UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

CENTRO DE INVESTIGACIONES EN ECOSISTEMAS

DISPERSIÓN DE SEMILLAS POR EL MONO ARAÑA (*ATELES GEOFFROYI*) EN FRAGMENTOS Y EN ÁREAS DE UN BOSQUE CONTINUO DE LA SELVA LACANDONA: IMPLICACIONES PARA LA CONSERVACIÓN

TESIS

QUE PARA OBTENER EL GRADO ACADÉMICO DE
DOCTOR EN CIENCIAS BIOLÓGICAS

PRESENTA
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MÉXICO, D.F. Junio, 2010

UNAM
POSGRADO
Ciencias Biológicas

COORDINACIÓN

Dr. Isidro Ávila Martínez
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Presente

Por medio de la presente me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día 8 de febrero del 2010, se acordó poner a su consideración el siguiente jurado para el examen de DOCTOR EN CIENCIAS del alumno **CHAVES BADILLA ÓSCAR MAURICIO** con número de cuenta **507451525**, con la tesis titulada: **"Dispersión de semillas por el mono araña (Ateles Geoffroyi) en fragmentos y en áreas de un bosque continuo de la Selva Lacandona: Implicaciones para la conservación"**, bajo la dirección de la **Dra. Kathryn E. Stoner.**

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Sin otro particular, quedo de usted.

Atentamente
"POR MI RAZA HABLARA EL ESPIRITU"
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Agradecimientos

Este proyecto se realizó gracias al apoyo del Posgrado en Ciencias Biológicas de la Universidad Nacional Autónoma de México (UNAM). El proyecto contó con el apoyo financiero del Consejo Nacional de Ciencia y Tecnología, México (CONACyT CB2005-C01-51043 y CB2006-56799). La Secretaría de Relaciones Exteriores de México otorgó una beca doctoral durante los tres primeros años del proyecto. Quiero agradecer a todo mi comité tutoral: Kathryn E. Stoner, Julieta Benítez y Alejandro Estrada por sus valiosos comentarios y recomendaciones para mejorar los diferentes manuscritos que componen esta tesis. Durante toda esta aventura académica de casi cuatro años, el apoyo incondicional y la amistad brindada por mi tutora fueron factores clave para que siguiera adelante.

Desde un inicio algunos colegas cuestionaron la factibilidad de este proyecto de tesis debido a las múltiples complicaciones que conlleva el estudio de los monos araña y a mi inexperiencia como primatólogo. Pero como a mí las cosas fáciles nunca me han atraído (porque las puede hacer cualquiera) decidí asumir el reto con trabajo duro y mucha pasión científica. Fueron muchas las personas que colaboraron con la realización de esta tesis en uno u otro momento. Pero por cuestiones de brevedad y porque la memoria a veces me falla, sólo mencionaré algunas. Al Laboratorio de Ecología del Hábitat Alterado, dirigido por la Dra. Julieta Benítez-Malvido, que junto con su grupo de trabajó generó las bases para el desarrollo de este proyecto. Celine Hauglustaine, Kathryn Amato, María Concepción Balderas, Santanita Martínez, Jeannet Herrera, Adolfo Jamangapé, Ana González y Rafael Lombera brindaron una importante ayuda durante diferentes etapas del trabajo de campo. A Víctor Arroyo por todas sus recomendaciones y la colaboración que brindó durante el diseño y revisión crítica de los manuscritos. A Mauricio Quesada por el apoyo logístico brindado en 2006 para mi ingreso al sistema de posgrado, por su amistad y por las sugerencias que realizó para el mejoramiento del capítulo II y IV de esta tesis. A Juan Manuel Lobato, Gumersindo Sánchez y Heberto Ferreira por la asistencia técnica. A mi amigo Marlon Delgado por apoyarme desde Costa Rica con diversas gestiones. A los habitantes de los ejidos Zamora Pico de Oro, Reforma Agraria, Loma Bonita, y Boca de Chajul por toda su colaboración y en especial a don Carlos Piceno y a toda su familia por el apoyo logístico brindado durante el trabajo de campo, por su amabilidad, y por su entrañable amistad.

