitan grandes áreas de forrajeo y tienden a desaparecer de parches pequeños y aislados de bosque (Chiarello 2000). Esos animales pueden actuar como dispersores de semillas, al menos ocasionalmente (Cadenasso y Pickett 2000). Por lo tanto, grandes mamíferos neotropicales juegan un importante papel ecológico relacionado a la dispersión de semillas y al mantenimiento de la diversidad de árboles, ya sea por dispersarlas propiamente o por eliminar selectivamente las semillas o plántulas no dispersadas (Asquith et al. 1997, Terborgh et al. 2008).

Existen respuestas más complejas de la comunidad de dispersores terrestres a la fragmentación. Un buen ejemplo de interacciones complejas entre defaunación y dispersores viene de los escarabajos coprófagos cuyo papel como dispersores de semillas es relativamente bien conocido. Esos Coleopteros (Familia: Scarabeideae) tienen reducidas sus poblaciones en sitios en donde vertebrados de gran talla fueron extirpados u ocurren en bajas densidades debido a la cacería, potencializando aún más la pérdida de servicios de dispersión en sitios defaunados y/o fragmentados (Wright y Duber 2001, Andresen y Laurance 2007). La cacería es un importante componente que agudiza los efectos negativos de la eliminación de la fauna decurrente de la fragmentación (Barlow et al. 2007). La fragmentación facilita el acceso de cazadores a grandes áreas de bosque que en general concentran sus presiones de cacería sobre grandes herbívoros/frugívoros (Chiarello 2000, Chiarello y de Melo 2001, Guariguata et al. 2002).

Por otro lado, hay poblaciones de dispersores que pueden aumentar su abundancia en paisajes fragmentados. Muchos murciélagos frugívoros de las subfamilias Stenodermatineae y Carollineae ocurren en altas densidades en paisajes fragmentados y/o perturbados (Bernard y Fenton 2003, Sampaio et al. 2003, Gorresen y Willig 2004, Bianconi et al. 2006, Montiel et al. 2006a). Esos murciélagos ejercen un reconocido papel como dispersores de semillas pequeñas de plantas muy abundantes en bosques fragmentados Neotropicales como *Piper* sp., *Cecropia* sp. y *Vismia* sp. (Godinez-Alvarez et al. 2002, Martinez-Garza y Gonzalez-Montagut 2002, Lobova et al. 2003, Mikich et al. 2003, Lopez y Vaughan 2004). Tomándose en cuenta que los murciélagos responden por gran parte de la abundancia de vertebrados en los Neotrópicos, es probable que su papel como dispersores de semillas aún esté subestimado. Es evidente que hay un sesgo en los estudios de murciélagos como dispersores de semillas pequeñas porque ya que esas son casi que exclusivamente las únicas colectadas en sus heces durante las capturas. Hay algunos reportes en la literatura, la mayoría careciendo de medidas experimentales, de especies de árboles con semillas grandes que son dispersadas por murciélagos (ver Mori y Lobova 2002). Por lo tanto, poco se sabe sobre el patrón de lluvia de semillas de gran tamaño generada por murciélagos frugívoros. Los murciélagos frugívoros son animales que se desplazan a grandes distancias en una única noche y pueden volar hasta 10km entre parches fragmentados en busca de alimento y contribuir significativamente para el flujo génico en poblaciones de árboles aisladas (Aldrich y Hamrick 1998, Montiel et al. 2006b).

Entre los pequeños roedores, las respuestas a la fragmentación en general contribuyen a un aumento en sus densidades. Se ha reportado para diversos bosques tropicales del mundo un incremento en la densidad de ratones en distintos órdenes de magnitud, dependiendo del tamaño del fragmento, de la disponibilidad de recursos alimenticios o de la densidad de depredadores (Bayne y Hobson 1998, Gascon et al. 1999, McCoy y Mushinsky 1999, Ringuet 2000, Pardini 2004, Vargas y Simonetti

2004, Saavedra y Simonetti 2005, Chung y Corlett 2006). Pequeños roedores actúan primariamente como depredadores de semillas pero eventualmente como dispersores debido a su hábito de enterrar semillas. Como consecuencia, varios estudios reportan aumentos en la depredación de semillas y de nidos artificiales que denotan que el reclutamiento de plántulas y la dispersión secundaria de las semillas probablemente sean afectados negativamente por incrementos en la densidad de pequeños mamíferos en paisajes fragmentados (Nupp y Swihart 1998, Stuart-Smith y Hayes 2003, Chauvet y Forget 2005, Githiru et al. 2005, Pardini et al. 2005, Pires et al. 2005)

Para las aves el escenario es un poco más delicado desde el punto de vista de los requerimientos del hábitat (Gascon et al. 1999, Van Houtan et al. 2007). Muchas familias de aves primariamente frugívoras como Ramphastideae, Cotíngideae y Cracideae comprenden animales de relativa gran talla y han sido más estudiados como dispersores de semillas (Galetti et al. 1997, Galetti et al. 2000). Sin embargo, por los mismos motivos que los mamíferos de gran talla, se ha reportado que sufren de las mismas limitaciones con respeto al requerimiento de área habitable y presiones de cacería que conducen a una reducción o hasta extinción local de sus poblaciones en paisajes fragmentados.

Por lo anterior, se puede concluir que la fragmentación afecta de manera variada a la comunidad de dispersores. No obstante, un patrón puede ser considerado relativamente constante: el efecto más contundente de la fragmentación se percibe sobre la fauna de gran talla, lo que probablemente afecta diferencialmente a la plantas con semillas más grandes desde el punto de vista de la probabilidad de dispersión de sus semillas (Fig. 1).

Fragmentación y poblaciones de plantas

La fragmentación del bosque aumenta la tasa de mortalidad de árboles en los bordes de los fragmentos con efectos perceptible hasta varios centenares de metros adentro del bosque (Ferreira y Laurance 1997, Laurance et al. 1998). La mayor parte de esta mortalidad de árboles se da en los estratos superior y emergente que comprenden árboles altos con copas frondosas y que producen gran cantidad de frutos que atraen una diversa gama de dispersores (Hanson et al. 2006). A largo plazo, esas especies tienden a ser sustituidas por especies pioneras y/o asociadas a estadios iniciales de sucesión que en su mayoría producen frutos y semillas pequeñas, atrayendo mayormente dispersores asociados a esos hábitats tales como murciélagos y pequeñas aves que son importantes consumidores de esos tipos de frutos (Galetti et al. 2003). Ello caracteriza un escenario en donde la alteración en la estructura y composición vegetal en dada porción del bosque podría generar cambios en la lluvia de semillas y posiblemente en el reclutamiento (Melo et al. 2006, Melo et al. 2007). Las consecuencias para otros árboles que permanecen en los bordes pueden ser importantes, dado que probablemente se altere la frecuencia y/o la calidad de las visitas de animales dispersores. La lluvia de semillas generada por cada grupo de dispersores puede ser influenciada por sus patrones de movimiento y por lo tanto por la distribución de los árboles que utilizan como recurso alimenticio (Kwit et al. 2004).

Algunas especies de árboles son consideradas como clave dentro del bosque por ter sus frutos consumidos masivamente por una inmensa gama de dispersores (Serio-Silva y Rico-Gray 2002). Es de esperarse que la lluvia de semillas bajo especies clave de árboles como las del género *Ficus* por ejemplo, sea significativamente más diversa que en otros sitios al azar dentro del bosque, dado que los árboles de esta especie atraen una inmensa gama de animales a sus copas en fructificación (Maycock et al.

2005, Wells y Bagchi 2005). Clark y colaboradores (2005) encontraron en Camerún que la lluvia de semillas colectada bajo especies de árboles que son dispersadas mayormente por monos son más ricas aunque menos abundantes, siendo el opuesto verdadero para la lluvia de semillas bajo especies de árboles dispersadas por aves. Por tanto, cambios en las proporciones de modos de dispersión en las comunidades vegetales de fragmentos de bosque tienen el poder de alterar patrones de lluvia de semillas. En la selva tropical Atlántica del Noreste de Brasil, la proporción de especies zoócoras en los bordes de un gran fragmento de bosque no se ve significativamente alterada con relación al interior del mismo (Oliveira et al. 2004). Sin embargo, esos autores encontraron claras diferencias con respeto al tamaño de los frutos y semillas en la lluvia de semillas estudiada en los en bordes e interior del fragmento, siendo que el borde carece de frutos y semillas grandes. Nuevamente, es probable que la lluvia de semillas en esas zonas sea distinta del interior del bosque, ya sea por el mismo cambio en las especies de árboles, ya sea por cambios en la frecuencia de visitas de dispersores (Galetti et al. 2003, Melo et al. 2006).

Aún considerando que no haya cambios significativos en la estructura de las comunidades vegetales en los fragmentos, la producción de frutos puede ser afectada por otros motivos como cambios en el éxito reproductivo de las plantas (Cascante et al. 2002, Fuchs et al. 2003). La producción de frutos en los fragmentos puede ser afectada por eliminación de polinizadores, reducción de frecuencias de visitantes florales o por cambios comportamentales de los polinizadores (Dick et al. 2003). En la isla de Barro Colorado, Panamá, la producción de frutos está correlacionada con la precipitación promedio anual e se han reportado eventos de sequía prolongada en donde hubo gran mortalidad de frugívoros por hambruna (Dalling et al. 1997, Barone 1998). Es probable que eventos de hambruna como esos sean recurrentes en los bosques tropicales y afecten de manera significativa la fauna residente en paisajes fragmentados potencializando los efectos sobre la dispersión de semillas.

Dispersión de semillas y regeneración en paisajes fragmentados.

Por toda la evidencia anteriormente presentada, parece razonable esperar que haya una real reducción en las tasas de dispersión de semillas en los paisajes fragmentados. Los cambios en la composición faunística, las alteraciones en la comunidad vegetal, las consecuencias genéticas de ello para los árboles, todo parece actuar en sinergismo para que el mantenimiento de la diversidad de árboles sea amenazado en esos hábitats (Tabarelli et al. 2004, Cramer et al. 2007). Por lo tanto, es posible y también necesario dar un salto conceptual con el intuito de entender como el mantenimiento de la diversidad de árboles en fragmentos de bosque es afectado por alteraciones en los patrones de dispersión de semillas.

El mecanismo de mortalidad denso-dependiente, promovido por Janzen (1970) y Connell (1971) puede actuar como promotor de diversidad en el bosque tropical al impedir que haya reclutamiento co-específico en las inmediaciones de los adultos reproductivos. Los patógenos y herbívoros al atacar diferencialmente a las semillas no dispersadas bajo la planta madre y las plántulas que fueron originadas de estas semillas, abren espacio para el reclutamiento de otras especies de árboles. Por lo tanto, escapar de esta “zona de riesgo” bajo la planta madre es crucial para el reclutamiento de nuevos individuos a través de las semillas. Así, la dispersión de semillas cobra un importante papel para la regeneración de las poblaciones de plantas a la vez que promueve y ayuda a mantener la diversidad de árboles en los bosques tropicales.

¿Qué consecuencias puede tener la eliminación de dispersores en los fragmentos de bosque para este mecanismo propuesto por Janzen y Connell? Algunos trabajos se han acercado a detectar ciertas alteraciones en el reclutamiento de plántulas resultantes de la no-dispersión de semillas, depredación diferencial de semillas y sus consecuencias para las poblaciones de plantas involucradas. Por ejemplo, Galetti y colaboradores (2006) consiguieron demostrar que los efectos combinados de la fragmentación y defaunación aumentan la depredación de semillas de palmas por insectos y reducen su dispersión, disminuyendo el reclutamiento de plántulas. En otro estudio, la distancia promedio de reclutamiento de plántulas de una especie de palma fue menor en fragmentos defaunados que en grandes masas de selva con fauna poco alterada (Lopez y Terborgh 2007). Esos autores argumentan que eso debe ser causado por el efecto combinado de la poca dispersión de las semillas y un probable relajamiento de la mortalidad denso-dependiente por eliminación de herbívoros que dejan de depredar las plántulas agregadas.

Además, es probable que la reducción en las tasas de dispersión resulte en efectos de distintas magnitudes en especies con distintos grados de susceptibilidad a la mortalidad denso-dependiente. Terborgh y colaboradores (2001) mostraron que la distancia de reclutamiento es naturalmente menor para especies más comunes en el bosque tropical del Perú. Esos autores argumentan que las especies más comunes de árboles son más resistentes a la mortalidad denso-dependiente y que por ello son naturalmente más abundantes. Sería razonable por lo tanto esperar que en fragmentos de bosque con bajas tasas de dispersión de semillas, esos sean florísticamente dominados por especies más comunes simplemente por la habilidad de estas en reclutar aunque sus semillas no sean dispersadas. Los tapetes monoespecíficos de plántulas reportados por Garcia-Guzman y Dirzo (2001) pueden ser una evidencia de ese proceso. Silva y Tabarelli (2000) llegan a argumentar que la probabilidad de extinción de árboles está asociada a la eliminación de dispersores y demuestran que 49% de los árboles del bosque atlántico de Brasil podrían extinguirse alargo plazo si las aves que dispersan sus semillas también lo fueron.

Entonces, si las tasas de dispersión de semillas son realmente reducidas en hábitats fragmentados, además si esta reducción se da diferencialmente según el tamaño de los propágulos, es probable que el factor “tamaño de semilla” pueda explicar, en parte, los patrones de reclutamiento y composición de plantas en fragmentos de bosque defaunado (Fig. 1). El tamaño de las semillas es asumido como una adaptación a gremios de dispersores pero también al hábitat preferencial de reclutamiento (Foster 1986). Especies de plantas con semillas grandes están asociadas a hábitats de bosque maduro y generalmente son el principal componente florístico del ensamble de plántulas en esos hábitats (Gentry 1982). Así, la eliminación de dispersores resultaría en una lluvia de semillas con “colas” más cortas, agregando las semillas cerca de la planta madre y sometiéndolas a una mayor probabilidad de mortalidad denso-dependiente, reduciendo así su reclutamiento específico (Cramer et al. 2007). Por otro lado, las especies de plantas pioneras con semillas menores necesitan más luz solar directa en la falta de cotiledones nutritivos. Esos hábitats con mayor incidencia de luz son representados por los claros cuya distribución en el tiempo y en el espacio es impredecible en un bosque maduro no perturbado (Brokaw 1985). Eso probablemente llevó a las especies pioneras a desarrollar semillas pequeñas y abundantes que resultarían probablemente en lluvias de semillas más abundantes y con colas más largas en comparación con las especies de semillas grandes. La amplia gama de dispersores capaces de transportar semillas pequeñas aumentaría la probabilidad de alcanzar más sitios ideales para el reclutamiento de esas especies en bosques que tienen, en promedio, apenas un 10% de su área como claros en el dosel (Brokaw 1985).

Sin embargo, en paisajes fragmentados los claros son más frecuentes, sobre todo en los bordes de los fragmentos y esas especies tienen chance de proliferar desproporcionadamente (Laurance et al. 2006). Si además se considera que los dispersores de estas especies pioneras siguen presentes en paisajes fragmentados, que por lo tanto sus colas de dispersión no se verían tan reducidas por la fragmentación, y que probablemente esas especies son más resistentes a la mortalidad denso-dependiente, entonces es de esperarse que proliferen en esos hábitats como se ha sugerido. El resultado sería una flora más homogeneizada con un sesgo hacia especies de semillas pequeñas.

El objetivo de esta tesis es determinar las consecuencias de la alteración en los patrones de dispersión de semillas para la regeneración del bosque en dos paisajes fragmentados, uno en el sureste de México y otro en Costa Rica. En la primera sección se evaluó como la fragmentación de la selva tropical subperemnifolia del estado de Quintana Roo, México, afecta los patrones espacio-temporales de la lluvia de semillas y el reclutamiento de plántulas de árboles. En el primer capítulo, se trató de evaluar como la fragmentación afecta la lluvia de semillas de árboles cuanto a: 1) densidad de semillas y especies por metro cuadrado; 2) patrón de agregación espacio-temporal; 3) proporción de semillas inmigrantes (dispersadas) y 4) como esos atributos se ven influenciados por la composición, estructura y diversidad funcional de la comunidad de árboles en fragmentos aislados y en un gran parche de bosque continuo no perturbado. En el segundo capítulo de ésta sección se evaluó en los mismos sitios, como la fragmentación afecta la composición y diversidad funcional del ensamble de plántulas. Traté de probar la hipótesis de que las especies de árboles con semillas grandes dispersadas por animales, como un grupo funcional, sufren una importante reducción en su reclutamiento debido a bajas tasas de dispersión ocasionadas por la eliminación de dispersores de gran talla en pequeños fragmentos defaunados.

En la segunda sección de esta tesis, que comprende el tercer capítulo de experimentación empírica, utilicé como modelo experimental una especie de murciélago frugívoro (*Artibeus watsoni*) para estimar el potencial de éste grupo de animales como dispersores de semillas grandes. Murciélagos frugívoros responden por una importante fracción de la biomasa animal de los bosques Neotropicales y pueden tener un importante papel en la dispersión de semillas de tamaño grande. Sin embargo un gran reto es encontrar sus perches de alimentación para poder estimar su real papel como dispersores de semillas de gran tamaño. Sin embargo, la especie de murciélago elegida tiene el hábito particular de construir refugios en hojas anchas de muchas especies de plantas del sotobosque, las que utiliza como sitios de alimentación. En la cuenca del río Sarapiquí, Costa Rica, utilicé una serie de fragmentos de bosque aislados (~20 ha) y dos grandes reservas (340 y 1500 ha) para estimar el real potencial de esos animales en dispersar semillas de gran tamaño (> 0.8 cm en este caso). Primero calculé el número observado y estimado de especies de semillas > 0.8 cm dispersadas por esos animales. Posteriormente comparamos como la densidad y riqueza de especies de semillas grandes encontradas debajo de los refugios fue afectada por el tamaño del parche. Finalmente, estimé la proporción de las especies más frecuentemente dispersadas por esos animales en ensambles de plántulas en el bosque maduro y en áreas de sucesión secundaria.

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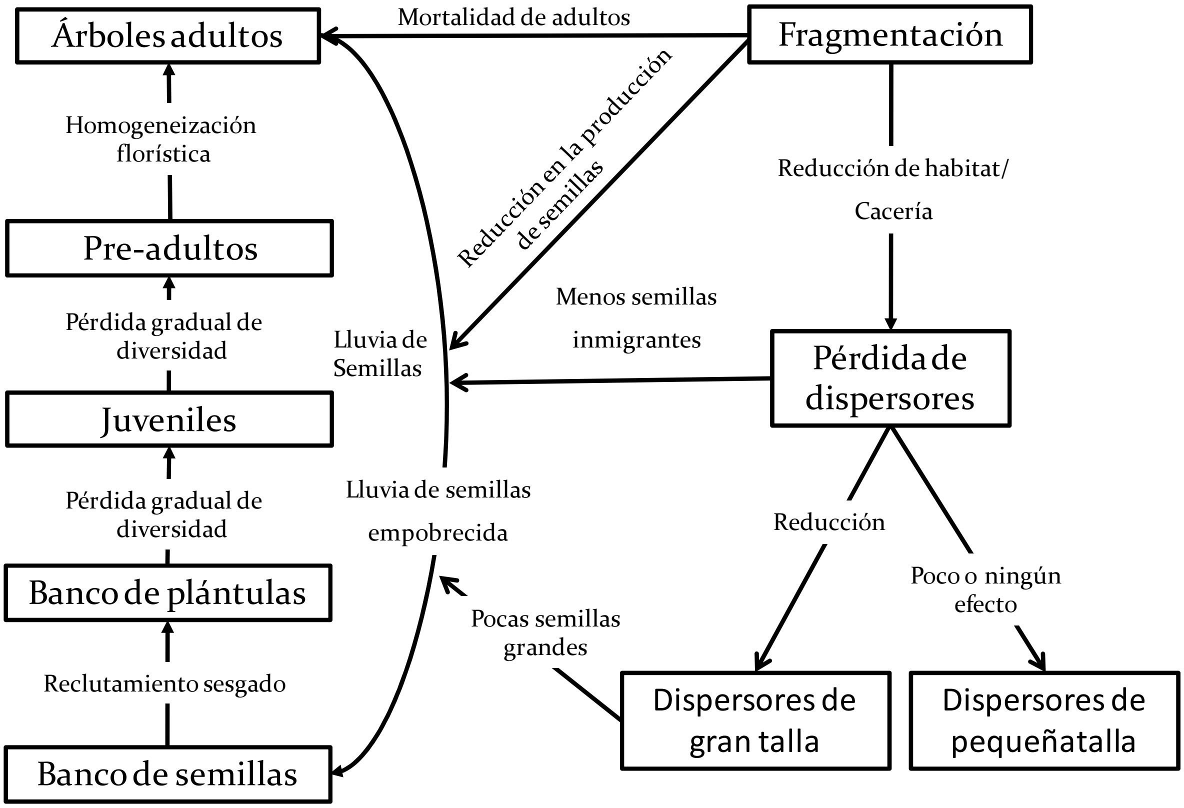

Figura 1. Diagrama de flujo conteniendo el marco conceptual hipotético de causas y efectos de la fragmentación del bosque sobre la dispersión de semillas y el reclutamiento de plántulas.

Sección 1

Efectos de la fragmentación sobre la lluvia de semillas y el reclutamiento de plántulas.

Spatiotemporal patterns of tree seed rain in a fragmented tropical forest of southern Mexico.

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Abstract

To predict future regeneration pathways of disturbed habitats is actually a major challenge for conservation purposes. In this study we test the hypothesis that functional attributes of seeds of tree species may drive differential responses seed rain to forest fragmentation and defaunation. We evaluated the tree seed rain for two consecutive years in a severe fragmented landscape in southern Mexico. Forest fragments were more sensitive to inter-annual variation in seed crop in comparison to continuous forest and small-seeded abitotically-dispersed seed species were the main group responding for such variation. Representation of immigrant seeds was higher in fragments < 3 ha but dispersed seeds were more abiotically-dispersed and clumped distributed in than in continuous forest. Yet, influence of vegetation structure on seed rain density was almost negligible but number of seeds was positive correlated with importance value of adults in all fragments. Finally, large-seeded species were more dispersal limited in small defaunated fragments and overall seed limitation in this forest patch size was mainly due to dispersal than to source limitation. Our results highlight that functional attributes of seed species together with composition of adult stands may help to predict different responses of seed deposition patterns to forest fragmentation that may be valuable for understand forest succession in fragmented landscapes.

Key words: Seed dispersal; Forest fragmentation; Defaunation; Landscape Management; Mexico.

Introduction

Forest fragmentation is known to cause shifts in tree species composition and disruptions on plant-animal interactions such as pollination and seed dispersal which may affect important traits of the seed rain (Guariguata and Pinard 1998, Melo et al. 2006). Patterns of seed input in the floor are the first step of forest succession and have a recognized importance in modeling forest structure, dynamics and composition (Harper 1977, Dalling et al. 1997, Hubbell et al. 1999). Functional attributes of tree species such as dispersal mode and seed size results in differential contributions to seed rain in terms of number of seeds and spatiotemoral distribution and may reflect differential responses of tree species to habitat modification (Melo et al. 2006). Therefore, to elucidate whether forest fragmentation affects spatiotemporal distribution of seed rain and the specific responses of functional groups of seeds may be key to improve knowledge on how forest succession undergoes in human modified landscapes (Zahwai and Augspurger 2006).

Spatiotemporal patterns of seed rain are particularly difficult to predict in undisturbed tropical forests where seed rain is highly heterogeneous with few composition overlap between sites, even nearly located (Hardesty and Parker 2002). This heterogeneity seems to be reduced in successional areas where seed rain is likely to be dominated by small-seeded species dispersed by abiotic means, small birds and bats (Arteaga et al. 2006, Standish et al. 2007). Furthermore, habitat preferences of seed dispersers and spatial distribution of seed sources are also important determinants of the likelihood seed arrival at a given forest site (Terborgh et al. 1996, Westcott et al. 2005). For example, forest edges seem to receive a biased seed rain in relation to forest interior habitats lacking large seeds that is strongly dominated by small-seeded abiotic-dispersed tree species (Melo et al. 2006, Melo et al. 2007). To assess seed rain in altered habitats may thus give important clues on future regeneration patterns of fragmented forests (Tabarelli and Peres 2002, Dosch et al. 2007).

Adults of vertebrate-dispersed tree species are likely to present a more spread spatial distribution in relation to more clumped pattern of abiotic-dispersed tree species (Seidler and Plotkin 2006). Patterns of movement of seed dispersers may thus be linked to composition and structure of tree community and patches with prevalence of zoochorous tree species may receive more visit of seed dispersers and present a more diverse seed rain than forest patches where dominates abiotic-dispersed trees with no attractive fruits for animals (Clark et al. 2001). Therefore, it is reasonable to expect that the vertebrate-dispersed component of the seed rain responds more prone to fragmentation and consequent elimination of disperser fauna than abiotic-dispersed species. Yet, among vertebrate-dispersed species, there should be functional groups (regarding seed size) that may be affected disproportionally by the extirpation of large mammals from isolated forest fragments that can disperse their seeds (Stoner et al. 2007, Wright et al. 2007). This turns to be extremely important since immigrant (dispersed) seeds may respond to ca. ~ 50% of all recruited seedlings per unit area of forest, even thought proportion of immigrant seeds is relatively smaller in the seed rain (Martinez-Ramos and Soto-Castro 1993, Webb and Peart 2001). Therefore, constrains in seed dispersal due to extirpation of vertebrates from forest fragments should be detected in the seed rain at a community-wide scale.

As a corollary, the fail in spread seeds over the forest (i.e. seed limitation) depend mostly on two components: seed production (i.e. source limitation) and how seeds are dispersed over the forest (i.e. dispersal limitation), thus limiting seedling recruitment and regeneration of tree populations (Clark 1998, Nathan and Muller-Landau 2000). Forest fragmentation is likely to affect both components of seed limitation by causing a fail in produce seeds due to disruptions in plants-pollinators interaction (Lobo et al. 2005, Newbery et al. 2006) and/or by reducing seed movement due to elimination of seed dispersers (Galetti et al. 2006, Stoner et al. 2007). Large seeds dispersed by large vertebrates are naturally more dispersal and source limited than small-seed species that conversely produce large seed crops dispersed by a wide range of the fauna. Therefore, differing seed sizes and dispersal modes are also important determinants for seed limitation and therefore, we may be able to identify differential responses to habitat fragmentation of trees differing in specific seed sizes (Clark et al. 2007).

In this study we evaluated the tree seed rain for two years in a fragmented landscape in Yucatan peninsula, southern Mexico that reflects also a defaunation gradient. We mainly report how spatiotemporal patterns of seed rain change with forest patch size. Specifically, we identify which functional groups of seeds are more likely to fluctuate in both spatial and temporal distribution and which are the main factors driving such changes in differing forest patch sizes. We also demonstrate differential changes in the components of seed limitation among seeds with contrasting dispersal modes and seed size categories. We than discuss future pathways of the tree community regeneration in defaunated forest fragments and its implications for forest management and conservation of the tree biodiversity in disturbed habitats.

Methods

Study site

The study took place in a severely fragmented area in the southeastern region of the Yucatan peninsula, state of Quintana Roo, Mexico. The zone is a communal land, called Ejido Palmar, (18° 27’N; 88° 35’W) which main economic activity is the plantation of sugar-cane what caused that a huge extension of plain lands was deforested for cropping (Fig.1a). However, in the western side of the Ejido, a large mass of continuous forest (~5,000 ha) remains with few or no disturbance. The remaining forest fragments are in small steeped hills where the predominant vegetation is medium semi-evergreen tropical forest, with canopy height of about 17 m (Sánchez-Sánchez and Islebe 2002). Forests of this region were previously exploited for extraction of “chicle” (gum) and selective logging of two species of timber wood, the caoba (*Swittenia macrophyla*) and cedro (*Cedrella fissilis*) which are almost locally extinct (Sánchez-Sánchez and Islebe 2002). Disturbance history in this forest goes back to ancient Mayan settlements which are thought to have caused severe modifications in the natural environment during pre-Colombian ages. However, such landscape represents a good opportunity for assessing changes in the seed rain traits in different fragment sizes and compares them to the continuous forest. All forest remnants in the region were isolated by the same time period (1970's) and the surrounding matrix is exactly the same (sugar-cane). Small scale disturbances such as wood consumption for fuel are still a usual practice of the local human inhabitants. Also, subsistence hunting is an important source of animal protein for local people and most fragments receive frequent incursions of poachers (F. Melo Pers. Obs.).

Seed rain surveys

To assess effects of forest fragmentation on seed rain patterns, we selected a series of forest remnants of different sizes that reflect different degrees of both changes in disperser fauna composition and vegetation structure. Small fragments category (hereafter SF) comprised two forest patches < 3 ha each distant about 4 km; medium-sized fragments (MF) comprised two isolated patches of 22 and 26 ha respectively (< 30 ha), distant 3 km between each other. In a large fragment of 640 ha (LF) and a continuous forest patch (CF) we established two independent sites separated by 1 km. In each fragment and independent site we demarcated five 20 x 20 m ($400m^2$) tree-plots > 100 m distant between each other where all trees > 5 d.b.h. (diameter at breast height) were identified to the finest possible taxonomic level and measured respecting d.b.h., height and crown area. We adopted the cut-off of 5 cm d.b.h. because many tree species in this forest are reproductive before reaching 10 cm. An importance value (IV) for each tree species was calculated by summing the relative basal area, the relative frequency and the relative abundance of each tree species per forest patch size (similar approach used by Hardesty and Parker 2002).

Within each of the tree-plots, we established a group of three $1m^2$ seed traps summing an area of 30 m^2 of seed traps per category of fragment size where seed rain was estimated during 24 months in regular intervals of ca. 15 days from January 2006 to December 2007. Each seed trap was made of 1 x 1 m plastic mesh ($1m^2$); 1 mm aperture and framed with galvanized wire. All traps were suspended 1.2 m above the forest floor and attached to adjacent trees with plastic cords (see Melo et al. 2006). Seed traps were placed more or less centered in tree-plots with an average distance of 4.87 m between each other

(Fig. 1).

Because life-forms other than canopy and understory trees were not taken in account in the tree-plots, we excluded from the analysis all lianas, herbs, and palm seeds. Tree seeds were collected and stored in individualized plastic bags per seed trap, counted, measured and identified. Afterwards, seeds were assigned into two dispersal modes, namely: vertebrate-dispersed (arils and pulp) and abiotically-dispersed (wings, plumes or any structure suggesting abiotic means of dispersal). Also, we divided seeds according to three categories of seed size measured in its longest length as follows: small seeds (< 6 mm); medium-sized seeds (6 - 14 mm) and large seeds (> 14 mm). Categories of seed size followed the mean ± 1 SD (standard deviation) of the distribution of seed species according to their specific longest length (see Melo et al. 2006). By comparing the list of seeds collected within each seed trap with the list of trees species inventoried in the correspondent tree-plot, we could assign the origin of each seed as: a) non-dispersed or local seeds, or; b) dispersed or immigrant seeds. All seeds collected in a given seed trap where a cospecific adult was also inventoried within the same tree-plot were considered as non-dispersed or local seed. On the other hand, seeds were considered as immigrant or dispersed, when no coespecific adult was inventoried within the correspondent tree-plot. By this way we could confidentially assign for each single seed if it was dispersed or simply dropped from any reproductive adult in the vicinity of seed traps (see Webb and Peart 2001). However, this estimation method of seed dispersal is likely to be conservative for one main reason: truly dispersed seeds of a given tree species may fall into a given seed trap in a tree-plot where a cospecific adult tree is present, hence, being considered non-dispersed.

Limitation measurements

We calculated seed limitation and its components: source limitation and dispersal limitation at 1m^2 scale (seed-trap) for each tree species per forest patch size. We used fundamental seed limitation as defined by the proportion of seed-traps failing to receive a seed over the entire sampling period (Nathan and Muller-Landau 2000). Source limitation consists in the expected proportion of seed-traps that would not receive seeds if these were randomly distributed over seed traps (here defined as a stochastically distribution of seeds; see Nathan and Muller-Landau 2000). Dispersal limitation is the relation between the proportion of traps that received seeds over the expected proportion of trap-hits under a random distribution of the seed rain (Nathan and Muller-Landau 2000). Therefore, limitation measurements may theoretically vary from 0 – 1; meaning no limitation and, maximum limitation respectively. Despite such approach is commonly used at a single-species scale, we also used in our analyses limitation measures pooled within both dispersal modes and categories of seed size.

Statistical analyses

Spatiotemporal variation in the traits of the tree seed rain was evaluated with respect to mean number of seeds and seed species at seed-trap (1m^2) scale after log(x + 1) transformation of data. We used repeated measures analysis of variance (repeated measures ANOVA) to assess temporal variations on mean number of seeds and seed species per forest patch size, within categories of seed size and dispersal mode. Another question of interest was how seeds are distributed in space and time at different forest patch sizes. For this, we used Pearson’s correlation between the relative abundance of seeds per seed-trap in each year of sampling and in each category of forest patch size. Furthermore, simple Morisita index of dispersion was used to measure spatial aggregation of seeds at each category of forest patch size per year. We used log-likelihood tests (G test) to compare proportion of immigrant seeds belonging to each seed size categories and dispersal modes among forest patch categories. Tree community structure per fragmentation treatment was reduced to two compound variables resulted from a principal component analysis (PCA) on the tree-plot level for the following variables: 1) number of tree stems; 2) number of tree species; 3) basal area and 4) sum of tree crown areas. Afterwards, MANOVA was used to assess differences among forest fragments respecting vegetation structure. To account for the effect of vegetation structure on mean number of all seeds as well as the subset of immigrant seeds we used general linear models (GLM) after log(x + 1) transformation of data on number of seeds with PC1-2 as factors. Possible relationships between species-specific abundance of seeds and importance value of adult species were tested by simple linear regression per habitat. We also used one-way ANOVA followed by Tukey *post-hoc* test to assessed effects of forest fragmentation on limitation measures for seed species pooled by categories of seed size and dispersal mode. For these last analyses we excluded seed species represented by a single seed due to uncertainty in calculate limitation measures. Finally, through multiple linear regressions we wanted to know whether source or dispersal limitation mainly respond for variation of fundamental seed limitation at each forest patch size. All statistical analyses we made using JMP version 7.

Results

Spatiotemporal structure of seed rain

Tree seed rain in this landscape totaled 16,623 seeds of 43 tree species after 24 months of samplings (Appendix 1). Mean number of tree seeds and species varied across fragments and year of sampling being almost four times more abundant in 2006 than in 2007 at the landscape level (repeated measures ANOVA; Year; $F_{1,116}$ = 107.92; p < 0.0001). Such decline in seed crop from 2006 to 2007 was stronger in most forest fragments than in continuous forest (Fig. 2; $F_{3,116}$ = 4.1444; p = 0.0079). Additionally, a significant decrease in mean number of tree seed species was found for all habitats (Fig, 2; $F_{3,116}$ = 6.4257; p = 0.0005). However, despite reduction in seed crop, CF experimented only a minor decrease in mean density of tree seed species and maintained the same absolute number of tree seed species from 2006 to 2007 (Fig. 2). These discrepancies were mostly due to a severe between-year reduction in the abundance of small-sized (< 0.6 cm) abiotic-dispersed seeds in all habitats (Appendix 1; Table 1). Spatial distribution of seeds was found to be aggregated in all habitats with very high values of Morista index of dispersion (I_d) mainly when seed crop was higher (Table 1). The exception was the SF where seed fall in 2007 though smaller, was more clumped than in the previous year. Also, seed rain was significantly more spatially congruent between years in MF and SF (Person's r = 0.50; 0.52 respectively; all $p < 0.05$) than in LF and CF (r = -0.03 and 0.35; all p >0.05; respectively). This means that in MF and SF traps that received highest proportion of seeds in 2006 also tended to receive many seeds in 2007 while such relationship was not found for CF and LF.

Influence of seed dispersal on seed rain

Immigrant seeds accounted for only 11.7 % of all seed sampled in CF; 9.5 % in the LF, 7.3% in MF and up to 20.7% of all seeds in SF (G = 294.18, df = 3; p < 0.0001). However, vertebrate-dispersed seeds accounted for more than 90% of all immigrant seeds in CF while this proportion was strongly reduced to less than 60% in isolated forest fragments (G = 171.68; df = 3; p < 0.0001; Fig. 3). Regarding categories of seed size, contribution of large seeds to the immigrant component of the seed rain was very similar in CF, LF and SF, all around 27%, but was strongly reduced to 13.7% in MF (G = 250.04; df = 6; p < 0.0001; Fig. 3). Otherwise, contribution of medium-sized seeds tended to increase with decreasing forest patch size, while representation of small seeds tended to decrease directly with forest patch size (Fig. 3).

Yet, spatial distribution of immigrant seeds tended to be more clumped in forest fragments than in continuous forest patch. In LF, MF and SF, dispersed seeds that reached up to two seed traps during the entire sampling period, represented 19.5; 12.3 and 32.1 % of all immigrant seeds respectively, while in CF these values responded for only a very small proportion of 3.1 % of all dispersed seeds (G = 179.88; df = 3; p <0.0001). For example in one of the < 3 ha fragments, a single seed-trap located under a palm leaf used as feeding roost site by bats, received 106 (84%) of the 125 immigrant large seeds collected during the study for this category of patch size.

Effects of vegetation structure on seed rain

All vegetation parameters assessed within tree-plots were reduced to two compound factors by principal components analysis that explained up to 84% (eingenvalues > 1.0) of the variance for those variables. First PC (PC-1) comprehended a positive relationship between sum of basal area and sum of crown areas. Second PC (PC-2), resulted to be formed by a positive association between number of tree stems and number of tree species. As a result, CF and LF had more tree biomass than MF and SF ($F_{3,116} = 21.80$; $p < 0.0001$) and PC-2 was not significantly different among habitats. The influence of vegetation structure on the density of both numbers of local and immigrant seeds was negligible for all habitats but for SF that presented a positive associations of mean density of local zoochorous and abiotic-dispersed seeds with PC-2 and PC-1 respectively (Table 3). Regarding tree species composition, NMDS grouping method accused that CF and LF are significantly different from MF and SF in terms of tree species composition. Notwithstanding, composition of adult tree stands seem not to influence composition of seed rian since partial Mantel test did not uncover any significant interaction between adult tree and tree-seed species composition for none of the categories of forest patch size (results not shown). The unique vegetation parameter influencing the species-specific abundance of seeds in each forest patch size was the importance value (IV) of each adult tree species (Fig. 4).

Limitation measures across forest fragments

Tree seed species in seed rain was highly seed, source and dispersal limited in all forest patch sizes with no significant difference at the community level. Abiotic-dispersed seeds did not vary in any limitation measure across fragments (Table 3), but vertebrate-dispersed seeds were more dispersal limited in MF and SF than in any other category of forest patch size ($F_{3,73} = 2.7326$; $p = 0.0498$). Small and medium-sized seed species did not differ significantly among fragments but large-seeded species tended to be more dispersal limited in SF than in any other category of forest size ($F_{3,27} = 3.7512$; $p = 0.0226$). We found the in CF, seed limitation was mainly explained by source limitation while dispersal limitation contributed with only 36% of the explained variance (Table 4). The same occurred for the LF and MF where both source and dispersal limitation was positively correlated with seed limitation but with a smaller contribution of the former, (32% and 25% respectively) to the fundamental seed limitation. However, an inverse trend was found for SF, where variation explained by the dispersal limitation component was greater (73%) than that of source limitation (27%; Table 5).

Discussion

Forest fragmentation significantly affected several aspects of the spatiotemporal distribution and functional traits of the tree seed rain. We demonstrate that forest fragments were more sensitive to inter-annual changes in seed crop with detectable consequences for the average seed input and number of seed species per unit area of forest. Likewise, other studies in tropical forests over the world have reported strong differences in seed rain patterns in relation to disturbance levels and/or successional stage of the forests (e.g. Loiselle et al. 1996, Grombone-Guaratini and Rodrigues 2002). Small-seeded tree species dispersed by abiotic means mostly accounted for the reduction in the abundance and richness of tree community seed rain. Seed rain in forest fragments < 30 ha and < 3 ha was strongly spatiotemporal homogeneous while in the large fragment (640 ha) and continuous forests spatial distribution of seeds tended to be more unpredictable among years. Vegetation structure proved to be of less concern to explain average seed input of immigrant seeds but had a slightly significant effect in predict number of both abiotically and vertebrate-dispersed only in fragments < 3 ha. Finally, despite most tree seed species was strongly seed limited among all forest patch sizes; source, rather than dispersal limitation was the main seed limitation component for all habitats but small fragments < 3ha, where the main factor driving seed limitation was the dispersal limitation.