Dedicatoria

Esta tesis está dedicada al maestro de maestros, Charles Darwin (1809-1882), ese hombre que demostró que cuando se combinan con pasión el intelecto, el raciocinio, y el método científico es posible "transformar" el mundo (o al menos una parte de él), es posible reemplazar las supersticiones milenarias por nuevas realidades fundadas no en los "dogmas" o en la ignorancia, sino en un arduo proceso de discernimiento y en las evidencias científicas. Gracias al magnánimo trabajo de Darwin, hoy es posible decir que quien tenga un conocimiento apropiado del evolucionismo, cuenta con una poderosa herramienta cognoscitiva para explicar y entender mejor lo que nos rodea, incluyéndonos a nosotros mismos. A través de sus enseñanzas aprendí a amar con pasión todas las maravillas del mundo orgánico, aprendí a aceptar mi propia finitud y a comprender que el ser humano es parte integral de ese fenómeno asombroso e infinitamente complejo que es la naturaleza. Que descanse en paz el gran maestro pues pese a que el mundo aún no ha comprendido los alcances de su legado y a la existencia de poderosos grupos religiosos que han saboteado (y siguen saboteando) la difusión de este conocimiento, Darwin se ha convertido en la inspiración de muchas generaciones de biólogos alrededor del mundo. Cierto es que la revolución sin parangón desatada a partir de la publicación del más importante tratado de biología y evolución jamás escrito, *Origin of Species by Means of Natural Selection* (1859), aún está lejos de terminar, pero muchos biólogos alrededor del mundo seguiremos difundiendo con pasión y valentía los conocimientos sobre la selección natural y demás mecanismos que gobiernan los procesos evolutivos ¿Y por qué tomarse semejante molestia? Porque al contrario de las "falacias sagradas" difundidas por los fundamentalistas religiosos y otros mercaderes de ilusiones, el evolucionismo cuenta con una sólida base científica que nos permite aproximarnos a la "verdad" sobre el mundo orgánico y sobre nosotros mismos. Por tanto, es nuestra responsabilidad ética luchar para que estos conocimientos científicos lleguen a todos los rincones de nuestras sociedades, es nuestra responsabilidad contribuir a demoler las supersticiones que limitan el desarrollo cognoscitivo del ser humano y por ende, que mutilan su capacidad de raciocinio.

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Resumen general

La dispersión de semillas por vertebrados es un proceso fundamental en la determinación de la estructura y dinámica de las poblaciones de plantas, y por tanto en la regeneración del bosque. En el caso de las zonas tropicales, los primates representan alrededor del 50% de la biomasa de frugívoros y diversos estudios sugieren que son dispersores altamente eficientes. Sin embargo, la mayoría de estos estudios han sido llevados a cabo únicamente en bosques continuos y se han enfocado en el estudio de aspectos descriptivos de la dieta y la dispersión de semillas (e.g., cantidad de semillas dispersadas, patrón de defecación) por primates folívoro-frugívoros de poca movilidad. Hasta la fecha son sumamente escasos los estudios que evalúen simultáneamente en bosque continuo y en fragmentos boscosos el comportamiento alimenticio de los primates frugívoros, así como su eficiencia en la dispersión de semillas, sus patrones de actividad y los efectos potenciales que tendría su desaparición sobre la regeneración del bosque. En el presente trabajo estudié durante 15 meses todos estos aspectos realizando observaciones de individuos focales en tres grupos de monos araña (*Ateles geoffroyi*) en la Reserva de la Biósfera Montes Azules, y otros tres grupos de monos en fragmentos boscosos del municipio de Marqués de Comillas, Chiapas. En el primer capítulo de la tesis: "Differences in Diet Between Spider Monkeys Groups Living in Forest Fragments and Continuous Forest in Lacandona, Mexico", evalué si las diferencias en la dieta del mono araña en ambos tipos de hábitat estaban relacionadas con diferencias en la estructura de la vegetación y la disponibilidad de alimento. En general, los fragmentos presentaron una menor disponibilidad de especies de frutos para los monos en comparación con el bosque. Como resultado, en fragmentos los monos incrementaron el tiempo dedicado al consumo de hojas y frutos inmaduros, e incrementaron el tiempo dedicado al consumo de partes vegetales de hemiepífitas y palmas. En el segundo capítulo: "Effectiveness of Spider Monkeys (*Ateles geoffroyi vellerosus*) as Seed Dispersers in Continuous and Fragmented Rainforests in Southern Mexico", comparé la manipulación de frutos y semillas, los patrones de defecación, la composición de las semillas defecadas, y la proporción de semillas defecadas en condición intacta en bosque continuo y en fragmentos, así como el efecto general del tracto digestivo sobre la germinación de las semillas. La eficiencia de los monos como dispersores fue mayor en el bosque continuo que en los fragmentos, ya que en los fragmentos: (1) se redujo la proporción de semillas tragadas y se