Our results match some patterns described before in the literature such as patchiness and between-years variation in the seed fall (Clark et al. 2001, Clark et al. 2005, Gomez-Aparicio et al. 2007). However, we could identify two types of responses of seed rain to forest fragmentation never reported before that are likely to have important implications for the understanding of forest regeneration in fragmented forests. The first, have to do with inter-annual reduction of seed crop that was higher in intermediate-sized forest fragments (640 ha; 75% reduction and < 30 ha; 85% reduction) than in continuous forest and small fragments (58.5 and 57.5% reduction in seed fall respectively). This may likely to be related to supra-annual reproduction of some tree species in such fragments since many seed species failed in hit traps 2007 (Appendix 1) resulting in a strong decline in both total and mean density of seed species (Muller-Landau et al. 2008). Otherwise, in continuous forest sites the reduction in seed fall of 58% did not affected the total number of tree seed species and presented only a slightly reduction in mean density of seed species and maintained the same total number of species in the seed rain. Fragments < 3 ha did not present a high relative decline in density of seeds but did so for number of seed species. The second important trend identified for the tree community seed rain is related with spatiotemporal distribution of seeds. In the two smaller categories of forest fragments, traps receiving a higher relative abundance of the seed rain in the first year tended to do so in second year, suggesting that seed input in such fragments may depend mainly on local seed production. Conversely, spatiotemporal distribution of seed rain in the 640 ha and continuous forest was unpredictable and this may be probably due to both supra-annual seed production of some tree species and the role of seed dispersers in moving seeds in those habitats.

Immigrant seeds may respond for a significant fraction of recruited seedlings in other Tropical forests (Webb and Peart 2001). Therefore, the proportions reported for this study (7.3-20.7%) may have a disproportionate impact in seedling recruitment of the forest.

However, they tended to be deposited in huge amounts in up to two seed traps in all categories of forest fragment size while in continuous forest those seeds were more widespread over the forest. Therefore, the per seed recruitment is likely to be reduced in relation to more spread patterns of dispersal due to density-dependent mortality (Terborgh et al. 2008). Additionally, since almost half of the immigrant seeds in forest fragments were comprised by species dispersed by abiotic means, seedling recruitment in those forest fragments may be biased to a stronger representation of such functional attribute in relation to continuous forest (Seidler and Plotkin 2006). This pattern may be explained to high seed limitation known for the majority of tropical tree species, that tend to be higher for larger seeds (Nathan and Muller-Landau 2000). However, the likely impoverished disperser’s fauna in small forest fragments may exacerbate dispersal limitation for the overall community of zoochorous seeds, especially for those species with seeds > 1.4 cm which depend on large-bodied vertebrates, that in our study site are almost completely absent from fragments smaller than 30 ha. Otherwise, abiotically-dispersed species did not presented any detectable pattern in relation to limitation measures suggesting that fragmentation do not affect significantly this functional group of seeds in such parameters.

Based on these results, the likely regeneration pathway for defaunated forest fragments is the gradual detriment of those species that lost their main seed dispersers (Cordeiro and Howe 2003, Cramer et al. 2007a, Cramer et al. 2007b). The trade-off: colonization-competition in such habitats may thus be biased toward favoring those ‘colonizer’ (small seeded) species that will enhance their success over the best ‘competitors’ (large-seeded) species is small defaunated forest fragments. On the long term, this may lead to an increasing homogenization of the flora of the fragments toward tree species that maintain large crops of small seeds easily spread over the forest (Laurance et al. 2006). Consequences for forest regeneration may be further perceived in old aged secondary forests that seems to be bunged in intermediate successional stages (Santos et al. 2008). For example, old edges of a 3.500 ha forest fragment of the northeastern Brazilian Atlantic forest failed to receive many medium-to large-seeded tree species after a year of seed rain sampling (Melo et al. 2006). In this same forest fragment, forest edges despite aged ~ 70 years have almost no adult trees or early-recruits of many large-seeded species still present in the interior of the fragment (Oliveira et al. 2004, Melo et al. 2007). Therefore forest regeneration undergoing in human-disturbed habitats may be deficient and may need to be assisted by seeking ways to enhance seed movement of those species lacking seed dispersers in order to improve their recruitment rates. This would permit small forest fragments to keep the entire functional diversity of tree community, improving their biological value in retain biodiversity at a landscape scale, thus justifying their conservation.

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Table 1. Functional attributes and a measure of spatial distribution of the tree seed rain in two consecutive years at the Ejido Palmar, southern Mexico.

Parameters of the seed rain	Continuous forest		Large fragment (640 ha)		Medium-sized fragments (< 30 ha)		Small fragments (< 3ha)	
	2006	2007	2006	2007	2006	2007	2006	2007
Abiotic-dispersed	39.1 ± 93.1	2.1 ± 3.1	9.1 ± 13.9	1.4 ± 3.1	174.9 ± 243.1	3.6 ± 13.3	16.8 ± 25.1	1.1 ± 2.8
Vertebrate-dispersed	30.0 ± 46.1	25.7 ± 42.4	94.7 ± 193.6	24.1 ± 40.4	44.9 ± 66.3	26.1 ± 44.6	35.2 ± 40.2	19.9 ± 37.8
Seeds > 1.4 cm	6.6 ± 11.5	3.1 ± 7.3	14.1 ± 16.2	8.4 ± 10.9	7.1 ± 11.1	1.3 ± 2.4	6.8 ± 17.5	8.9 ± 32.5
Seeds 06-1.4 cm	15.6 ± 37.1	13.7 ± 11.1	26.3 ± 26.2	10.6 ± 11.6	38.1 ± 44.9	26.9 ± 28.9	34.6 ± 35.7	13.1 ± 15.8
Seeds < 0.6 cm	47.5 ± 92.9	12.4 ± 41.8	63.4 ± 197.9	6.6 ± 36.5	174.8 ± 242.3	3.2 ± 13.3	10.4 ± 24.2	0.03 ± 0.18
Morista index of dispersion (Id)	3.001	2.942	4.299	3.282	2.216	1.894	1.649	3.853

Table 2. Values of t-ratios of the general linear models for the influence of vegetation structure on mean density of all seeds and the subset of immigrant seeds per dispersal mode at Ejido Palmar, southern Mexico.

Model terms	All seeds/m2		Immigrant seeds/m2	
	Abiotic-dispersed	Vertebrate-dispersed	Abiotic-dispersed	Vertebrate-dispersed
Continuous Forest				
PC-1 (Basal area + Crown area)	1.45	0.37	-0.38	-0.06
PC-2 (Tree species + Tree stems)	-0.63	0.96	-0.67	-1.66
Large fragment (640 ha)				
PC-1 (Basal area + Crown area)	-0.30	0.04	1.29	0.50
PC-2 (Tree species + Tree stems)	-0.08	2.03	0.06	0.67
Medium-sized fragments (< 30ha)				
PC-1 (Basal area + Crown area)	-1.66	-0.77	-1.23	-1.00
PC-2 (Tree species + Tree stems)	0.10	-0.22	0.32	0.95
Small fragments (< 3 ha)				
PC-1 (Basal area + Crown area)	-1.20	**3.51 ****	0.53	1.16
PC-2 (Tree species + Tree stems)	**2.80****	-0.70	0.35	-2.01

** $p < 0.01$

Table 3. Values of limitation measures pooled by dispersal mode and categories of seed size for each of the categories of forest patch size at the Ejido Palmar, southern Mexico.

Limitation measures (angular transformed)	Continuous forest	Large fragment (640 ha)	Medium-sized fragments (< 30 ha)	Small fragments (< 3 ha)
Abiotic-dispersed seeds				
Seed Limitation	1.10 ± 0.10 a	1.07 ± 0.12 a	1.10 ± 0.14 a	1.01 ± 0.11 a
Source Limitation	0.56 ± 0.24 a	0.44 ± 0.36 a	0.65 ± 0.39 a	0.20 ± 0.29 a
Dispersal limitation	0.86 ± 0.08 a	0.91 ± 0.04 a	0.95 ± 0.13 a	0.99 ± 0.09 a
Vertebrate-dispersed seeds				
Seed Limitation	1.08 ± 0.03 a	1.14 ± 0.05 a	1.18 ± 0.03 a	1.14 ± 0.03 a
Source Limitation	0.64 ± 0.09 a	0.78 ± 0.10 a	0.84 ± 0.07 a	0.62 ± 0.08 a
Dispersal limitation	0.86 ± 0.03 a	0.86 ± 0.04 a	0.89 ± 0.03 a	**1.01 ± 0.04 b**
Seeds > 1.4 cm				
Seed Limitation	1.11 ± 0.06 a	1.04 ± 0.11 a	1.12 ± 0.06 a	1.13 ± 0.07 a
Source Limitation	0.74 ± 0.15 a	0.63 ± 0.20 a	0.80 ± 0.12 a	0.54 ± 0.17 a
Dispersal limitation	0.81 ± 0.07 a	0.80 ± 0.06 a	0.84 ± 0.04 a	**1.12 ± 0.11 b**
Seeds 0.6-14 cm				
Seed Limitation	1.12 ± 0.04 a	1.19 ± 0.06 a	1.18 ± 0.04 a	1.14 ± 0.04 a
Source Limitation	0.72 ± 0.12 a	0.88 ± 0.12 a	0.82 ± 0.10 a	0.65 ± 0.11 a
Dispersal limitation	0.87 ± 0.04 a	0.91 ± 0.03 a	0.90 ± 0.03 a	0.96 ± 0.04 a
Seeds < 0.6 cm				
Seed Limitation	0.94 ± 0.04 a	1.11 ± 0.07 a	1.18 ± 0.13 a	1.03 ± 0.11 a
Source Limitation	0.12 ± 0.12 a	0.53 ± 0.29 ab	**0.76 ± 0.14 b**	0.31 ± 0.22 ab
Dispersal limitation	0.92 ± 0.04 a	0.91 ± 0.04 a	1.00 ± 0.11 a	0.94 ± 0.10 a

Numbers in the same line followed by different letters are significantly different at $p < 0.05$ by Tukey *post-hoc* test.

Table 4. Multiple linear regressions for the effect of the two components of the fundamental seed limitation for each category of fragment size and continuous forest at the Ejido Palmar, southern Mexico.

Habitat	df	Sum of squares	F-ratio	P	Adjusted R^2
Continuous Forest					
Source limitation	1	0.628	119.420	<0.0001	0.906
Dispersal limitation	1	0.359	68.340	<0.0001	
Large fragment (640 ha)					
Source limitation	1	0.899	180.270	<0.0001	0.951
Dispersal limitation	1	0.431	86.460	<0.0001	
Medium-sized fragments (< 30ha)					
Source limitation	1	0.988	413.640	<0.0001	0.964
Dispersal limitation	1	0.341	142.860	<0.0001	
Small fragments (< 3 ha)					
Source limitation	1	0.195	9.610	0.007	0.698
Dispersal limitation	1	0.522	25.764	<0.0001	

List of Figures

Figure 1. Study site located at the Ejido Palmar reserve, State of Quintana Roo in southern México. The fragments and continuous forest used for experiments (a) and demonstrative illustration of tree-plots and seed traps (b) are shown.

Figure 2. Mean (bars) and total number (line-scatter) of seeds and seed species in 2006 (black bars and circles) and 2007 (grey bars and circles) in four categories of forest patch size at the Ejido Palmar, Mexico.

Figure 3. Proportion of seeds within each dispersal mode and categories of seed size among all immigrant seeds sampled at the Ejido Palmar, Mexico.

Figure 4. Linear regressions between importance values of adult trees and total seeds for continuous forest (black circles); 640 ha fragments (open circles); < 30 ha fragments (black triangles) and < 3 ha fragments (open triangles). Each symbol corresponds to a single species.

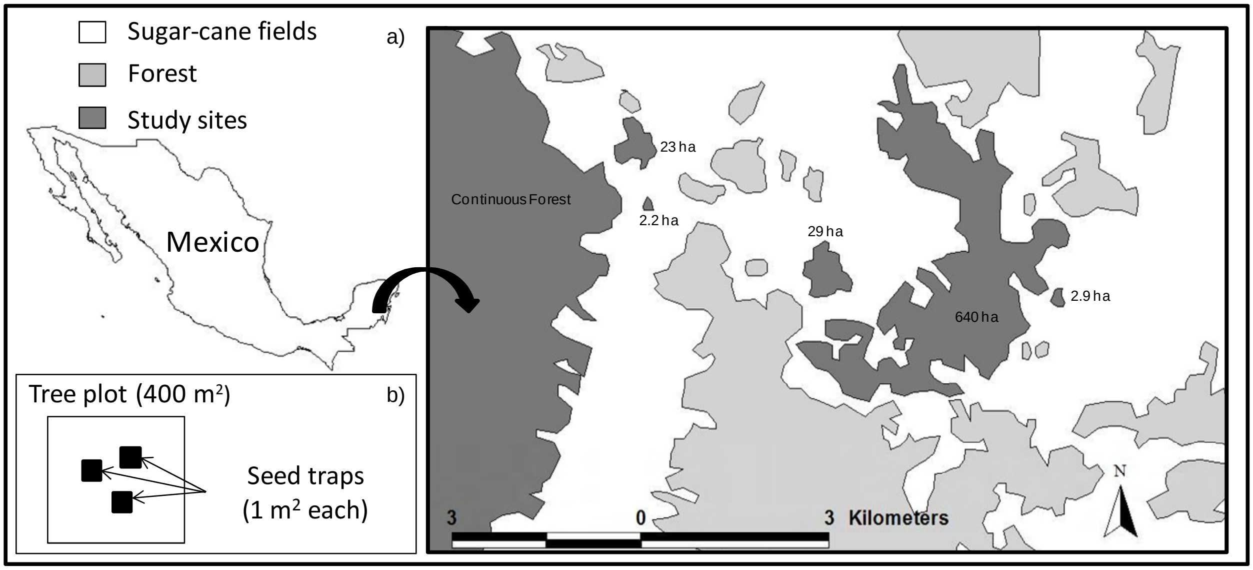

Sugar-cane fields
Forest
Study sites
a)
Mexico
Continuous Forest
23 ha
2.2 ha
29 ha
640 ha
2.9 ha
3
0
3 Kilometers
N
Tree plot (400 m²)
b)
Seed traps
(1 m² each)

Figure 1.

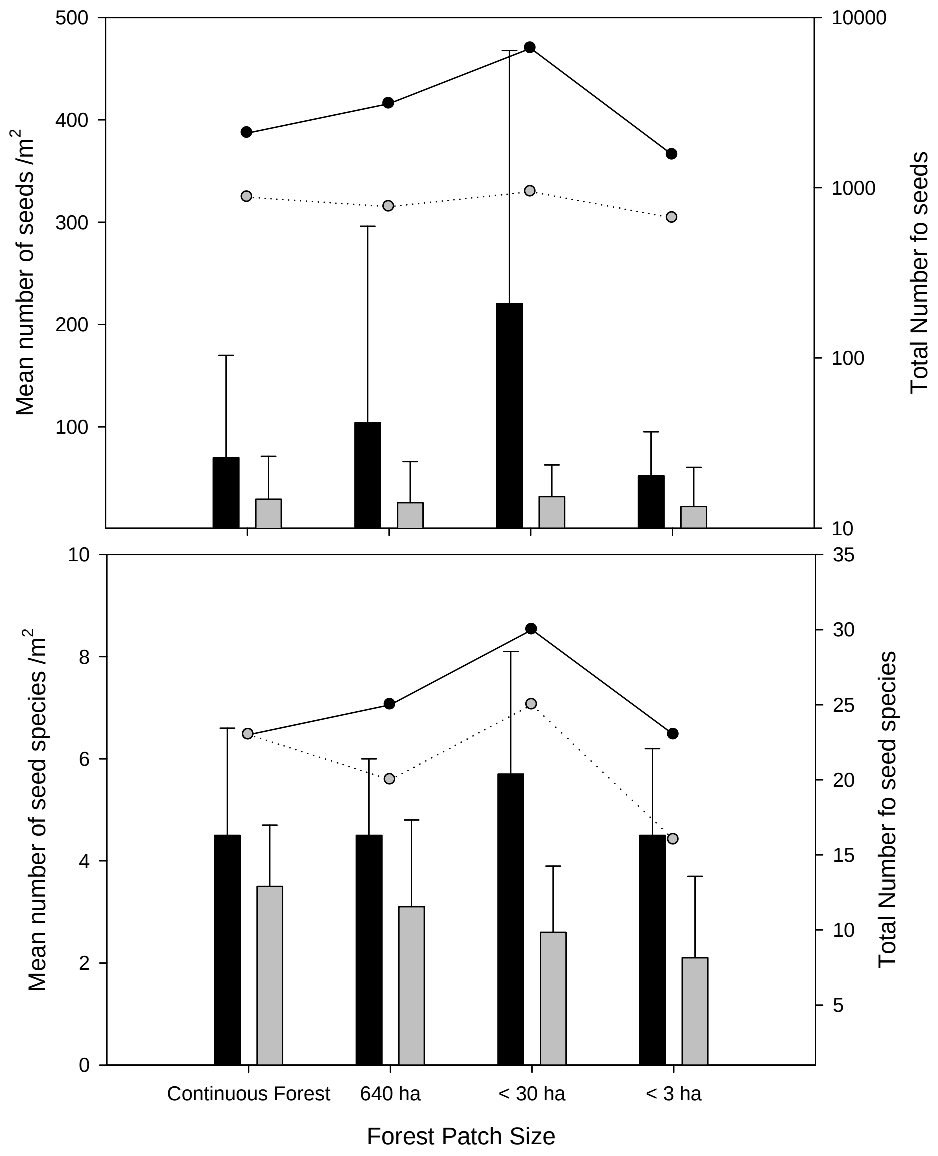
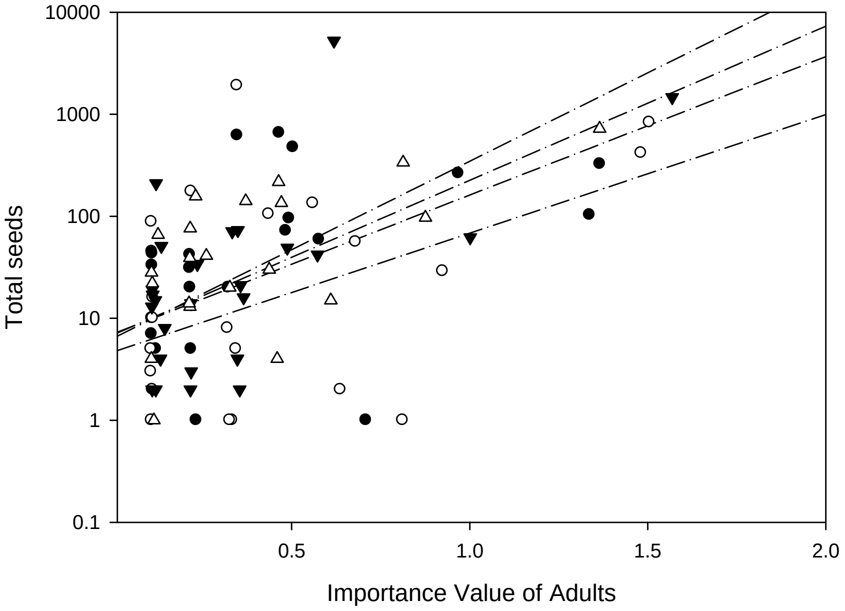

500
400
300
200
100
Mean number of seeds /m^2
10000
1000
100
10
Total Number fo seeds
10
8
6
4
2
0
Mean number of seed species /m^2
35
30
25
20
15
10
5
Total Number fo seed species
Continuous Forest
640 ha
< 30 ha
< 3 ha
Forest Patch Size

Figure 2.



Total seeds
10000
1000
100
10
1
0.1
0.5
1.0
1.5
2.0
Importance Value of Adults

Figure 3.

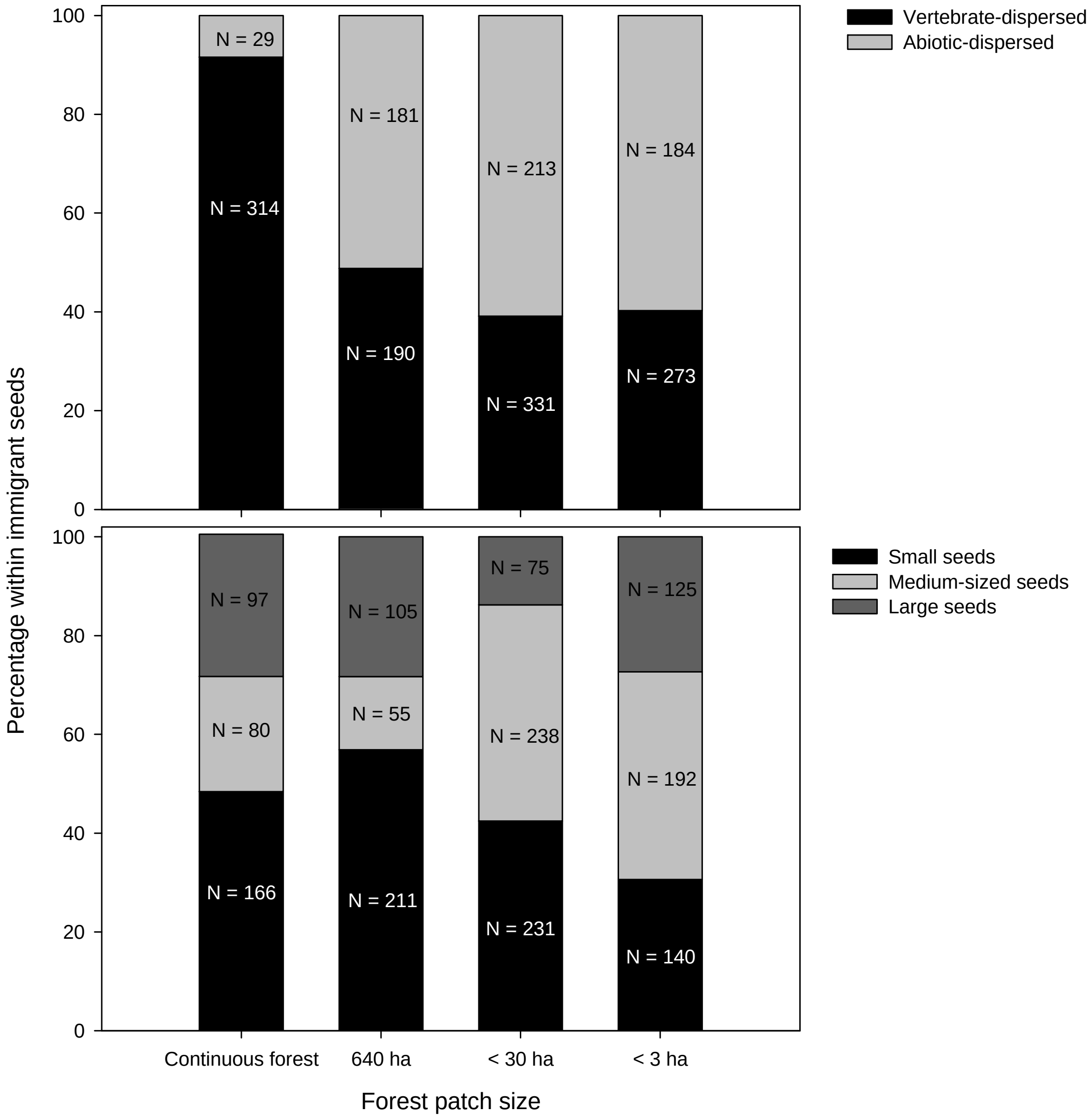

Vertebrate-dispersed
Abiotic-dispersed
Small seeds
Medium-sized seeds
Large seeds
Percentage within immigrant seeds
100
80
60
40
20
0
N = 29
N = 314
N = 181
N = 190
N = 213
N = 331
N = 184
N = 273
N = 97
N = 80
N = 166
N = 105
N = 55
N = 211
N = 75
N = 238
N = 231
N = 125
N = 192
N = 140
Continuous forest
640 ha
< 30 ha
< 3 ha
Forest patch size

Figure 4.

Appendix 1. List of species with number of seeds collected in each year with number of traps reached (trap hits) for the entire sampling period per forest patch size at Ejido Palmar, southern Mexico.

Species	Family	Seed size	Dispersal mode	Continuous Forest			Large Fragment (640 ha)			Medium-Sized Fragments (< 30ha)			Small Fragments (< 3ha)		
				2006	2007	trap hits	2006	2007	trap hits	2006	2007	trap hits	2006	2007	trap hits
Acacia gentlei	Leguminoseae	M	abio	0	3	2	0	0	0	0	0	0	21	18	3
Brosimum alicastrum	Moraceae	G	zoo	0	0	0	0	0	0	0	21	4	0	0	0
Callyptranthes pallens	Myrtaceae	M	zoo	3	0	1	3	0	1	2	0	1	12	0	3
Casearia nitida	Flacourtiaceae	M	zoo	29	2	6	1	3	2	190	20	13	76	0	9
Casimiroa tetramerea	Rutaceae	G	zoo	0	5	3	42	5	6	0	1	1	28	0	1
Coccoloba reflexiflora	Polygonaceae	P	zoo	0	0	0	0	0	0	16	0	2	0	0	0
Coccoloba spicata	Polygonaceae	M	zoo	194	69	7	10	19	5	11	31	6	26	4	6
Cordia sp	Boraginaceae	M	zoo	0	0	0	9	0	1	0	0	0	0	0	0
Cupania belizensis	Sapindaceae	M	zoo	22	20	7	0	0	0	0	0	0	0	1	1
Diospyros salicifolia	Ebenaceae	G	zoo	5	54	9	18	87	12	65	6	10	19	198	10
Eugenia sp	Myrtaceae	M	zoo	11	9	3	1	1	2	0	4	3	8	5	5
Ficus sp.	Moraceae	P	zoo	0	0	0	0	0	0	15	0	1	0	0	0
Hamphea trilobata	Malvaceae	M	abio	0	0	0	1	0	1	10	3	3	1	0	1
Jatropha gaumeri	Euphorbiaceae	G	abio	23	10	3	0	0	0	0	0	0	0	0	0
Lisiloma latisiliqua	Leguminoseae	M	abio	42	61	15	93	41	12	10	3	6	324	13	12
Lonchocarpus xull	Leguminoseae	M	zoo	1	0	1	0	1	1	0	0	0	4	0	2
Malmea depresa	Annonaceae	M	zoo	0	10	3	10	0	1	2	15	4	0	15	5
Nectandra salicifolia	Lauraceae	G	zoo	20	0	10	85	3	10	13	5	7	20	0	8
Pouteria campechiana	Sapotaceae	G	zoo	0	0	0	5	0	3	16	0	5	27	14	9
Pouteria reticulata	Sapotaceae	G	zoo	0	0	0	0	0	0	3	0	1	0	0	0

Protium copal	Burseraceae	M	zoo	1	0	1	0	0	0	1	1	2	0	0	0
Simauba glauca	Simarubaceae	G	zoo	0	5	3	1	7	3	0	2	1	0	4	4
Swartzia cubensis	Leguminoseae	G	zoo	0	1	1	0	1	1	0	0	0	0	0	0
Sideroxylon foetidisimo	Sapotaceae	G	zoo	0	0	0	0	0	0	8	0	4	0	0	0
Thevetia gaumeri	Apocynaceae	G	abio	2	0	1	1	0	1	0	0	0	1	0	1
Thouinia paucidentata	Sapindaceae	P	abio	654	3	15	175	0	9	5142	98	26	156	1	12
Trichilia americana	Meliaceae	P	zoo	0	1	1	0	0	0	2	0	1	0	0	0
Trophis racemosa	Moraceae	M	zoo	28	0	6	0	0	0	17	0	2	26	0	3
Zygia stevensonii	Leguminoseae	G	zoo	0	0	0	1	0	1	0	0	0	0	0	0
Allophylus sp	Sapindaceae	P	zoo	35	10	10	14	0	5	24	0	6	22	0	8
Anona primigenia	Annonaceae	M	zoo	0	7	4	11	5	6	5	0	2	12	2	3
Bursera simaruba	Burseraceae	M	zoo	121	204	30	606	224	30	802	665	30	466	256	30
Ceiba schotii	Bombacaceae	M	abio	0	0	0	0	1	1	43	8	7	0	0	0
Celtis trinervia	Euphorbiaceae	M	zoo	0	0	0	1	0	1	9	10	4	1	0	1
Exotea diphyla	Sapindaceae	G	zoo	0	0	0	0	2	1	1	0	1	0	0	0
Luehea speciosa	Tiliaceae	P	abio	469	5	9	5	0	2	34	0	2	1	0	1
Metopium brownei	Anacardiaceae	M	zoo	15	28	9	33	23	13	7	7	6	61	80	9
Pimenta dioica	Myrtaceae	M	zoo	0	0	0	11	1	6	33	40	12	0	0	0
Sideroxylon salicifolia	Sapotaceae	P	zoo	268	353	9	1708	200	9	4	0	2	135	0	5
Spondias mombim	Anacardiaceae	G	zoo	93	2	10	1	0	1	61	1	17	74	23	10
Vitex gaumeri	Verbenaceae	G	zoo	56	16	12	268	148	23	44	5	11	37	29	1
Cochlospermum vitifolium	Cochlospermacea	P	abio	0	0	0	0	0	0	9	0	1	0	0	0
Aegiphylla sp.	Verbenaceae	M	zoo	1	0	1	0	0	0	0	0	0	0	0	0

Reduced recruitment of large-seeded seedlings in small rain forest patches of Southern Mexico.

Running title: seedling recruitment in small forest patches

Key words: Fragmentation; Regeneration; Seed dispersal; Seedling recruitment; Tropical forest.

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ABSTRACT

Understanding biological dynamics of fragmented rain forests is a major task to assess possible successional trajectories in disturbed habitats. In this study we test the hypothesis that elimination of large-bodied seed dispersers rather than shifts on adult tree communities may strongly affect both taxonomic and functional composition of seedling assemblages in a fragmented landscape of Southern Mexico. In six forest patches (2.3 - 5,000 ha) we inventoried disperser's fauna and collected a total of 653 tree seedlings that were classified according to dispersal mode, categories of seed size and whether they were local (*i.e.* from dropped seeds) or immigrant (*i.e.* from actively-dispersed seeds). Number of medium- to large-bodied seed dispersers (> 1 kg) decreased with forest patch area, but around 50% of all seedlings were considered as immigrants irrespective to forest area. Although adult tree communities did not vary significantly among forest patches in terms of both taxonomic and functional composition, large-seeded seedlings tended to be low-represented within the smallest forest patches (< 30 ha). We conclude that forest fragmentation and defaunation may seriously reduce dispersal rates of large-seeded tree species (> 1.4 cm length), negatively affecting regeneration pathways of small defaunated forest patches.

INTRODUCTION

Understanding the biological dynamics of tropical forest patches is a fundamental challenge for biological conservation, particularly if we are to maintain or increase biological diversity in altered landscapes. For plants, both physical and biotic disruptions resulted from forest fragmentation can lead to population declines and reduced species richness (Fischer & Lindenmayer 2007) affecting as well, the ecological interactions among plant and animals (Terborgh *et al.* 2001). Among other threats, remaining plant communities in isolated forest patches can be negatively affected by habitat loss, isolation, edge-effects and defaunation (Arroyo-Rodriguez *et al.* 2007, Laurance & Peres 2006). Is a common sense, however, that synergisms among the mentioned fragmentation-derived effects results in significant shifts on plant communities that should be perceivable in early life stages such as seedlings (Laurance *et al.* 2006, Tabarelli *et al.* 2004).

Forest fragmentation exposes fauna to hunters that can strongly deplete, or even locally extinguish populations of their preferred game species (Corlett 2007). For example, larger-bodied vertebrates such as cracids, monkeys and terrestrial ungulates are more prone to be extirpated from forest fragments due to habitat loss and/or poaching (Chiarello 2000). Currently, vertebrate populations are severely reduced or have become locally extinct over large regions in the Neotropics affecting many biological interactions in which they are involved (Ceballos & Ehrlich 2006, Terborgh *et al.* 2001). Elimination of seed dispersers reduces seed movement and may strongly alter both taxonomic and functional composition of regenerating stands in ‘empty forests’ (Terborgh *et al.* 2008). Although relatively few seeds are dispersed away from parent plants in tropical forests (Martinez-Ramos & Soto-Castro 1993), recruitment probability appears to be strongly influenced by seed dispersal as approximately half of the seedlings originate from immigrant (*i.e.* actively dispersed) seeds

(Webb & Peart 2001). Otherwise, local seeds (*i.e.* those dropped from parent plant) are more prone to herbivore and pathogen attack succumbing shortly after recruitment (Janzen 1970, Wyatt & Silman 2004).

There is a plenty of seed dispersal strategies within tropical tree species that depend on vertebrates of different body masses as illustrated by the astonishing six orders of magnitude (0.001-100 g) regarding seed mass of tropical species (Foster 1986). Large-seeded species are associated with mature forest environments, comprise a great part of plant species richness in tropical forests and are supposed to depend on larger frugivores to have seeds successfully dispersed (Terborgh & Nuñez-Iturri 2006). Large ungulates, peccaries, monkeys and many large birds may act as effective seed dispersers for large-seeded plants but also as important seed predators (Ickes *et al.* 2001, Stoner *et al.* 2007). Their disappearance from disturbed landscapes should therefore, reduce both seed predation and dispersal rates of large-seeded plants giving place to contrasting predictions on the future flora of defaunated forests (Silva & Tabarelli 2000, Wright *et al.* 2007).

In this sense, Silva and Tabarelli (2000) suggested that up to 34% of the flora of the Brazilian Atlantic forest, mainly comprised by large-seeded species, will become locally or regionally extinct due to elimination of large frugivorous birds. Alternatively, recent studies argued that altogether: 1) the lack of large-bodied seed predators and 2) biased seed predation by small rodents towards smaller seeds would constitute an ecological release that favors the prevalence of large-seeded species in defaunted forests (Dirzo *et al.* 2007, Wright *et al.* 2007). For example, non-dispersed (local) seeds may form monospecific carpets of seedlings in the absence of large-bodied seed predators (Dirzo & Dominguez 1995). These seedlings, however, have little or no probability of survival in the long term due to attacks of pathogens or other species-specific invertebrate herbivores (Janzen 1970).

Therefore, though reduced seed-predation rates may theoretically favor large-seeded plants, the stronger “bottleneck” for successful recruitment should be the effective seed dispersal away from parent plant (Howe & Miriti 2004).

Following this rationale, impoverished disperser fauna in fragmented landscapes may reduce recruitment of zoochorous seedlings in general (Cordeiro & Howe 2001). However, some small-bodied seed dispersers such as frugivorous birds (Uezu *et al.* 2005) and bats (Gorresen & Willig 2004) are known to persist in relatively large abundances in fragmented landscapes, thus keeping some dispersal service mainly for small-seeded plants. Alternatively, it is reasonable to expect that large-seeded species would experience a stronger decline in dispersal rates due to disappearing large frugivores from small forest patches (Cramer *et al.* 2007). As a consequence, few large-seeded seedlings are expected to recruit in small, defaunted forest remnants, affecting composition of the regenerating stands of these habitats. A feasible manner to test such predictions is to quantify the representation of seedlings of differing sizes and how many of them are originated from local (non-dispersed) or immigrant (dispersed) seeds in forest patches of differing areas (Webb & Peart 2001).

In this study, we first test whether functional composition (*i.e.* representation of differing dispersal modes and categories of seed size) of both adult tree and seedling communities vary with forest patch area in the Yucatan Peninsula, Mexico. Secondly, we explore whether taxonomic compositions of adult tree and seedling communities are correlated and whether they vary with forest patch area. Thirdly, we correlate forest patch area with defaunation level and test if there is a dispersal mode or seed-size related reduction in the proportion of immigrant seedlings with decreasing forest patch area. We finally discuss the possible causes and consequences of a biased seedling community in small isolated forest patches and its consequence for the successional trajectories in highly disturbed landscapes.

MATERIALS AND METHODS

Study site

The study was carried out in the communal lands of the Ejido Palmar (18° 27’N; 88° 35’W), Yucatan Peninsula, Mexico (Figure 1a). Deforestation accompanied the establishment of sugar-cane plantations in the mid 1970’s. However, a large forest patch (> 5,000 ha) was left in the western zone of the Ejido (Figure 1a) that is contiguous with other communal lands of less intensive uses than sugar-cane cultivation. The remaining forest patches are in small hills where the predominant vegetation type is semi-deciduous tropical forest, with canopy height of about 17 m (Sánchez-Sánchez & Islebe 2002). All forest patches in the region suffered selective logging prior to establishment of sugar-cane and were isolated in the same time period (1970's). Wood collection for fuel is practiced in the area, and most forest patches receive frequent incursions by hunters.

To test our hypotheses we selected five completely isolated forest fragments ranging from 2.3 to 640 ha plus the large forest patch of 5,000 ha (Figure 1a). These areas were selected among many isolated forest patches in this landscape because they did not present signs of recent fires that could strongly influence our results. In addition to area (in hectares), we measured for each forest patch, the degree of isolation – expressed as the proportion of forested area in a 1-km radius from the border of each forest patch. For purposes of analyzes we attributed the value of 1 (*i.e* no isolation) to the 5,000-ha forest patch because of its large size and the fact that it is not completely isolated. Since degree of isolation and forest patch area were correlated ($r = 0.83$; N = 40; $p < 0.01$), we opted to use forest patch area as explanatory variable in our analyses.

Defaunation

In each forest patch we conducted faunal inventories to know whether patch size is related to the defaunation level. For this, 30 h of visual censuses per site were conducted during dry and wet season of 2006 using linear transects ranging from 200 to 1,500 m length according to patch size as described by Chiarello (1999). Second, we placed 5 camera-traps for seven consecutive days in dry and rainy season at each experimental site arrayed 100 m apart in transect lines. We registered the presence/absence of any large-bodied terrestrial vertebrates (> 1 kg; plus < 1 kg *Sciurus* spp.) that might act as seed dispersers and three of the largest birds: *Ramphastus sulfuratus* (Keel-billed Toucan); *Ortalis vetula* (Plain Chachalaca) and *Tityra semifasciata* (Tityra). Since sightings were rare we also recorded footprints, carcasses and reports of encounters made by local hunters. Because of the low number of records and the inability to conduct more extensive faunal surveys in the forest sites we could not use abundance or density of any vertebrate group in our analyses. Alternatively, we are confident on the presence/absence of the selected species in each forest site as a three-year study by two of the authors was conducted in the same forest sites with 15-day interval visits with no new record of any vertebrate species than that reported here. Based on this information we estimated the number of species present at each site.

Adult tree and seedling surveys

We randomly established five 400 m^2 (20 x 20 m) sampling plots within each forest fragment ranging from 2.3 to 29 ha. In both the 640-ha and 5,000-ha patches we sampled two areas separated by at least 1 km where five 400 m^2 were set, totaling ten sampling plots for these forest patches. To avoid spatial scale effects of sampling forest patches of very contrasting sizes we standardized the arrangement of each group of five sampling plots based on the average distance among sampling stations set in the smallest forest fragment sampled (2.3 ha). Within each sampling plot, all trees larger than 5 cm diameter at breast height (d.b.h.) were mapped and identified to species or genus level. The cutoff criterion of 5 cm d.b.h. (rather than the usual 10 cm criterion) was chosen because of the large number of tree species that may reach maturity under 10 cm d.b.h. in this type of forest (Sánchez-Sánchez & Islebe 2002). Within each 400 m^2 sampling plot we established three smaller (9 m^2; 3 x 3 m) plots centered at three equidistant points (~ 5 m) within which we collected all seedlings 10-50 cm height (Figure1b).

Since we did not consider life forms other than trees within the 400 m^2 sampling plots, we restricted our analysis to tree seedlings that were identified to the lowest possible taxonomic level. We classified adult trees and tree seedlings into two contrasting dispersal modes: vertebrate-dispersed vs. abiotic-dispersed; and into three seed-size categories according to their longest length: small-seeded, < 0.6 cm; medium-sized, 0.6-1.4 cm; and large-seeded species, > 1.4 cm. Dispersal mode was assigned to each tree seedling species according to characteristics of the fruits of each species; whereas the categories of seed sizes were chosen based on the frequency distribution of the mean specific longest seed length of seeds collected in a seed rain study carried out at the same site as proposed by Silva and Tabarelli (2000).