incrementó la de semillas arrojadas bajo el parental, y (2) se redujo la proporción de excretas que contenían semillas. No obstante, la proporción de semillas defecadas en condición intacta fue igualmente alta en ambos tipos de hábitat (> 86%) y en las cinco especies analizadas, el paso por el tracto digestivo favoreció la germinación. En el tercer capítulo**:** "Seasonal Differences and Shifts in Activity Patterns of Spider Monkeys Living in Forest Fragments in Southern Mexico", evalué la influencia de la reducción de recursos alimenticios en fragmentos y durante la estación seca sobre la cantidad de tiempo dedicado a la alimentación, al descanso y a la locomoción. En fragmentos el mono invirtió más tiempo en alimentación y menos en locomoción que en boque continuo. Por otro lado, como respuestas a las condiciones imperantes en la estación seca, el mono redujo el tiempo de alimentación e incrementó el tiempo de descanso. Estos resultados sugieren que el mono araña es capaz de lidiar con la limitación espacial y estacional de recursos a través de ajustes conductuales que minimizan los gastos energéticos. Sin embargo, desconocemos si esta flexibilidad conductual es suficiente como para permitir la sobrevivencia del mono araña a largo plazo, particularmente en los fragmentos. Finalmente, en el cuarto capítulo: "Absence of spider monkeys in small forest fragments affects the composition of seedlings in Southern Mexico", evalué la hipótesis de que la ausencia de los monos araña en fragmentos priva a las especies con semilla grande de sus dispersores eficientes, lo cual se traduce en un menor reclutamiento de este tipo de plántulas en comparación con bosques que presentan monos araña. Para esto, durante 16 meses realicé muestreos del reclutamiento de plántulas en tres áreas de bosque continuo, tres fragmentos con monos y tres fragmentos sin monos. Clasifiqué las plántulas en tres categorías de dispersión: dispersadas por primates, dispersadas por vertebrados pequeños, y dispersadas por medios abióticos (viento y gravedad). Los resultados indicaron que la ausencia del mono araña alteró la composición de plántulas, reduciendo la abundancia y riqueza de especies de semilla grande y favoreciendo tanto la riqueza de especies dispersadas por vertebrados pequeños como la abundancia de especies dispersadas por medios abióticos. Sin embargo, para tener un panorama más claro sobre la contribución del mono araña a la regeneración del bosque y sobre su capacidad para sobrevivir a la limitación espacial y estacional de recursos es crucial realizar más estudios que evalúen estos aspectos en otros bosques continuos y fragmentados de Mesoamerica.

Abstract

Animal seed dispersal may affect the distribution and structure of vegetation, and has crucial implications for forest regeneration. In tropical areas, primates represent ca. 50% of the frugivore biomass and several studies suggest that they have a diverse diet, are efficient seed dispersers, and can make important behavioral adjustments in response to environmental stresses. However, most of these studies have focused on isolated descriptive aspects of their diet and feeding behavior, and activity patterns. Furthermore, most have focused only on a small group of more folivorous primates. Studies evaluating feeding behavior, seed dispersal efficiency, and activity budgets of highly frugivorous primates in continuous and fragmented forests are extremely scarce, and the potential effects of their disappearance on seedling recruitment dynamics has not been evaluated. In this work, I evaluated these aspects in the largest Mesoamerican frugivorous primate – spider monkeys (*Ateles geoffroyi*) –using focal observations from six monkey groups living in continuous and fragmented forests of the Selva Lacandona rainforest, Chiapas, southern Mexico. In the first chapter of this thesis: "Differences in Diet Between Spider Monkeys Groups Living in Forest Fragments and Continuous Forest in Lacandona, Mexico", I evaluated the feeding behavior in three sites of continuous forest and three forest fragments, and relate differences in diet to differences in composition and structure of vegetation between habitats. Overall, I found that in response to food scarcity in fragments, spider monkeys diversified their overall diet and increased the consumption of fallback foods (e.g., leaves) in comparison with the continuous forest. In the second chapter: "Effectiveness of Spider Monkeys (Ateles geoffroyi vellerosus) as Seed Dispersers in Continuous and Fragmented Rainforests in Southern Mexico", I determined the efficiency of spider monkeys as primary seed dispersers in quantitative and qualitative terms and if this interaction is altered in forest fragments. My results indicate that efficiency of spider monkeys as seed dispersers may be limited in fragments as a consequence of changes in seed handling and a reduction of the percentage of feces with seeds. However, the number of defecated seed species was similar between habitats and in both cases most seeds (> 86%) were undamaged. Similarly, defecated seeds showed greater germination percentages than control seeds in all of the five plant species evaluated. In the third chapter: "Seasonal Differences and Shifts in Activity Patterns of Spider Monkeys Living in Forest Fragments

in Southern Mexico”, I evaluated the influence of food resource scarcity in fragments and during the dry season on activity patterns of spider monkeys. Overall, in fragments the monkeys increased the time devoted to feeding and reduced the time devoted to traveling in comparison with continuous forest. Furthermore, in response to high temperature and food scarcity in the dry season monkeys reduced their time devoted to feeding and increased their time devoted to resting. Although these findings confirm that spider monkeys are able to make behavioral shifts in order to deal with fruit scarcity in Lacandona, further studies are necessary to assess if these behavioral changes are adequate to assure their health, fitness, and most importantly, their long-term persistence in fragmented and seasonal habitats. Finally, in chapter IV: “Absence of spider monkeys in small forest fragments affects the composition of seedlings in Southern Mexico”, I address the hypothesis that in forest fragments the lack of spider monkeys (*Ateles geoffroyi*) deprive large-seeded plants of efficient dispersers and hence limit community-wide recruitment of primate-dispersed species in comparison with forests containing monkeys. For this, during a 16-moths period I carried out samplings of seedling recruitment in three areas of continuous forest, three fragments with monkeys and three fragments without monkeys. I classified the seedling species into four categories according to their dispersal mode: primate-dispersed species (seeds >1.5 cm), small and medium vertebrate-dispersed species, wind-dispersed species, and gravity-dispersed species. Overall, my results suggest that the disappearance of spider monkeys could ultimately affect tree composition, reducing both the abundance and richness of large-seed species, and favoring small and medium seed-size vertebrate-dispersed species and abiotic-dispersed species. Nevertheless, to improve our understanding about the relative contribution of spider monkeys to forest regeneration and their behavioral responses to environmental stresses imposed by fragmentation and seasonality, more studies evaluating these and other important factors in populations of monkeys living in continuous and fragmented forests of Mesoamerica are crucial.

INTRODUCCIÓN GENERAL

Importancia de los dispersores de semillas

La relación mutualística entre las plantas y sus dispersores animales representa una de las interacciones más ampliamente distribuidas en el mundo. Por ejemplo, a nivel global, la dispersión por animales se presenta en el 64% de las familias de gimnospermas y en un 46% del total de especies de este mismo grupo; mientras que otro 39% de especies son dispersadas tanto por medios bióticos como abióticos (Herrera 1989). En el caso particular de la dispersión de semillas por vertebrados, se estima que oscila entre 70 y 94% en las plantas leñosas de los bosques neotropicales, entre 82 y 88% en los bosques lluviosos de Australia, entre 50 y 70% en algunos bosques tropicales secos y, entre 30 y 40% en los bosques de coníferas de las zonas templadas (Jordano 2000).

Entre los principales factores ecológicos que favorecen la dispersión por vertebrados sobresalen cinco. Primero, el escape de la alta mortalidad de semillas y plántulas cerca de parentales y conespecíficos debido a la acción densodependiente de los enemigos naturales (Jazen 1970, Connell 1971). Segundo, la colonización de sitios distantes (Howe & Miriti 2004), lo cual puede repercutir directamente en la distribución geográfica de las plantas. Tercero, el escape de la competencia intraespecífica (e.g., autosombreo, competencia por agua y nutrientes del suelo) entre individuos emparentados (Willson & Traveset 2000). Cuarto, la dispersión directa de las semillas por animales que las defecan en sitios específicos que favorecen su germinación y establecimiento (e.g., aves: Wenny & Levey 1998, Wenny 2001). Finalmente, los efectos de desinhibición, escarificación y fertilización que tiene el paso de las semillas por el tracto digestivo y la defecación comúnmente favorecen la germinación (Robertson *et al.* 2006). Cualquiera de estos factores que esté actuando, podría aumentar la probabilidad de que las semillas y las plántulas sobrevivan hasta la etapa adulta, en comparación con las semillas que no han sido dispersadas (Howe & Miriti 2004). Por tanto, no es casualidad que la mayoría de los árboles tropicales produzcan frutos adaptados para el consumo y la dispersión por vertebrados (Tiffney 2004, Eriksson 2008). No obstante, debido a que las relaciones coevolutivas entre plantas y dispersores no son estrechas, sino más bien "difusas" (i.e., es una coevolución entre grupos de organismos y no entre pares: Herrera 1985), la desaparición de un dispersor rara vez traerá como consecuencia la extinción de las especies de plantas que produce sus frutos preferidos (o viceversa). Pese a esto, existe evidencia que indica que la desaparición de los dispersores eficientes puede reducir considerablemente el flujo génico y alterar la composición del banco de plántulas, especialmente en el caso de especies con semilla grande, como se explicará más adelante para el caso de algunos primates frugívoros como el mono araña (*Ateles* spp.).