Tree seedlings were also classified as “immigrants seedlings” or “local seedlings” based on whether they originated from dispersed (*i.e.* actively dispersed away from parent plant) or local seeds (*i.e.* dropped from the parent tree) respectively. For this, we compared the list of all tree species within each of the 400 m^2 tree-plots with the list of tree seedlings collected within it. We considered a seedling as originating from a dispersed seed (hereafter “immigrant seedling”) only when no conspecific adult was present within the sampling site (see Webb & Peart 2001). When both seedling and adult of the same species were present at the same 400 m^2 sampling plot we considered all seedlings of such species as “local”. This method for the estimation of seed dispersal is likely to be conservative if: 1) a seedling of a given species *a* may have not came from the seeds dropped from a conspecific adult *a* within the sampling site, but from seeds of another adult of the species *a* distant from the sampling site; and if 2) we were unable to exclude males of dioecious tree species from the potential parent list. Otherwise, overestimation of seed dispersal would occur if seedlings sampled were actually originated from seeds dropped from adults that have died, thus not being considered in the parent plant list. Also, frequent adult tree species would be less likely to be considered as immigrant than rare tree seedling species. Even considering such methodological constrains, this approach proved to be effective to account for the importance of seed dispersal in other tropical forests (see Martinez-Ramos & Soto-Castro 1993, Webb & Peart 2001).

Statistical analysis

Because of the small number of forest patches we opted to use each sampling plot (N = 40) as a replication unit for our analysis (pooling the three 9m^2 seedling plots). To be confident of the independence of sampling plots, we used a Mantel test to detect spatial autocorrelation of data sets of both adult tree and seedling communities. Spatially correlated data sets were analyzed pooling all sampling plots within the same forest patch or within each 1km separated sites within the two largest forest patches. To assess changes in the functional composition (dispersal mode and seed size) of both tree and seedling assemblages we used GLMM’s (Generalized Linear Mixed Models) where fixed effects were: patch area, dispersal mode and categories of seed size as well as second level interaction among these terms. To control for unavoidable pseudoreplication effects of our study design, we set sampling plots nested within each forest patch as a random effect in the models. Residual maximum likelihood method (REML) was used to separate variances of both fixed and random effects of the models (Grafen & Hails 2002). Partial Mantel test was used to test if there was a correlation between similarity matrices of adult tree and seedling communities and their interaction with geographical distance. Afterwards, we used non-metric multidimensional scaling (NMDS) based on Bray – Curtis abundance based similarity index to generate a two-dimension representation of both adult tree and seedling community (Dufrene & Legendre 1997). To test for the effects of patch area on tree and seedling species composition we used NMDS dimensions as response variables in general linear mixed models (GLMM) with forest area as fixed effects and sampling plots nested within forest patches as a random factor. All response variables (excepting NMDS values) as well as forest patch area were $\log_{10}(x+1)$ transformed prior to analyses. Adequacy of each GLMM was tested by checking studentized residuals against a normal distribution through the Shapiro-Wilk test. We used Pearson´s correlation to know whether recorded number of medium-to large mammal species and large birds and forest patch area were correlated. Generalized linear models for binomial data sets (Crawley 2007) were used to assess effects of forest patch area on: 1) proportion of immigrant seedlings; 2) proportion of each dispersal mode within immigrant seedlings and 3) proportion of each category of seed size within zoochorous immigrant seedlings. We made all analyses using JMP version 7 and Primer-E version 5 (Clarke & Warwick 2001, SAS 2007).

RESULTS

In all sites pooled, we found a total of 967 tree stems (> 5cm d.b.h.) from 93 species and 38 families, and 653 seedlings belonging to 63 tree species and 30 families. Mantel test detected a small but significant spatial autocorrelation of data sets for adult trees ($\rho = 0.19$; $p < 0.05$) what impeded us to use sampling sites as replicates for the analyses on tree community (note degrees of freedom reported in the analyses). However, no spatial autocorrelation was found for seedling community ($\rho = -0.05$; $p = 0.20$). Average number of seedling individuals and species (at 27 m^2 scale) as well as tree stems and species (at 400 m^2 scale) was not related to forest patch area (Table 1). Categories of seed size and dispersal mode were strongly correlated for both seedlings and trees (Table 1). Abiotically-dispersed seedlings were mainly small seed-sized while vertebrate dispersed seedlings were mostly medium to large seed-sized (Figure 2). Functional traits of adult tree and seedling communities were differentially influenced by forest patch area. First, neither seedling nor adult tree communities varied with forest patch area in terms of average density of individuals or species belonging to differing dispersal modes (Table 1). Otherwise, a significant interaction between forest patch area and categories of seed size was evidenced for the seedling community, but not for adult trees (Table 1). This interaction was mainly due to a marked decrease in mean number of large-seeded seedlings with reducing forest patch area, while in the two smallest categories of seed size the average number of individuals and species were not related to forest area (Figure 3).

Data sets of adult tree and seedling communities were not correlated in terms of species composition (Mantel's $\rho = 0.003$; $p = 0.97$), neither was their interaction with geographical distance among sampling sites (trees*seedlings/distance; $\rho = 0.01$; $p = 0.46$). Furthermore, ordination method (NMDS) for the seedling community accused a discrete grouping pattern (negative values of MDS-2; Figure 4a). This method did not uncover any evident grouping pattern for adult tree community, however (Figure 4b). Forest patch area significantly influenced species composition of seedling community as suggested by the regression analysis between axis-2 of the NMDS for seedlings and the logarithm of forest patch area (Figure 5). However, no influence of patch area was detected for any axis of the NMDS for tree community (all $F_{1,6} < 1.1$; $p > 0.32$).

Faunal inventory suggests that forest patch area is negatively related to the number of medium to large-bodied mammals and large birds that may act as seed dispersers ($r = 0.86$; N = 6; p = 0.02; Table 2). Forest patches smaller than 30 ha lacked many of the large frugivores common to the study region and the two smallest forest patches lacked almost all large frugivores excepting for a common species of large bird (Table 2). However, proportion of immigrant tree seedlings, irrespective to dispersal mode or seed size, was not related to patch area (L-R Chi-square = 0.02; df = 1; p = 0.88; Table 3). Also, proportion of each dispersal mode within immigrant seedlings did not vary with patch area (L-R Chi-square =1.19; df = 1; p = 0.28; Table 3), what does not support the hypothesis that zoochorous seedlings, in general, are low represented within small/defaunated forest remnants. However, proportion of zoochorous large-seeded seedlings (> 1.4 cm length) decreased with patch area (L-R Chi-square = 14.26; df = 1; p < 0.01), comprising around half of immigrant seedlings in the largest patches (640 and 5,000 ha) while their contribution was not greater than 25% of all zoochorous seedlings within forest sites smaller than 30 ha (Table 3). No correlation was found between species-specific abundance of adults and the respective number of seedlings considered as immigrant ($r = 0.21$; N = 43, p = 0.19) thus, our classification of seedlings as immigrant or local was not affected by species-specific abundance of adults.

DISCUSSION

Our results suggest that seedling assemblages in small defaunated forest patches are strongly biased towards a low representation of large-seeded seedlings. This may have caused the observed variation in both taxonomic and functional composition of seedling assemblage that significantly varied with forest patch area. Such pattern could not be attributed, however, to shifts on adult tree species composition across forest patches as our data suggest no drastic changes in adult tree community among sites. Although forest patch area and defaunation are correlated and thus confounded in our analyzes the elimination of large-bodied seed dispersers from < 30-ha forest patches should be the most important factor influencing seeding assemblages. The stronger evidence for such a conclusion is the reducing representation (in both absolute and relative terms) of large-seeded tree seedlings originated from immigrant seeds with decreasing forest patch size. Although small forest patches still harbor large-seeded tree species as adults they lacked many of the large frugivores of the region suggesting that low dispersal rates of large-seeded species may be responsible for the observed shifts in tree seedling assemblages.

Habitat loss and fragmentation are known to cause severe changes in tree communities mainly caused by edge effects (Laurance & Peres 2006). Shade tolerant species; emergent trees; dispersed by vertebrates and pollinated by specialists seem to comprise the most affected groups of tree species in fragmented forests (Girão 2007, Santos *et al.* 2008). However, adult tree community in the studied sites did not vary with forest patch area in terms of taxonomic or functional composition while seedling community did so, suggesting that effects of habitat disturbance should be more insidiously in the early successional stands than in adult trees. This is reasonable as relatively recent history of fragmentation of this landscape (1970´s) may be insufficient to cause perceivable changes in adult tree communities in the studied site, although in other tropical forests a few years are sufficient to cause important shifts on adult tree stand (Laurance *et al.* 2002). Alternatively, tropical forests of this region evolved under a periodical, large-scale canopy disturbance regime caused by pre-Colombian human settlements and hurricanes (Islebe *et al.* 1996, Sánchez-Sánchez & Islebe 2002). Hurricanes are frequent in the Yucatan Peninsula and may have hit the studied area prior to forest fragmentation (Hjerpe *et al.* 2001). This may have influenced actual tree species composition, increasing taxonomic similarity of tree stands in a regional scale by promoting massive recruitment of light-demanding tree species after canopy opening. For example, *Bursera simaruba* (Burseraceae), a typical pioneer tree species of this region, comprised around 20% of all adult tree stems irrespective to forest patch area (unpubl. data) but was never found as seedlings. In resume, there are little or no evidences to suggest that shifts in adult tree community may have caused the observed changes in the seedling assemblage we documented in this study.

Throughout the tropics, defaunation has been proposed as an important driving force of changes in seedling communities (Cordeiro & Howe 2001, Rodriguez-Cabal *et al.* 2007). Few studies, however, demonstrated how impoverished communities of seed dispersers (specifically lacking large-bodied frugivores) may drive biased changes on seedling assemblages of fragmented forests (but see Cordeiro & Howe 2001, 2003). In our study site, large mammals seemed to be almost completely extirpated from patches smaller than 30 ha, except for spider monkeys (*Ateles geoffroyi*) recorded in a 22-ha patch and only one common large bird species, chachalaca (*Ortalis vetula*) registered within the < 3-ha patches. Several old-growth forest species common in our study area, including small forest patches, hold seeds larger than 1.4 cm in length (*e.g., Manilkara zapota*, *Brosimum* *alicastrum*, and *Vitex gaumeri*) but were absent as seedlings in forest patches smaller than 30 ha. Several large-seeded tree species, including those mentioned above are important components of the diet of the two largest monkeys of Central America whose dispersal service is decaying together with declining populations their species in fragmented landscapes (Cristobal-Azkarate & Arroyo-Rodriguez 2007, Gonzalez-Zamora *et al.* 2009). Also, large-seeded tree species are adapted to germinate and grow in shaded environments, they are associated with large trees, typical of mature forest whose fruit production represent a crucial food supply for many frugivore species (Foster 1986). The lack of large-bodied seed dispersers in defaunated forest patches should, therefore, contribute to the reduced taxonomic and functional diversity of the remaining flora documented for forest fragments (Laurance *et al.* 2006, Oliveira *et al.* 2004).

Contrary to our results, some recent studies argued that large-seeded tree species may be favored in defaunated forests by the reduced seed predation (Dirzo *et al.* 2007, Wright *et al.* 2007). But like our results, other studies have documented that an important limiting factor for seedling recruitment should be the seed dispersal, thus dispersal failing may significantly deplete seedling recruitment (Galetti *et al.* 2006, Wyatt & Silman 2004). The ecological release of large-seeded species has been suggested based on the preference of small rodents for small seeds and/or on the predominance of large-seeded species within seedling communities of some Central American defaunated forests (Dirzo *et al.* 2007, Wright *et al.* 2007). However, robust conclusions on whether exists such an ecological release of large-seeded species must consider whether seedlings originate from dispersed or local seed and thus are susceptible to differential survival probability. Our results showed that immigrant seedlings respond for 41-61% of all recruits, what correspond to similar values reported by Webb and Peart (2001) in Malaysia as an evidence for the importance of seed dispersal to the community-wide seedling recruitment.

Limitations of this study rely on the small number of tree seedlings collected and on possible misclassifications of seedlings as immigrant or local. The number of tree seedlings was surprising low – 653 seedlings in 1080 m^2 – in comparison to other tropical forests (*e.g.* Benitez-Malvido 1998). Limited number of seedlings reduces power of the analyses but the statistical methods we employed were sufficiently robust to exclude the probability of a pattern resulted from a sampling artifact. Classification of seedlings as immigrants or locals might be definitely confident only with genetic analyses that are unfeasible in a community study. The method of comparing species lists of adults and seedlings has been successfully used elsewhere (Martinez-Ramos & Soto-Castro 1993, Webb & Peart 2001) and we have no reasons to assume that associated error would be different in our study. Additionally, forest fragmentation consists in more than area contraction, involving for example, proximity to edge and isolation effects (Fischer & Lindenmayer 2007) that were not directly treated in this study. Fortunately in the studied landscape, distance of sampling plots to nearest edge and isolation level were all positively correlated with forest area as well as number of frugivores species, allowing the use of a single explanatory variable for the analyses (forest patch area in our case). However, the use of forest area as explanatory variable does not mean that other variables associated with landscape configuration or species-specific abundances of frugivores in each forest patch are not as good predictors as forest area for the documented drifts in tree seedling community.

The patterns observed in this study claims a striking importance for conservation purposes if this biased seedling represents a loss of large-seeded tree species in disturbed forest sites (Michalski *et al.* 2007). Few large-seeded tree species may represent reduced food supply for large frugivores, reducing attractiveness of defauntated forest patches to vertebrates affecting dispersal function as whole. The conservation and proper management of the remaining fauna in fragmented landscapes may help to maintain dispersal services and prevent the impoverishment of the future flora (Silva & Tabarelli 2000). Efforts to conserve fragmented landscapes must to take in account all possible manners to keep dispersal function. This is critical for old, severely fragmented landscapes that have been subject to several disturbance pressures acting in synergism that may accelerate the loss of species (Tabarelli *et al.* 2004). The paradigm of the empty forest (*i.e.* forest lacking a significant portion of the original fauna; sensu Redford 1992) and the implications it brings to the maintenance of the biodiversity in tropical forest must be considered more seriously to turn fragmented forests into viable conservation units.

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TABLES

Table 1. Results of the general linear mixed models fitted for functional composition of both seedling and tree communities at the Ejido Palmar, Southern Mexico. Random effects responded for less than 10% of the unexplained variance of all models.

Model terms	df	F-ratio	p	Whole model R^2
Seedling individuals				
Log_{10}(Area)	1,38	0.23	0.64	0.55
Dispersal Mode	1,192	92.41	0.00	
SeedSize	2,192	11.48	0.00	
Log_{10}(Area)*Dispersal Mode	1,192	3.21	0.08	
Log_{10}(Area)*Seed Size	2,192	9.00	0.00	
Dispersal Mode*Seed Size	2,192	59.79	0.00	
Seedling species				
Log_{10}(Area)	1,38	0.19	0.66	0.51
Dispersal Mode	1,192	82.14	0.00	
SeedSize	2,192	9.87	0.00	
Log_{10}(Area)*Dispersal Mode	1,192	1.72	0.19	
Log_{10}(Area)*Seed Size	2,192	3.06	0.05	
Dispersal Mode*Seed Size	2,192	52.21	0.00	
Tree stems				
Log_{10}(Area)	1,6	0.30	0.61	0.74
Dispersal Mode	1,32	78.88	0.00	
SeedSize	2,32	10.70	0.00	
Log_{10}(Area)*Dispersal Mode	1,32	0.35	0.56	
Log_{10}(Area)*Seed Size	2,32	0.30	0.74	
Dispersal Mode*Seed Size	2,32	15.28	0.00	
Tree species				
Log_{10}(Area)	1,6	1.55	0.26	0.76
Dispersal Mode	1,32	115.42	0.00	
SeedSize	2,32	0.43	0.66	
Log_{10}(Area)*Dispersal Mode	1,32	2.38	0.13	
Log_{10}(Area)*Seed Size	2,32	1.27	0.30	
Dispersal Mode*Seed Size	2,32	13.39	0.00	

Table 2. Faunal composition of forest patches studied in the Ejido Palmar, Southern Mexico. Potential large-bodied seed dispersers with both terrestrial (mammals) and aerial (birds) habits are indicated. Presence is indicated with + signs.

Vertebrate group	Forest patch size (ha)					
	2.3	2.9	22	29	640	5,000
Large birds						
Ramphastus sulfuratus			+	+	+	+
Ortalis vetula	+	+	+	+	+	+
Tityra semifasciata			+	+		+
Medium-to large mammals						
Sciurus sp.	+	+	+	+	+	+
Dasyprocta punctata	+	+	+	+	+	+
Agouti paca			+	+	+	+
Ateles geoffroyi			+			
Mazama americana				+	+	+
Odocoileus virginianus						+
Tayassu pecari					+	+
Tapirus bairdii						+

Table 3. Absolute numbers and percentage values (in parenthesis) of tree seedlings found in six forest patches in the Ejido Palmar, Southern Mexico. Values are indicated considering: (1) the origin (i.e. whether seedlings originated from a local or immigrant seeds); (2) the dispersal mode of immigrants (i.e. whether immigrant seedling have abiotic or zoochorous dispersal mode); and (3) seed size of zoochorous immigrants (i.e. what category of seed size the zoochorous immigrant seedlings belong to).

Patch Area (ha)	Origin		Dispersal mode		Categories of seed size		
	Local	Immigrant	Abiotic	Zoochorous	> 1.4 cm	0.6-14 cm	< 0.6 cm
2.3	26 (38.8)	41 (61.2)	16 (39.0)	25 (61.0)	4 (16.0)	21 (84.0)	0 (0.0)
2.9	50 (53.2)	44 (46.8)	7 (16.3)	37 (83.7)	9 (24.3)	26 (70.3)	2 (5.4)
22	19 (44.2)	24 (55.8)	4 (16.6)	20 (83.4)	5 (25.0)	9 (45.0)	6 (30.0)
29	24 (38.7)	38 (61.3)	9 (23.7)	29 (76.3)	4 (13.8)	18 (62.1)	7 (24.1)
640	115 (59.0)	80 (41.0)	11 (10.5)	69 (75.9)	40 (58.0)	26 (37.7)	3 (4.3)
5,000	76 (39.6)	116 (60.4)	22 (24.1)	94 (89.5)	43 (45.7)	50 (53.2)	1 (1.1)

LEGENDS TO FIGURES

Figure 1. Study site located at the Ejido Palmar, State of Quintana Roo in southern Mexico with the six forest patches used for experiments (a) and a demonstrative illustration of the sampling station with containing adult tree and seedling plots (b).

Figure 2. Mean number of seedling individuals (a) and tree stems (b) per categories of seed size and dispersal mode at the Ejido Palmar, Southern Mexico. Small-seeded (< 0.6 cm in the longest length); medium-size seeded (0.6 - 1.4 cm) and large-seeded seedling individuals (> 1.4 cm). Similar pattern was observed for adult tree and seedling species.

Figure 3. Relationship between logarithm of forest patch area and mean number (with standard error bars) of small-seeded (< 0.6 cm in the longest length); medium-size seeded (0.6 - 1.4 cm) and large-seeded seedling individuals (> 1.4 cm) at the Ejido Palmar, Southern Mexico. NS = non significant. Similar pattern was observed for seedling species.

Figure 4. Nonmetrical multidimensional scaling for seedling (a) and adult tree (b) communities in a 5,000-ha patch (grey circles); a 640-ha patch (grey squares); a 29-ha patch (open triangles - up); a 22-ha patch (open triangles - down); a 2.9-ha patch (thin crosses) and a 2.3-ha patch (filled crosses). Stress values are 0.14 and 0.2 for seedling and adult tree data sets, respectively.

Figure 5. Relationship between logarithm of forest patch area and the average values of the axis – 2 of the nonmetric multidimensional scaling analysis (NMDS) based on Bray-Curtis similarity index (with standard error bars) for the seedling data set at the Ejido Palmar, Southern Mexico.

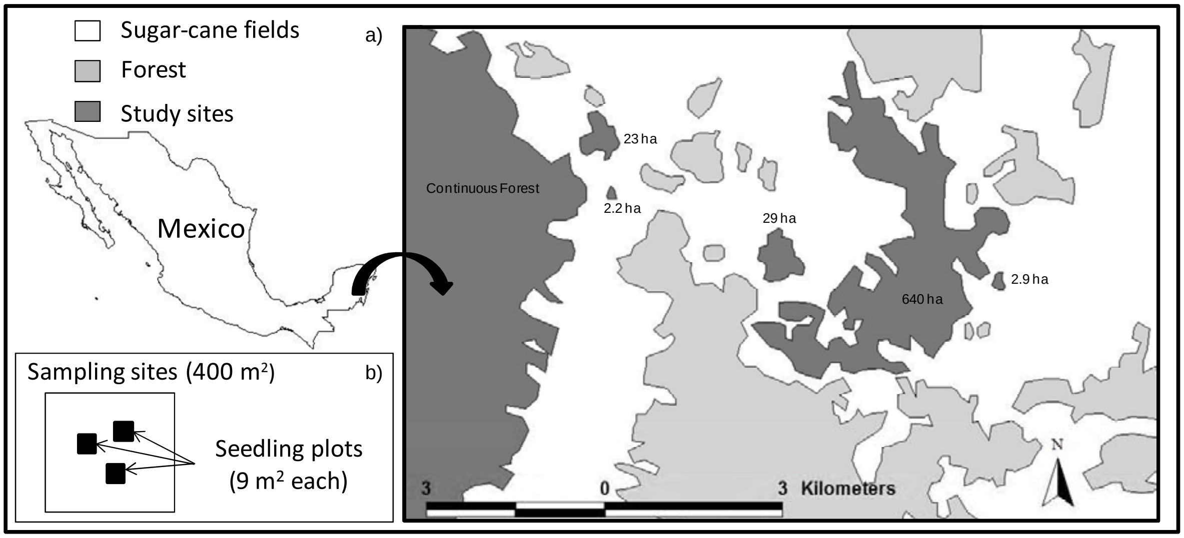

Sugar-cane fields
Forest
Study sites
a)
Mexico
Continuous Forest
23 ha
2.2 ha
29 ha
640 ha
2.9 ha
3
0
3 Kilometers
N
Sampling sites (400 m²)
b)
Seedling plots
(9 m² each)

Figure 1.

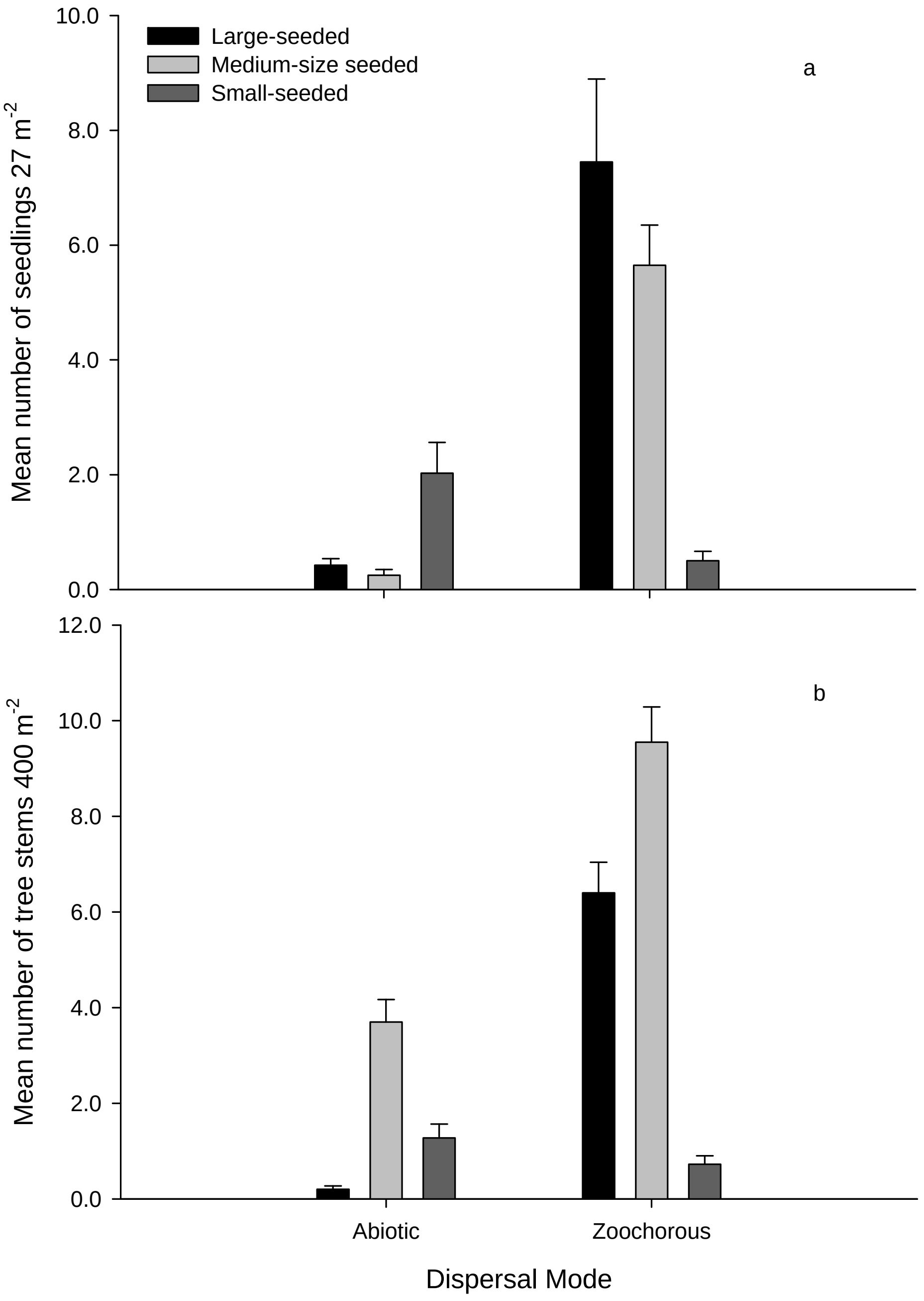

10.0
8.0
6.0
4.0
2.0
0.0
Large-seeded
Medium-size seeded
Small-seeded
a
Mean number of seedlings 27 m^{-2}
12.0
10.0
8.0
6.0
4.0
2.0
0.0
b
Mean number of tree stems 400 m^{-2}
Abiotic
Zoochorous
Dispersal Mode

Figure 2.

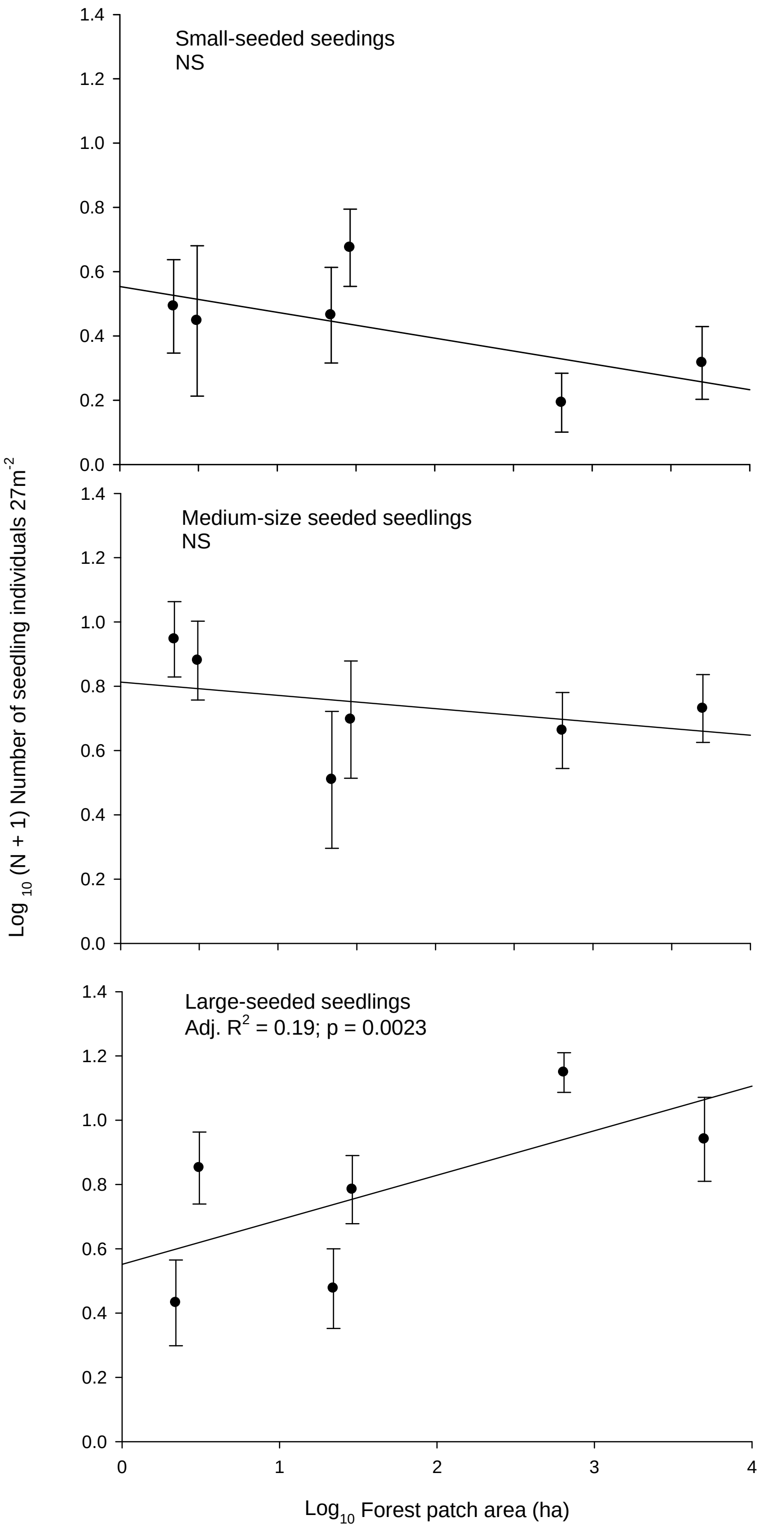

Small-seeded seedings
NS
Medium-size seeded seedlings
NS
Large-seeded seedlings
Adj. R^2 = 0.19; p = 0.0023
Log$_{10}$ (N + 1) Number of seedling individuals 27m^{-2}
Log$_{10}$ Forest patch area (ha)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
0
1
2
3
4

Figure 3.

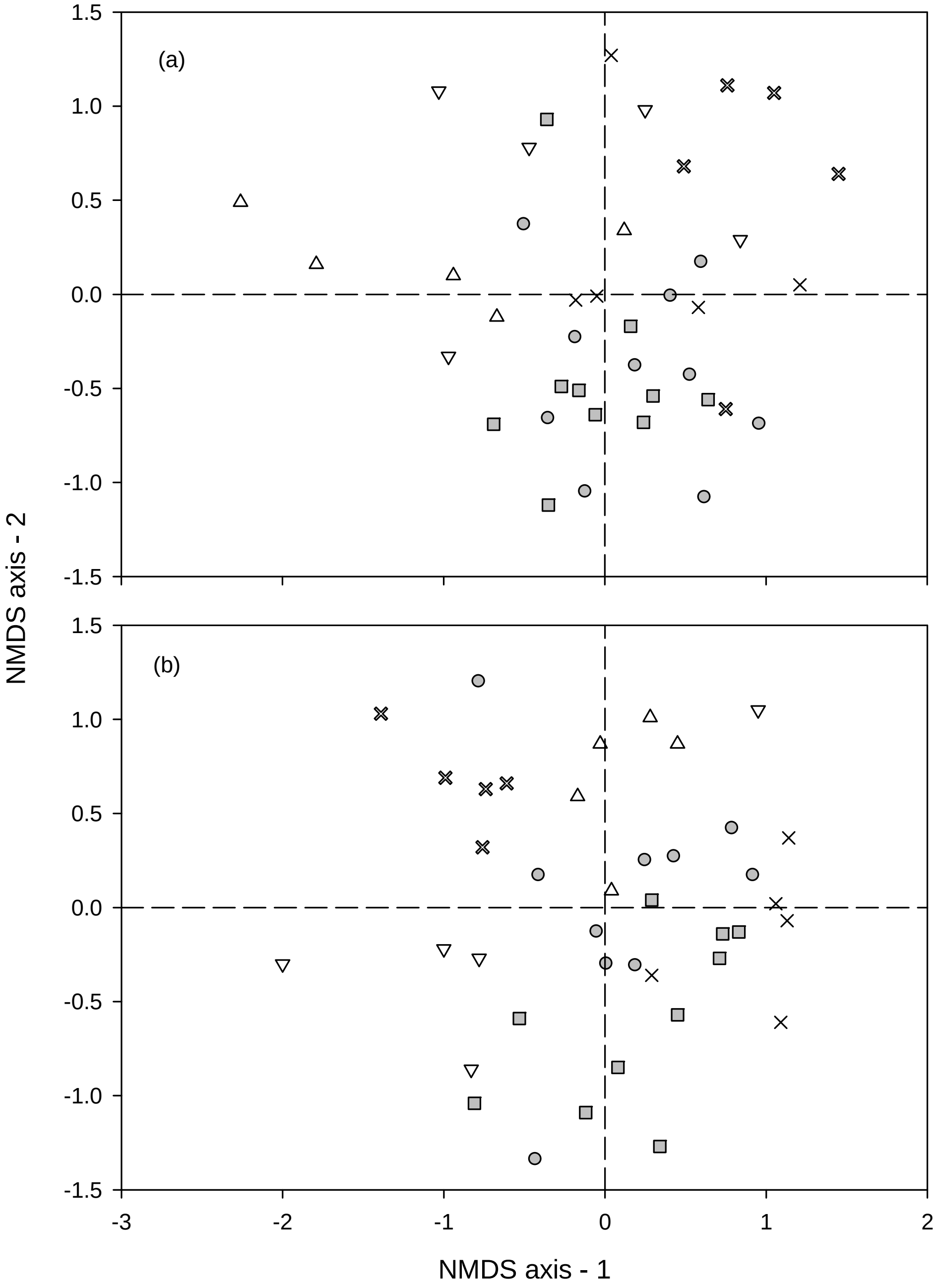
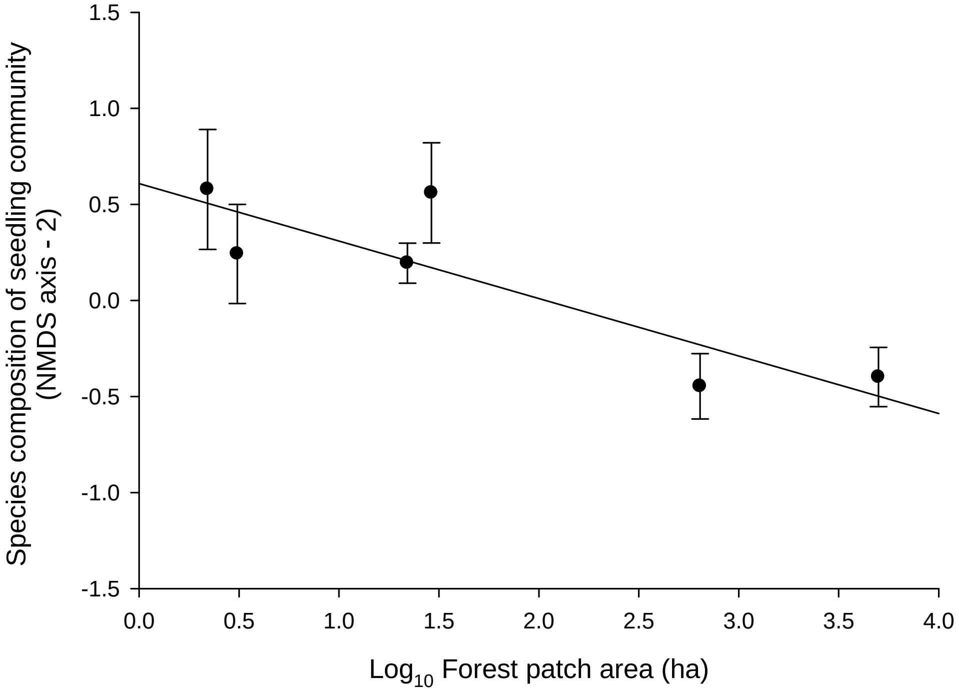


Figure 4.



Species composition of seedling community (NMDS axis - 2)
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
Log$_{10}$ Forest patch area (ha)

Figure 5.

Sección 2

El papel de la fauna remanente en la dispersión de semillas en paisajes fragmentados.

Small Tent-Roosting Bats Promote Dispersal of Large-Seeded Plants in a Neotropical Forest

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Abstract

In Neotropical regions, fruit-bats are among the most important components of the remaining fauna in disturbed landscapes. These relatively small-bodied bats are well known disperal agents for many small-seeded plant species, but are assumed to play a negligible role in the dispersal of large-seeded plants. We investigated the importance of the small tent-roosting bat *Artibeus watsoni* for dispersal of large seeds in the Sarapiquí Basin, Costa Rica. We registered at least 43 seed species > 8 mm beneath bat roosts, but a species accumulation curve suggests that this number would increase with further sampling. Samples collected beneath bat feeding roosts had, on average, 10 times more seeds and species than samples collected 5 m away from bat feeding-roosts. This difference was generally smaller in small, disturbed forest patches. Species-specific abundance of seeds found beneath bat-roosts was positively correlated with abundance of seedlings, suggesting that bat dispersal may influence seedling recruitment. Our study demonstrates a greater role of small frugivorous bats as dispersers of large seeds than previously thought, particularly in regions where populations of large-bodied seed dispersers have been reduced or extirpated by hunting.

Key words: Costa Rica; Defaunation; Forest Regeneration; Frugivorous bats; Seed dispersal.

Resumen

En las regiones Neotropicales los murciélagos frugívoros son uno de los principales componentes de la fauna que persiste en paisajes perturbados donde dispersan muchas especies de plantas con semillas pequeñas. Sin embargo, debido a su relativa pequeña talla su papel en dispersar semillas de gran porte es considerado irrelevante. Este estudio evaluó el papel del murciélago constructor de tiendas *Artibeus watsoni* en la dispersión de semillas grandes en la región del río Sarapiquí, Costa Rica. Se registró al menos 43 especies de semillas > 8 mm bajo las tiendas de esos murciélagos pero la curva de acumulación de especies sugiere un aumento en este número. Los murciélagos que acampan en hojas aumentaron la densidad y riqueza del banco de semillas en 10 veces en promedio pero esos valores fueron reducidos en los pequeños parches de bosque. Encontramos una correlación positiva entre la abundancia especie-específica de semillas bajo las tiendas de los murciélagos y la respectiva abundancia de plántulas tanto en bosque maduro como en secundario. Este estudio demuestra que el papel de murciélagos frugívoros en dispersar semillas de gran porte es mucho mayor de lo que previamente se asumía, lo que les atribuye un crucial papel en dispersión de semillas de gran porte actualmente amenazadas por la eliminación de dispersores de gran talla.

FRUGIVOROUS BATS REPRESENT AN IMPORTANT PROPORTION OF MAMMAL BIOMASS and diversity within the Neotropics (Emmons & Feer 1997). Frugivorous bats are at least as abundant as frugivorous birds, and they persist in relatively high abundances in medium-to highly disturbed habitats (*e.g.* Gorresen & Willig 2004, Faria 2006, Montiel *et al.* 2006). Neotropical bats are widely recognized as effective seed dispersers for small-seeded pioneer trees during early stages of forest regeneration (Medellin & Gaona 1999, Bernard & Fenton 2003, Lobova & Mori 2004). Because of their small body size, fruit-bats of the Netropics are thought to play a negligible role in dispersal of larger uningested seeds, however (see Muscarella & Fleming 2007). This assumption might stem from the fact that studies evaluating the role of Neotropical fruit-bats as seed dispersers are based on the collection of feces during bat captures, which limits records to endozoochoric seed dispersal (Kunz 1988). Few studies have documented epizoochorous events of seed dispersal by bats and very few report bat dispersal of, large uningested seeds (but see Lopez & Vaughan 2004, Mello *et al.* 2005).

Tropical tree species present an astonishing range of up to six orders of magnitude in seed mass (0.001 – 100 g), and exhibit a wide spectrum of seed dispersal and recruitment strategies; approximately 90 percent are animal-dispersed (Gentry 1982, Foster 1986). In Neotropical forests, small-seeded species in the genera *Cecropia*, *Vismia*, *Solanum,* and *Piper* are associated with early-successional areas and may have a wide range of seed dispersers available, from ants to monkeys, including many frugivorous bats in the subfamily Stenodermatinae that scatter seeds widely while defecating during flight (Bonaccorso & Gush 1987). An important component of the flora of mature forests is comprised by large-seeded tree species (*e.g.* those belonging to Lecythidaceae, Chrysobalanaceae and Sapotaceae families) that are thought to be dispersed primarily by medium to large-bodied animals (Poorter & Rose 2005, Wright *et al.* 2007a).