Eficiencia en la dispersión de semillas

Desde la perspectiva de la planta, lo importante no es tanto la cantidad de dispersores, sino, la eficiencia con que éstos dispersen sus semillas, lo cual afecta directamente los patrones de reclutamiento y regeneración de los bosques tropicales (Cordeiro *et al.* 2009). En términos generales la eficiencia de un dispersor depende dos componentes principales: (1) la cantidad de semillas dispersadas, que es una función del número de visitas realizadas y el número de semillas defecadas en cada visita, y (2) la calidad de la dispersión (i.e., la probabilidad de que las semillas sean defecadas en condición intacta en sitios apropiados para su germinación y establecimiento) (Schupp 1993, Jordano & Schupp 2000). Ambos componentes son afectados por el tipo de manipulación de los frutos y semillas, lo cual depende tanto de las características morfológicas del fruto y las semillas, como de las características conductuales y morfológicas del dispersor (Jordano 2000, Izhaki 2002). Debido a esto, se presenta un *continum* en la eficiencia de dispersión (Jordano 2000), de modo que un mismo dispersor puede comportarse algunas veces como depredador de semillas y otras como verdadero dispersor, con múltiples grados de eficiencia.

El componente cuantitativo es relativamente fácil de comparar y ha sido objeto de numerosos estudios alrededor del mundo (e.g., Howe & Smallwood 1982, Garber 1986, Levey *et al.* 1994, Lobova *et al*. 2009). En cuanto a la calidad de dispersión la mayoría de estudios realizados hasta la fecha se han centrado en describir y/o cuantificar la selección y manipulación de los frutos y semillas (Jordano 2000, Stevenson 2004), el efecto del paso de las semillas por el tracto digestivo (Stevenson 2000, Robertson *et al.* 2006), los patrones de deposición (Wehncke *et al.* 2004, McConkey & Chivers 2007) y la distancia de dispersión (Link & Di Fiore 2006, Levey *et al.* 2008). No obstante, son muy escasos los estudios que han considerado simultáneamente ambos componentes de la eficiencia y aún menos los que han evaluado cómo ésta se puede ver afectada por diferentes presiones antropogénicas (e.g., fragmentación).

Fragmentación y el papel de los primates en la regeneración de los bosques tropicales

En las zonas tropicales, millones de hectáreas de bosque son convertidas en campos agrícolas y pastizales cada año. Por ejemplo, sólo durante la década de 1981 a 1990, en los Neotrópicos se perdieron 74 millones de hectáreas de bosque a una tasa de deforestación anual del 0.75% (Whitmore 1997). En América Latina (excluyendo México y la selva Atlántica de Brasil), durante el período de 1990-1997 esta tasa fue del 0.38%, siendo superada únicamente por la de las zonas tropicales de África y del Sudeste de Asia (Achard *et al.* 2002). En los paisajes fragmentados resultantes, la reducción en la diversidad de hábitats a nivel local y del área total de hábitat disponible, propicia la extinción de muchas especies de flora y fauna (Burkey & Reed 2006, Watlin & Donnelly 2006). Esta situación es especialmente grave en el caso de México, ya que después de Indonesia, Nueva Guinea y Brasil es el cuarto país con mayor deforestación a nivel mundial, y sólo durante el período 2000-2005 se perdieron 1.3 millones de hectáreas de bosque (FAO 2007). Para revertir esta situación y establecer estrategias de conservación apropiadas, es prioritario realizar estudios más profundos sobre la contribución relativa de las diferentes especies de dispersores en la regeneración de los hábitats fragmentados.

En este sentido, los primates representan uno de los grupos de dispersores primarios más importantes en los bosques tropicales (Stevenson 2000, Peres & van Roosmalen 2002, Chapman & Russo 2006, Stevenson & Aldana 2008), y se ha comprobado que en conjunto pueden movilizar el doble del total de semillas dispersadas por las aves (Clark *et al.* 2001). De acuerdo con Sussman (1991), la gran diversificación evolutiva de las angiospermas en los trópicos está estrechamente asociada con la evolución de los primates frugívoros, hace unos 65 millones de años (Milton 1993). Sin embargo, no todos los primates son igualmente eficientes como dispersores de semillas y, por tanto, su contribución relativa a la regeneración del bosque puede variar considerablemente. Por ejemplo, algunos primates actúan principalmente como depredadores, y son capaces de masticar y digerir las semillas (e.g., *Propithecus diadema*; Overdorff & Strait 1998). Otros primates pueden actuar ya sea como depredadores de semillas o como dispersores para una misma especie de planta (e.g., *Papio anubis*; Kunz & Linsenmair 2007). Finalmente, muchos primates en el Paleotrópico (e.g., *Gorilla gorilla*: Voysey *et al.* 1999; *Pan troglodytes, Cercopithecus ascanius*:

Lambert 1998; *Hylobates muelleri*: McConkey & Chivers 2007) y en el Neotrópico (e.g., *Ateles* spp: Chapman 1989, Dew 2008; *Lagothrix lagotricha*: Stevenson 2000, 2007; *Cebus capucinus*: Wehncke *et al.* 2003) funcionan como dispersores especializados, y son capaces de tragar, defecar en condición intacta, y dispersar a una distancia considerable (> 100 m) las semillas de muchas especies de plantas. Esto pese al costo energético que representa para el animal acarrear en su estómago grandes volúmenes de semillas que limitan la cantidad total de alimento que puede ingerir a lo largo del día.

En el Neotrópico la mayoría de estos estudios, se han enfocado en un pequeño grupo de primates que habitan en bosques continuos y se han evaluado solamente algunos aspectos aislados de la ecología alimenticia (diversidad dietética: Nunes 1998, Pinto & Setz 2004, Cristóbal-Azkarate & Arroyo-Rodríguez 2007; variación estacional en la dieta: Hemingway & Bynum 2005); y de la eficiencia de dispersión (e.g., selección de frutos: Stevenson 2004, Martins 2008, Stevenson & Link 2010; cantidad de semillas dispersadas: Link & Di Fiore 2006). Además, la contribución relativa de los primates frugívoros a la regeneración de la comunidad vegetal en fragmentos y en bosques continuos es un tema que permanece prácticamente inexplorado (pero ver Stevenson & Aldana 2008).

Pese a lo anterior, la evidencia disponible sugiere que la eficiencia de los primates neotropicales como dispersores es muy variable en términos del porcentaje de frutos en la dieta, el número de semillas en las excretas, el patrón de defecación y el efecto del tracto digestivo sobre la germinación. Por ejemplo, el porcentaje de frugivoría puede variar entre un 2% (*Alouatta seniculus*: Orihuela-López *et al*. 2005) y un 87% (*Ateles belzebuth*: Dew 2008). La diversidad de semillas en las excretas varía de 9 especies (*A. palliata*: Wehncke *et al*. 2004) hasta133 especies (*Ateles belzebuth*: Link & Di Fiore 2006). De igual forma, el patrón de defecación en algunos casos puede ser agregado (e.g., *Alouatta seniculus*:

Andresen 2002) y en otros es espaciado (e.g., *Cebus capucinus*: Wehncke *et al*. 2004, *Ateles belzebuth*: Di Fiore *et al*. 2008). Finalmente, se han encontrado efectos variables del tracto digestivo sobre la germinación de las semillas, pero en términos generales prevalecen los efectos positivos (e.g., en el 75% de especies defecadas por *Alouatta guariba*: Martins 2006; y en el 56% de las defecadas por *Cebus capucinus*: Wehncke & Dalling 2005).

Los servicios ecológicos brindados por los primates frugívoros (e.g., *Ateles* spp.) pueden tener considerables repercusiones a nivel de conservación. Por ejemplo, éstos podrían ser importantes aliados para lograr la regeneración y el mantenimiento de ecosistemas severamente fragmentados, como es el caso de la gran mayoría de bosques tropicales (FAO 2007). Diversos estudios con poblaciones de primates frugívoros en fragmentos y bosques continuos de África, indican que estos animales contribuyen activamente a la regeneración de los parches boscosos puesto que facilitan el flujo de semillas entre parches (Onderdonk & Chapman 2000, Chapman *et al.* 2007). En Sudamérica se ha encontrado que el reclutamiento de las especies con semilla grande (>1 cm de diámetro) en bosques con o sin presiones de cacería, depende principalmente de un pequeño grupo de dispersores como *Ateles*, *Alouatta* y *Lagothrix* (Julliot 1997, Peres & van Roosmalen 2002, Nuñez-Iturri & Howe 2007, Nuñez-Iturri *et al.* 2008). Así, se ha demostrado que la desaparición de especies de primates frugívoros como *Ateles belzebuth* y *L. lagotricha* afecta negativamente el reclutamiento y la abundancia de especies de semilla grande en el bosque tropical húmedo de La Macarena, Colombia (Stevenson & Aldana 2008). Un patrón similar también se ha observado para fragmentos boscosos de la Selva Lacandona, México, en los que ha desaparecido *Alouatta prigra* (A. González-Di Pierro *et al.* datos no publicados). Todo esto sugiere que la eventual desaparición o reducción de las poblaciones de los primates, acarrearía profundos cambios en las tasas de reclutamiento de plántulas y por ende, en la estructura y la composición de las futuras comunidades de plantas.