Deforestation causes both loss and alteration of natural habitats, converting large forested areas to mixed landscapes composed of isolated patches of forests and human-modified areas (Daily *et al.* 2003, Laurance 2004, Tabarelli *et al.* 2005, Mayfield *et al.* 2006). Faunal composition in such disturbed landscapes is affected by both reduction in area and overhunting that may strongly deplete populations of large-bodied vertebrates (Peres & Palacios 2007). Thus, the remaining disperser fauna of highly disturbed landscapes is often composed of a subset of the original fauna comprised mainly by small to medium-sized rodents, small birds, and bats that are thought to disperse primarily small-seeded pioneer plants with few or none importance to disperse large-seeded plant species (Terborgh *et al.* 1997, Melo *et al.* 2006). As a result, extirpation of large frugivores was proposed to be the main cause of long-term extinction of a high percentage of the flora comprised by large-seeded (> 1.5 cm) trees species in Northeastern Brazil (Silva & Tabarelli 2000).

Few studies have documented the role of remaining small-bodied fauna, especially frugivorous bats, in the dispersal of large-seeded species. Because large-seeded fruits cannot be ingested by small-bodied bats, alternative methods are required to detect their dispersal. Such fruits are usually processed by bats in feeding roosts where seeds are deposited after the pulp is consumed (Rodriguez-Herrera *et al.* 2007). One type of feeding roost is the modified leaves used by tent-roosting bats. In the Neotropics, tent-roosting bats comprise 17 species with both broad and restricted geographical distribution and represent about 22 percent of all Neotropical frugivorous bat species (Rodriguez-Herrera *et al.* 2007).

Many tent-roosting bats belong to the genus *Artibeus* (47%; N = 8), one of the most abundant frugivorous bat genera in the Neotropics (Bonaccorso 1979, Medellin *et al.* 2000). Thus, it is reasonable to expect that if small-bodied Neotropical bats are important seed dispersers of large uningested seeds, we might encounter dispersed seeds of many species beneath feeding roosts.

In this study we suggest, contrary to what is commonly assumed in the literature, that Neotropical fruit-bats can disperse a vast diversity of seeds they cannot ingest (large seeds). For this, we sampled the seeds deposited beneath leaf tents used for food processing by the small tent-roosting bat *Artibeus watsoni* in a Costa Rican tropical wet forest. We first report the observed number of seed species > 8 mm found under leaf tents. Second, to evaluate how tent-roosting bats may influence overall patterns of large seed rain in the forest we compare the abundance, richness and composition of seeds present in samples under bat roosts with samples collected 5 m away from leaf tents. Furthermore, we compare bat-generated seed rain between large, undisturbed reserves and small, disturbed forest patches. Finally, we correlate species-specific abundance of seeds found under bat roosts with the respective abundance of seedlings in both mature and secondary forests. We provide evidence here that Neotropical fruit-bats disperse a vast diversity of uningested large seeds, contrary to the common assumptions in the literature.

METHODS

STUDY SITES. - Our study was carried out in three disturbed small forest patches and two large forest reserves of tropical wet forest in the Sarapiquí basin, Costa Rica (Fig. S1). All study areas are in Submontane Wet Tropical Forest and are located in the same watershed (Sarapiquí Basin) with similar soil and elevation conditions (35-235 m asl) and are separated by a maximum of 6 km (Guariguata *et al.* 1997). Annual rainfall in the region is around 4,000 mm and mean temperature is around 25° C (McDade *et al.* 1994). Study areas included mature (LS, TR and RM; Table 1) to secondary forests (BJ and SC; Table 1).

BAT ROOST SAMPLING. – Leaf tents, or bat-constructed roosts in leaves, are used by bats as sleeping roosts during daylight and as feeding roosts at night (Rodriguez-Herrera *et al.* 2007). We searched for a specific type of bat-roost, namely bifid tents, constructed from leaves of several understory palm species and palm-like Cyclanthaceae that are usually 1-1.5 m above the soil. These tents are formed by bats making elongated “J” or “V” cuts along both sides of the midrib on leaves with bifurcated tips and folding them down along the midrib. Neotropical tent-roosting bats may use up to 77 species of plants to construct tents in at least 8 types of architectures (Rodriguez-Herrera *et al.* 2007). We chose to focus on this specific type of tent (bifid) because: 1) they are more abundant and conspicuous in the forest understory of the study sites than other tent types; 2) by concentrating sampling within a single type of tent we excluded, or at least reduced, any possible effect of tent type on the bat-generated seed rain and 3) these tents are mostly constructed and used by *A. watsoni* bats, although they may be used by other bat species such as *A. cinereus*, *Mesophylla macconnelli*, *Rhinophylla pumilio*, and *Uroderma bilobatum* (Rodriguez-Herrera *et al.* 2007).

Our sampling design consisted of walking through the forest sites looking for as many tents as we could find, assuring that each sampled leaf tent was at least 100 m apart. For all leaf tents found, 1 m^2 of soil surface immediately beneath the tent was scanned for seeds using a wooden frame to delimit the search area. If no seeds were found in a first scan, we recorded a seedless tent that was excluded from further analysis. We excluded seedless tents, as these tents may be used by bats for purposes other than feeding roosts, such as protection against rainfall, regulation of body temperature, protection against predators and parasites, or in sexual selection (Rodriguez-Herrera *et al.* 2007). When seeds were found, the leaf litter was first carefully removed and all seeds > 8 mm in length were collected. This cutoff criterion was based on the ability to identify collected seeds without germination treatments. Seeds smaller than this threshold are more likely to be rapidly buried and were often covered by fungus or were too deteriorated to be reliably assigned to species or morphospecies. No buried seeds were collected to avoid including seeds prior to tent construction by the bats. For each leaf tent with seeds underneath, we also scanned for seeds (using the same cutoff criterion) in four additional quadrats (control quadrats) of the same area (1 m^2) established in the four cardinal directions about 5m away from the tent quadrats. This procedure was necessary to: 1) compare the bat-generated seed rain with the seed rain sampled in the same forest site but away from the tent influence; 2) exclude from tent quadrats any seed species also found in at least one of the nearby control quadrats, thus distinguishing and eliminating seeds that could be present in tent quadrats due to contagious seed rain of fruiting trees in the vicinity. The four tent quadrats were pooled for all subsequent analyses and compared against tent quadrats with seeds. This experimental design was suitable for testing our hypothesis since we could compare the effect of bat tents on seed rain while controlling for local tree species composition. However, resources for construction of tents (understory palms and Cyclanthaceae) are more abundant in mature forest sites than in disturbed areas (Capers et al. 2005), thus number of seeds and species in tent and non-tent quadrats were standardized to a quadrat basis (1 m^2) for statistical comparisons. All leaf tents were visited once between April and June 2007, prior to the peak fruiting period for the flora of this region (August–October). All seeds collected were identified to the finest taxonomic level possible by comparison with herbarium specimens of fruits at LS and consultations with a plant taxonomist (Orlando Vargas from La Selva staff). Species were also classified according to their preferred habitat (mature forest *vs.* successional forest) and life form based on the descriptions available in the “Flora Digital de La Selva” database available online (http://sura.ots.ac.cr/local/florula3/en/index.htm).

BAT SEED DISPERSAL AND SEEDLING RECRUITMENT. - To assess the potential contribution of bat-generated seed rain for the seedling community in both mature and secondary forests, we used data on woody seedling recruitment previously collected in 1-ha forest monitoring plots in four secondary and two mature-forest sites within the study region. In each plot, we surveyed all tree seedlings ≥ 20 cm tall and below 1 cm DBH within 1000 1 x 2 m^2 quadrats (total area = 0.2 ha). Seedling survey data from 2006 were then scored for all seed species found beneath bat tents and control quadrats (excepting lianas). Thus, we could assess the correlation between species-specific abundance of seeds under bat roosts and respective seedling abundance in both mature and secondary forest plots. Since we did not follow the seed fate under bat roosts, these data provided a reasonable proxy for estimating the importance of *Artibeus watsonii* dispersal for seedling regeneration.

STATISTICAL ANALYSIS. - We used log-likelihood ratio tests (G tests) to account for differences in the proportion of leaf tents with seeds between large undisturbed and small disturbed habitats. We generated a species accumulation curve based on 1000 randomizations using the program EstimateS 7.5.2 (Colwell 2005) to was assess the completeness of our sampling effort. EstimateS was also used to calculate the Chao-Jaccard similarity index between tent and control plots based on 1000 randomizations. We chose this particular index of similarity because it fits well for small samples with many rare species (Chao *et al.* 2005). To determine whether forest patch size affects the abundance and species richness of the bat-generated seed rain we used generalized linear models with a log-link function for a Poisson distribution of data (McCullagh & Nelder 1989). Forest patch size (large vs. small reserves), treatment (tent vs. control quadrats) and their interaction were used as factors in the model. Pearson's correlation analyses on *log* (x+1) transformed data (to improve normality) on both seeds and seedlings abundance were used to assess the correlation between species-specific abundance of seeds in both tent and control quadrats and the respective abundance of seedlings registered in mature and secondary forest plots. All statistical analyses were performed using JMP version 7.

RESULTS

SEEDS DISPERSED BY BATS. —We found 194 leaf tents, from which 103 tents had seeds >8 mm underneath. The percentage of seedless tents varied from 20 to 68 percent among forest sites and was higher in the large reserves ($G = 16.963$; df = 1; $P < 0.0001$; Table 1). A total of 1030 seeds from 46 species were found in all tent quadrats pooled. After excluding seeds potentially originating from neighbor fruiting trees and those species dispersed by abiotic means, a total of 810 seeds from 43 species were included in the analyses. These animal-dispersed seed species comprised trees, palms, and lianas associated with different habitats and forest successional stages (Appendix S1).

All seeds found under bat roosts showed signs of manipulation, such as tooth marks and total or partial removal of pulp/arils from seeds. Thirteen out of 43 seed species (30.2%) had a total of 10 or more seeds and accounted for 89.3 percent of all seeds sampled in all tent quadrats. *Spondias radlkoferi* accounted for 50.5 percent of all seeds collected ($N = 410$) under leaf tents, followed by *Calophyllum brasiliense* with 9.7 percent ($N = 79$) of all seeds. Only these more abundant seed species occurred in 10 or more leaf tents (Appendix S1). Remaining seed species (69.8%; $N = 30$) occurred in low abundances (≤ 10 seeds found across all tents) and most seed species (90.4%; $N = 38$) were found in fewer than 10 tent quadrats. Twenty species (45%) were found in only one leaf tent.

The large number of rare seed species affected species-accumulation curve that showed a non-asymptotic pattern, suggesting that more extensive sampling would yield a significant increase in the number of plant species dispersed by leaf-roosting bats (Fig. 1). In control quadrats sampled away from leaf tent influence we found only 268 seeds from 34 seed species, averaging 0.65 ± 1.5 seeds/m^2 and 0.18 ± 0.23 species/m^2. In contrast, the average density of seeds and species under bat roosts were almost ten times greater than in control quadrats averaging 7.86 ± 12.5 seeds /m^2 and 1.78 ± 1.18 species /m^2, respectively. Tent quadrats shared only 25 seed species with control quadrats, representing 58 percent of total species found under bat tents (Chao-Jaccard estimator = 0.754).

HABITAT TYPE EFFECTS AND INFLUENCE ON SEEDLING RECRUITMENT. - The generalized linear model suggests that tent influence had a significant direct effect on density of both seeds and species, whereas forest habitat had no direct effect (Table 2). We sampled fewer large seeds underneath bat roosts in small/disturbed than in large/undisturbed forest habitats (Fig. 2A), but virtually the same number of species under leaf tents in both types of habitat (Fig. 2B). The distribution of leaf tents according to the abundance of seeds found underneath was strongly right-skewed in both large reserves and small forest patches; high densities of seeds under bat roosts were very infrequent (Fig. 2A,B). Furthermore, the seedling community may be partially influenced by dispersal patterns of tent-roosting bats. Species-specific abundance of seed species (excluding lianas) found beneath leaf tents was positively correlated with the respective abundance of recruited seedlings in both mature and secondary forests (Fig. 3 A,B). In contrast, no significant associations were found between species-specific abundance of seeds in control quadrats and the respective abundance of seedlings in any type of forest (Fig. 3 C,D).

DISCUSSION

Our results demonstrate that Neotropical fruit bats play a far more important role in dispersing large seeds than previously thought. In our study area, tent-roosting bats disperse at least 43 species of several plant families with differing habitat preferences and life forms, suggesting that these bats have a broad dietary habit including fruits from mature forest and successional tree species. Bat dispersal may significantly shape the seed rain of both large-undisturbed and small-disturbed forest patches, as comparisons between bat-generated and nearby non-tent samples showed strong differences in seed abundance, species richness, and species composition. Further, the positive correlations between species-specific abundance of bat-dispersed seeds and regenerating seedlings in both mature and secondary-forest plots indicate that bats can influence seedling community composition. Habitat disturbance, however, may affect this dispersal system as we detected a significant decrease in the abundance of bat-generated seed rain in small forest patches.

Considering the contribution of other larger fruit bats (both tent and non tent-roosting) to community-wide seed dispersal, the importance of Neotropical frugivorous bats for the dispersal of large-seeded plants could potentially be even greater. This study focused on a only a single type of leaf tent primarily used by *Artibeus watsoni*, one of the smallest fruit-bats that occurs in the study area (ca. ~ 11g) that use mainly lower-canopy and understory strata. However, this kind of leaf tent may also be used by larger fruit-bats such as *A. jamaicensis* (Rodriguez-Herrera *et al.* 2007). This may explain why several plant genera with seeds > 2 cm were frequently found under leaf tents. Small *A. watsoni* and other larger *Artibeus* (*e.g. A. jamaicensis* and *A. lituratus*) are closely related phylogenetically and have similar dietary habits (Giannini & Kalko 2004), so it is not surprising that they may occupy the same leaf tents. Species belonging to genera *Spondias*, *Calophyllum, Otoba* and *Quararibea* (Appendix S1) are among the largest seeds of the regional flora and, excepting *Spondias,* all mentioned species are associated with mature forest habitats and upper-canopy layer (McDade *et al.* 1994). Moreover, some of the recorded plant species (*e.g. Virola* spp., *Simarouba glauca,* and *Protium* spp.) are thought to be mainly dispersed by large birds (*e.g.* toucans and guans) but were frequently found under bat roosts, supporting the assertion that even distantly related taxa such as bats and birds may compete for resource (Palmeirim *et al.* 1989). These findings strongly contradict the argument that Neotropical furgivorous bats, due to morphological and ecological constrains, are irrelevant to the dispersal of large-seeded tree species from mature forest, a role played in Old-world tropical forests by larger Pteropodid bats (flying-foxes; Muscarella & Flemming 2007).

The elevated seed rain under bat tents in comparison with adjacent non-tent quadrats raises questions regarding the benefits of dispersal by leaf-roosting bats, as clusters of seeds may be more susceptible to natural enemies and/or intraspecific competition (Janzen 1970). However, 69 percent of all seed species found underneath leaf-tent roosts had fewer than 10 seeds across all leaf tent, and half of the species were represented by a single seed (Appendix S1). Absolute numbers of seeds per tent quadrat ranged widely (1–88 seeds), but high densities of seeds were infrequent (Table 1; Fig. 2). Furthermore, secondary seed dispersal by rodents may significantly scatter seeds over the forest floor (Vander Wall *et al.* 2001). Analogous to the clumped dispersal patterns created by monkeys or tapirs, seed dispersal by tent-roosting bats may increase seedling establishment at the population level for seeds deposited far away from co-specific adults (Romo *et al.* 2004, Queenborough *et al.* 2007). Moreover, dispersal by tent-making bats in secondary forests may promote colonization and seedling establishment of mature forest species, such as *Calophyllum brasiliense, Welfia spp,* and *Protium spp* that are not present as fruiting trees in secondary forest in our study sites (Norden *et al*. 2009). Tent and non-tent quadrats shared only 25 seed species and only three out of 46 seed species were excluded from our samples due to possible contagious seed rain from neighbor trees. Thus, tent-making bats may significantly enhance the density and diversity of allochtonous seed rain at the local scale (Martinez-Ramos & Soto-Castro 1993).

Although we did not account for the eventual fate of bat-dispersed seeds, we found significant correlations between the species-specific abundance of seeds dispersed by bats and the abundance of respective seedlings in both mature and secondary forests (Fig. 3). If differential seedling abundance within our study areas is simply due to species differences in local fruit availability (and therefore higher local rates of frugivory, dispersal, and recruitment), we would also expect to find a significant correlation between species-specific abundance of seeds and seedlings in adjacent non-tent samples. Our results therefore suggest that tent-making bats may influence the local seed rain and therefore the abundance of seedlings of the tree species they feed on and disperse. This influence may still persist even though other vertebrate species such as monkeys and birds also serve as dispersal agents for these seed species.

Dispersal of large seeds by bats can assume critical importance for plant dynamics in defaunated forest fragments and large tracts of forests from where large frugivores have been depleted or extirpated due to hunting or loss of habitat (Wright *et al.* 2007b). Mature forest tree species developed larger seeds than their early-succesional counterparts as an adaptation for germination and establishment in shaded environments, and are considered to be depend on disappearing large frugivores for successful seed dispersal (Terborgh & Nuñez-Iturri 2006). Therefore, bats are an important component of the remnant fauna that may help to maintain tree diversity and promote forest regeneration in disturbed landscapes (Wright *et al.* 2007b). Our results highlight the need for further study of Neotropical frugivorous bats and their role in the dispersal of large seeds in tropical forest ecosystems.

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TABLE 1. *Number of leaf tents with seeds and seedless tents at each forest site sampled also showing median values and range of number of seeds and seed species > 8 mm found under leaf tents at the Sarapiqui basin, Costa Rica.*

Site	Forest type	Tents with seeds	Seedless tents	Number of seeds (median; range)	Number of seed species (median; range)
La Selva (LS)	mature, large reserve	30	30	433 (5; 1-88)	17 (2; 1-5)
La Tirimbina (TR)	mature, large reserve	12	26	58 (6.5; 1-10)	13 (2.5; 1-4)
El Bejuco (BJ)	secondary, small patch	8	10	31 (3.5; 1-7)	7 (1.5; 1-4)
Socorro (SC)	secondary, small patch	8	3	41 (3.5; 1-12)	12 (2.5; 1-5)
Ramirez (RM)	mature, small patch	53	14	247 (3; 1-36)	29 (1; 1-5)

TABLE 2. *Results of the generalized linear models fitted to number of seeds and seed species /* m^2 *as a function of the treatment (tent quadrats vs. control quadrats) and reserve size (large vs. small).*

Model terms	df	Chi-square	*P*
Number of seeds /m^2			
Treatment	1	101.0644	0.0000
Habitat type	1	0.2680	0.6046
Treatment*Habitat type	1	4.1602	0.0414
Number of seed species /m^2			
Treatment	1	62.7304	0.0000
Habitat type	1	0.2109	0.6460
Treatment*Habitat type	1	0.9219	0.3370

Figure Legends

FIGURE S1. The Sarapiquí basin in Northeastern Costa Rica. Black shaded areas were study sites for tent survey and seed collection; LS = La Selva Biological Station (1,536 ha); TR = La Tirimbina Rainforest Center (345 ha); BJ = El Bejuco (20 ha); RM = Ramirez (25 ha); SC = Socorro (20 ha).

FIGURE 1. Mean species accumulation curve for number of seed species found under leaf tents based on 1000 randomizations of the data set (Sobs) in the Sarapiquí Basin, Costa Rica.

FIGURE 2. Distribution of leaf tents according to abundance of seeds (A) and number of seed species (B) at the Sarapiquí basin, Costa Rica. Also shown, mean values for large reserves (solid line) and small forest patches (dashed line).

FIGURE 3. Pearson’s correlations between species-specific abundance of seed species found in both tent quadrats (A,B) and non-tent quadrats (C,D) and respective abundance of seedlings in both mature and secondary forest at the Sarapiqui, Basin, Costa Rica. Each dot corresponds to a single tree species.