Escasez de recursos y cambios conductuales en los primates

La escasez espacial y temporal de recursos alimenticios puede alterar considerablemente el comportamiento de muchas especies de primates (Jones 2005). Por ejemplo, la diversidad y abundancia de especies de árboles que producen frutos carnosos importantes en la dieta de los primates frecuentemente es menor en fragmentos (Onderdonk & Chapman 2000, Arroyo-Rodríguez *et al.* 2007) y durante la estación seca (Chapman 1987, Hemingway & Bynum 2005). Entre los principales ajustes adaptativos que pueden realizar los primates en respuesta a la escasez de alimento y/o condiciones climáticas adversas se encuentran: (1) diversicar la dieta incluyendo un mayor consumo de partes vegetales de bejucos, arbutos y palmas (e.g., Onderdonk & Chapman 2000, Cristóbal-Azkarate & Arroyo-Rodríguez 2007), (2) compensar la menor disponibilidad de frutos con un mayor consumo de material foliar (Onderdonk & Chapman 2000, Hemingway & Bynum 2005, González-Zamora *et al.* 2009), y (3) reducir el tiempo invertido en actividades energéticamente costosas como la locomoción mientras que incrementan el tiempo dedicado al descanso (Campos & Fedigan 2009, Korstjens *et al.* 2010). En este último caso, los primates se ven forzados a descansar más tiempo debido a que es una demanda fisiólogica de una dieta más folívora (Milton 1981, Lambert 1998).

En el caso particular de los primates frugívoros, los ajustes conductuales anteriores se podrían traducir en un menor nivel de frugivoría (e.g., *C. capucinus*, *Ateles geoffroyi*: Chapman 1987, *A. chamek*: Wallace 2008), lo cual afectaría directamente la cantidad y diversidad de semillas defecadas, y por ende, la composición del banco del plántulas, tal y como se mencionó anteriormente en el caso de *A. belzebuth* y *L. lagotricha*. Además, se ha reportado que la menor calidad y abundancia de recursos alimenticios en fragmentos y el aumento de la temperatura durante la estación seca, puede obligar a ciertos primates frugívoros a incrementar el tiempo dedicado a la alimentación para obtener suficientes nutrientes del material foliar, lo cual también puede alterar el tiempo dedicado a la locomoción y al descanso (e.g., *Papio* spp.: Dunbar 1992; *A. geoffroyi* Korstjens *et al.* 2010).

Importancia de *Ateles geoffroyi* como dispersor de semillas

El mono araña (*Ateles geoffroyi*) es uno de los más importantes dispersores de semillas del Neotrópico debido a su alto nivel de frugivoría y a la diversidad de frutos que consumen (Russo *et al.* 2005, González-Zamora *et al.* 2009). La evidencia disponible indica que los monos araña son dispersores importantes para la regeneración de las comunidades de plantas. Por ejemplo, *Ateles* spp. es capaz de ingerir semillas hasta de 5 cm (Peres 1994), y de dispersar miles de semillas de cientos de especies (van Roosmalen 1985, Link & Di Fiore 2006, Dew 2008), por distancias > 100 m (Suarez 2006, Di Fiore & Campbell 2007). En la Isla Barro Colorado, Panamá y en diferentes países de Sudamérica, *Ateles* spp. dispersa semillas de más de 100 especies de plantas distribuidas en unos 59 géneros (Campbell 2000, Russo *et al.* 2005, Dew 2008). A través de Mesoamérica, *A. geoffroyi* se alimenta de 364 especies de plantas de 76 familias (González-Zamora *et al.* 2009) y es un importante dispersor de diferentes especies de *Brosimum, Bursera, Ficus, Poulsenia, Pouteria, Spondias* y *Virola* entre otras (Estrada *et al.* 2004a, Russo *et al.* 2005, González-Zamora *et al*. 2009).