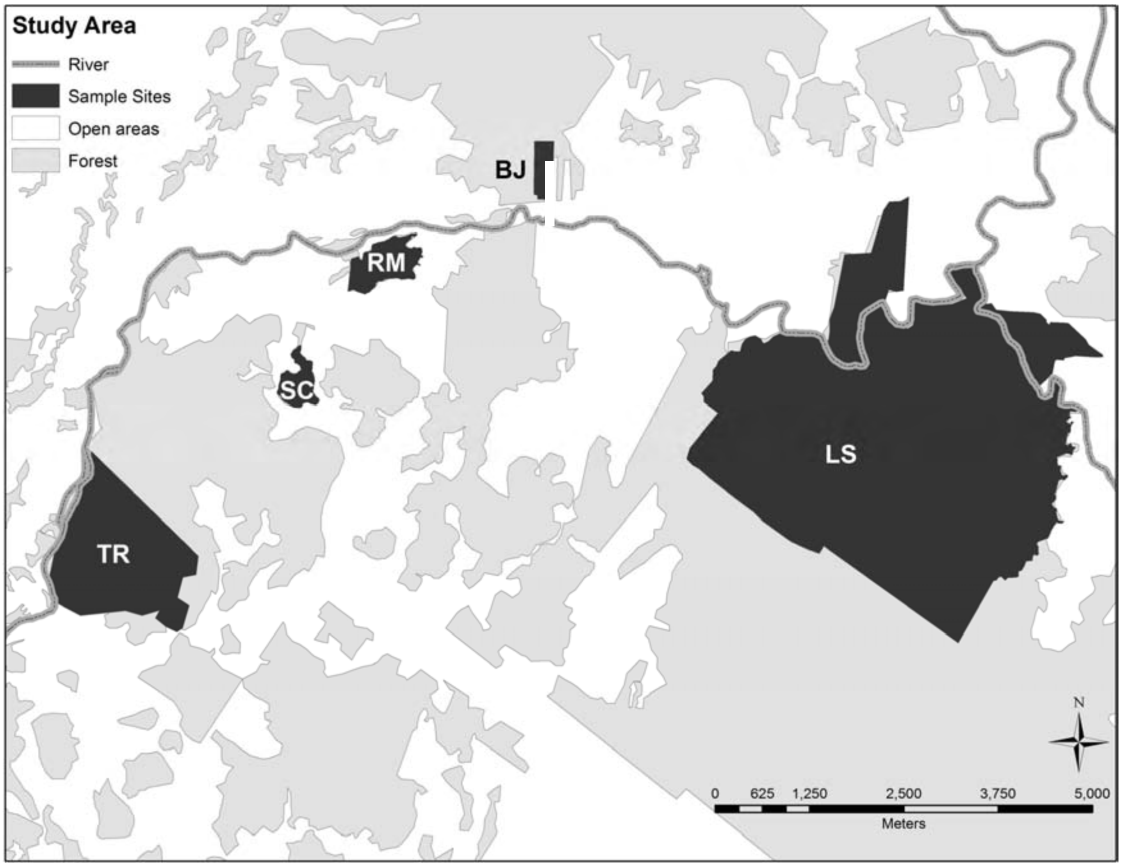

FIGURE S1.

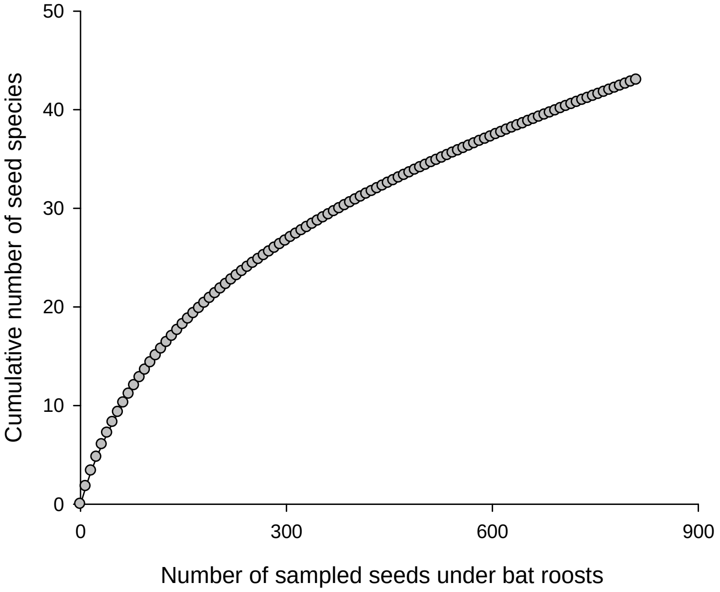

FIGURE 1.

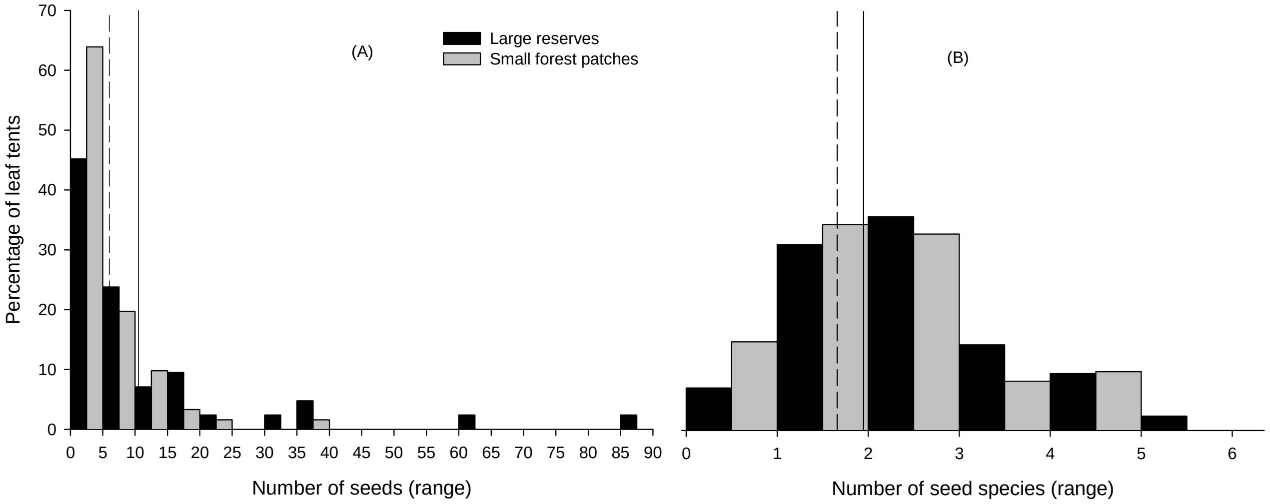

FIGURE 2.

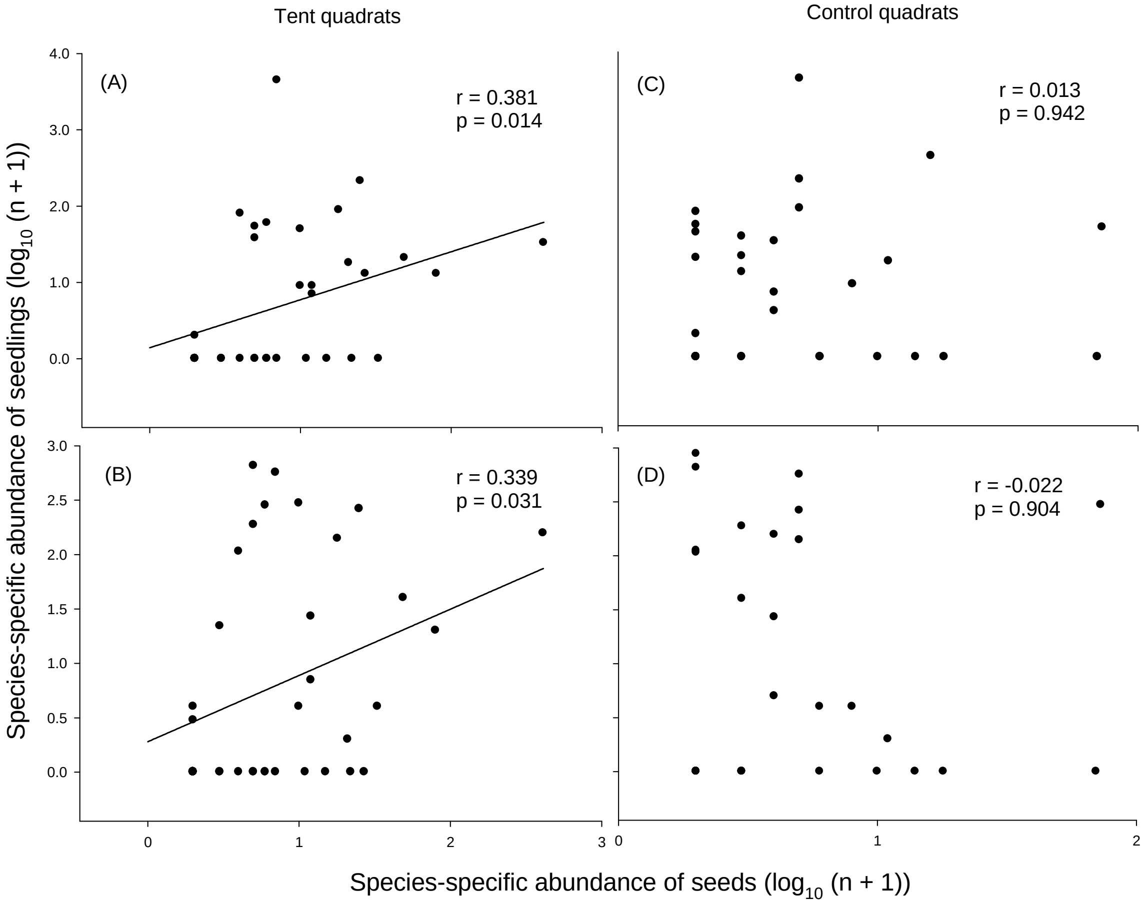

FIGURE 3.

DISCUSIÓN GENERAL

El conjunto de resultados presentados en este trabajo da más fuerza al papel de la dispersión de semillas como un proceso clave para el mantenimiento de las poblaciones de árboles en bosques tropicales. Los patrones de dispersión de semillas al moldar la deposición de propágulos en el suelo del bosque tropical demostraron tener importantes consecuencia para el subsecuente reclutamiento de plántulas y la regeneración del bosque tropical (Harper 1977, Cramer et al. 2007b, Standish et al. 2007). El patrón de regeneración al que son llevados los “bosques vacios” (sensu Redford 1992) parece eliminar, a largo plazo, todo un grupo de especies de árboles que depende de los servicios de dispersión realizados por los vertebrados de gran talla (Terborgh et al. 2008). Aunque se detectó que los murciélagos frugívoros, como parte importante de la fauna remanente en hábitats fragmentados (Willig et al. 2007), pueden mantener un cierto nivel de dispersión de semillas de gran porte, su papel como dispersor de este grupo de plantas parce no ser suficiente para mantener niveles e reclutamiento equivalentes al encontrados en el bosque continuo. Así, el resultado final del sinergismo entre fragmentación forestal y eliminación de la fauna de gran talla es el gradual empobrecimiento y la homogeneización de la flora de los paisajes fragmentados (Tabarelli y Peres 2002, Laurance et al. 2006, Santos et al. 2008).

Actualmente, la mayoría de los estudios sobre patrones de lluvia de semillas en bosques tropicales se ha enfocado en contestar preguntas acerca del mantenimiento de la diversidad de árboles (Harms et al. 2000, Svenning y Wright 2005), colonización de los claros en el bosque (Hubbell et al. 1999) y detectar diferencias en patrones espaciales en bosques conservados (Loiselle et al. 1996, Hardesty y Parker 2002). Estudios sobre la lluvia de semillas en hábitats que presentan diferentes niveles de perturbación son relativamente recientes. Los patrones hasta ahora descritos por estos estudios sugieren que áreas alteradas presentan cambios asociados al aumento de la representatividad de semillas dispersas por medios abióticos (Barbosa y Pizo 2006); reducción de la presencia de semillas de gran porte (Melo et al. 2006); una probabilidad de llegada de la semillas fuertemente asociada a la presencia de adultos reproductivos (Martini y Santos 2007) que determinan significativamente las tasas de colonización de áreas abandonadas (Dosch et al. 2007). El presente estudio pudo identificar importantes cambios en la lluvia de semillas de fragmentos aislados en comparación con el bosque continuo que no habían sido descritos anteriormente.

Por ejemplo, variaciones interanuales en la producción de semillas redujeron drásticamente la densidad promedio y el número de total de especies de semillas colectadas en fragmentos mientras que el bosque continuo fue el sitio que sufrió la menor reducción relativa en la densidad promedio y ningún cambio en el número total de especies colectadas. La congruencia espacio-temporal encontrada en la lluvia de semillas de fragmentos < 30 ha sugiere una lluvia de semillas sesgada cuya distribución se influencia básicamente por la producción local de semillas y denota una menor importancia del papel de los dispersores en distribuirlas por el bosque. Tal conclusión es reforzada por otros hallazgos de este estudio como por ejemplo. La lluvia de semillas, especialmente de las especies zoócoras de gran porte, sufren fuerte limitación de dispersión en los pequeños fragmentos defaunados. Esos resultados dan soporte a la hipótesis de que la homogeneización florística causada por la fragmentación del bosque tropical (Laurance et al. 2006) tiende a eliminar las especies de árboles cuyas interacciones ecológicas con la fauna son más afectadas (Girão 2007).

Recientemente, un gran número de trabajos ha explorado las consecuencias de la eliminación de la fauna sobre la comunidad de plántulas (ver Biotropica volumen 39 del 2007 especial sobre defaunación) pero las conclusiones con frecuencia son contradictorias. Por ejemplo, algunos autores proponen que la defaunación favorece las semillas de gran tamaño debido a un relajamiento en sus tasas de depredación decurrente de la eliminación de vertebrados de gran talla (Dirzo et al. 2007, Wright et al. 2007). Sin embargo, otros autores sugieren que el principal “cuello de botella” para el reclutamiento de la mayoría de las especies de árboles es su proceso de dispersión y que la eliminación de dispersores de gran talla (los mismos que por veces también actúan como depredadores de semillas) reduce drásticamente las tasas de reclutamiento de semillas de gran porte (Cramer et al. 2007a, Cramer et al. 2007b, Terborgh et al. 2008). Tamaña es la incertidumbre sobre cuál proceso es más importante; si el relajamiento de la depredación o la reducción en tasas de dispersión, que Stoner y colaboradores (2007b) en una revisión sobre el tema reconocen que más estudios son necesarios para esclarecer este punto.

El segundo capítulo de ésta tesis confiere una evidencia robusta acerca del sobresaliente papel de la dispersión de semillas en limitar el reclutamiento de plántulas. Se pudo demostrar que el ensamble de plántulas parece responder a la eliminación de vertebrados dispersores de los fragmentos de bosque. Primero, documentamos para los fragmentos de bosque defaunados una importante reducción en el número promedio de plántulas cuyas semillas son dispersadas por vertebrados. Segundo, esa reducción fue más fuerte entre plántulas cuyas semillas son dispersadas por vertebrados de gran talla. Finalmente, al distinguir entre plántulas inmigrantes y locales, pudimos notar que la representatividad de plántulas de semillas grandes entre el grupo de las inmigrantes (o sea, dispersadas) fue drásticamente reducida en pequeños fragmentos. La evidencia más contundente acerca de la importancia de los dispersores en influenciar el reclutamiento de plántulas se expresó en el alta proporción (~50%) de plántulas originadas de semillas dispersadas en los ensambles tanto de fragmentos cuanto del bosque continuo.

Las rutas de regeneración de un bosque fragmentado y defaunado parecen ser, por lo tanto, fuertemente influenciadas por los patrones de dispersión de semillas (Terborgh y Nuñez-Iturri 2006, Terborgh et al. 2008). Eso no significa que la depredación de semillas y la herbivoría de plántulas, igualmente afectadas por la fragmentación, no actúen de manera significativa en moldar los patrones de reclutamiento. Por ejemplo, se ha demostrado que un exceso de herbivoría por artrópodos aumenta la mortalidad de plántulas en islas de bosque aisladas por la construcción de una presa en Venezuela (Lopez y Terborgh 2007). En la selva tropical Atlántica de Brasil, los efectos combinados de la depredación de semillas y reducción en las tasas de dispersión de una especie de palma del sotobosque altera sus patrones de reclutamiento y la distribución de nuevos reclutamientos agregándolos cerca de la planta madre (Galetti et al. 2006). Esa misma agregación se ha documentado para otras especies de palma en diferentes bosques tropicales, que al perder servicios de dispersión y también tener reducida tasas de depredación, siguen reclutando pero de manera agregada (Pimentel y Tabarelli 2004, Wyatt y Silman 2004). Aparentemente, las plantas tropicales presentan diferentes niveles de susceptibilidad a la mortalidad denso-dependencia ya que especies de árboles más comunes tienden a presentar distancias promedios de reclutamiento menores que las especies más raras (Terborgh et al. 2001). Por lo tanto, las especies más raras, y que responden por la mayor parte de a diversidad de los bosques tropicales (Gentry 1982) deben ser las más susceptibles a una eventual reducción en sus tasas de dispersión, lo que limitaría seriamente su reclutamiento. Además si consideramos entre estas especies muchas poseen semillas de gran tamaño como son las de las familias Lecythidaceae, Sapotaceae, Chrysobalanaceae, Lauraceae, entre otras, la hipótesis de que la dispersión, no la depredación de semillas es el principal factor limitante al reclutamiento, gana aún más fuerza.

Otro factor que se debe considerar al intentar predecir rutas de regeneración en bosques tropicales perturbados es la fauna dispersora remanente. La historia de perturbación de cada sitio incluyendo: presiones de caza (Parry et al. 2007), extracción de recursos madereros (Michalski y Peres 2005) y no madereros (Arnold y Perez 2001, Prance 2002), incidencia de incendios (Barlow et al. 2007) y edad de los remanentes de bosque (Santos et al. 2008) influencian de manera significativa a la composición de la fauna remanente. Como regla, especies de aves generalistas y mamíferos de pequeña talla son los principales componentes de la fauna vertebrada en áreas perturbadas (Daily et al. 2003). Su papel como dispersores de semillas tiene una limitación intrínseca respeto al tamaño máximo de propágulos que pueden remover (Foster 1986). Sin embargo, la relación *"bocas grandes - semillas grandes"* puede no aplicarse para todas las especies de vertebrados.

Éste parece ser el caso de los murciélagos frugívoros Neotropicales que según el tercer capítulo de ésta tesis tienen un papel mucho más importante para la dispersión de semillas de lo que se estimaba previamente en la literatura (ver Muscarella y Fleming 2007 para una revisión reciente). Los murciélagos frugívoros parecen ser favorecidos por perturbaciones moderadas del hábitat como es el caso del paisaje estudiado en Quintana Roo, México (Willig et al. 2007). Eso implica que esos animales de relativa pequeña talla pasen a representar una importante proporción de la biomasa vertebrada en zonas perturbadas y posiblemente los vuelva más abundantes que las aves (Bonaccorso 1979). Datos acerca de dispersión de semillas de gran talla por murciélagos son en su mayoría anecdóticos (ver la base de datos en línea de Mori y Banchard 2002). Según nuestros datos, claramente subestimados, apenas una de las menores especies de murciélagos frugívoros neotropicales, *Artibeus watsoni* (~11g), es capaz de dispersar hasta 43 especies de semillas mayores de 0.8 cm de largo con importantes consecuencias para el ensamble de plántulas. Así, las implicaciones del papel de los murciélagos como dispersores de semillas grandes son patentes para el mantenimiento de la diversidad de árboles en paisajes defaunados. La presencia de murciélagos en los fragmentos estudiados en esta tesis fue responsable, por ejemplo, por más de 80% de los eventos de dispersión de semillas grades en los fragmentos < 3 ha y que se concentraron en una única trampa que se localizaba debajo de una palma usada como refugio por esos animales. La dispersión de semillas por murciélagos es apenas un factor aditivo en las tasas de dispersión de especies de árboles de semillas grandes y obviamente esos no pueden sustituir el servicio de dispersión realizado por una fauna vertebrada en buen estado de conservación.

Por lo tanto, podemos concluir que la fragmentación de los bosques tropicales y sus consecuencias inmediatas como la defaunación sesgada hacia vertebrados de gran talla tienen un fuerte potencial para alterar patrones de regeneración de paisajes modificados (Cordeiro y Howe 2001, Babweteera et al. 2007, Stoner et al. 2007a). El resultado a largo plazo de las alteraciones en procesos ecológicos como la dispersión de semillas aún debe ser mejor estudiado para generar modelos más fidedignos de regeneración del bosque tropical bajo perturbación antropogénica. La necesidad de conservar interacciones ecológicas, más que especies o poblaciones se hace cada vez más patente si esperamos restaurar o manejar hábitats alterados. El paradigma de los “bosques vacíos” (sensu Redford 1992) se encuentra cada vez más vigente y el futuro de las selvas tropicales del mundo puede estar íntimamente enlazado con el de sus habitantes más notables - la fauna vertebrada - que de alguna manera son componentes del proceso de generación y mantenimiento de su gran diversidad biológica.

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