Sin embargo, a lo largo de la distribución geográfica de *A. geoffroyi*, las investigaciones realizadas se han enfocado en aspectos como la filogenia (Collins & Dubach 2000, Collins 2008), la demografía (Cant 1978, Estrada *et al.* 2002, 2004a), la conducta y la estructura social (Riba-Hernández *et al.* 2005, Ramos-Fernández *et al.* 2006, 2009), la fisiología (Milton 1981, Laska *et al.* 2006, Rangel-Negrín *et al.* 2009), y la dieta en bosques continuos (Di Fiore *et al.* 2008, González-Zamora *et al*. 2009). Pero los estudios sobre su dieta en hábitats contrastantes (e.g., bosques continuo y fragmentos boscosos), su función en la dispersión de semillas, su capacidad para realizar ajustes en los patrones de actividad en respuesta a la escasez de alimento, y sobre el efecto que pueda tener en la composición del banco del plántulas en hábitats alterados (e.g., fragmentos boscosos de diferentes tamaños) están prácticamente ausentes. La ausencia de estos estudios es evidente en el caso de México, ya que *A. geoffroyi* ha sido considerablemente menos estudiado que las dos especies de *Alouatta* (*A. palliata* y *A. pigra*), y el 90% del total de investigaciones sobre esta especie (44% de las cuales se han realizado en cautiverio) se han enfocado en aspectos ecológicos y demográficos (Estrada & Mandujano 2003, Estrada *et al.* 2004a,b), en la dieta (ver González-Zamora *et al*. 2009), en la estructura social (Ramos-Fernández *et al.* 2009) y más recientemente, en el efecto de su ausencia sobre el reclutamiento de algunas especies de semilla grande (e.g., *Manilkara zapota*: Gutiérrez-Granados & Dirzo 2010).

Esta información es de gran importancia para: (1) entender mejor las interacciones entre los monos araña y las plantas de las que se alimenta, (2) mejorar nuestro conocimiento sobre la contribución de esta especie (y otros primates frugívoros) a la regeneración de la selva, y (3) dilucidar cuáles son los mecanismos que le permiten a esta especie lidiar con el estrés ambiental en fragmentos y durante la estación seca. En el contexto de ecosistemas altamente degradados, como en el caso de ciertas regiones de la

Selva Lacandona (ver Mendoza & Dirzo 1999), la información que se presenta en los cuatro capítulos de esta tesis contribuirá a mejorar nuestro conocimiento sobre la ecología de *A. geofroyi* en bosque continuo y en fragmentos y, en particular, al entendimiento de los factores bióticos y abióticos que afectan la regeneración del bosque y la sobrevivencia de frugívoros críticamente amenazados, como es el caso de los monos araña.

Objetivo general

Determinar la contribución relativa de *A. geoffroyi vellerosus* a la regeneración de las comunidades de plantas presentes en un bosque continuo y en fragmentos de bosque en la Selva Lacandona, y su capacidad para realizar cambios conductuales que le permitan lidiar con la menor disponibilidad de frutos en fragmentos y durante la estación seca.

Objetivos específicos

Capítulo I.

1) Someter a prueba la hipótesis de que los cambios en la disponibilidad de alimento entre fragmentos y bosque continuo resultan en cambios en la dieta de las comunidades de monos araña en ambos tipos de hábitat.
2) Determinar la diversidad de la dieta en bosque continuo y en fragmentos.
3) Determinar cuáles son las especies de plantas, módulos vegetales, y formas de crecimiento más importantes en la dieta del mono araña en ambos hábitats.
4) Evaluar la relación de la variación en la dieta con cambios en la disponibilidad de alimento en ambos hábitat.

Capítulo II

1) Someter a prueba la hipótesis de que *A. geoffroyi* es un dispersor eficiente tanto en bosque continuo como en fragmentos.
2) Evaluar cómo varía la eficiencia como dispersor del mono araña en bosque continuo y en fragmentos.
3) Determinar el tipo de manipulación de las semillas de las especies más importantes en la dieta en bosque continuo y fragmentos.
4) Determinar el patrón de defecación y la diversidad y condición de las semillas defecadas en ambos hábitats.
5) Determinar el efecto del tracto digestivo sobre el porcentaje de germinación de las semillas.

Capítulo III

1) Someter a prueba la hipótesis de que para lidiar con la limitación de alimento en fragmentos y durante la estación seca, los monos araña son capaces de de ajustar el tiempo que invierten en sus actividades vitales (i.e., alimentación, descaso y locomoción) para minimizar los costos energéticos de las mismas.
2) Determinar el efecto del hábitat (continuo y fragmentado), la estación (seca y lluviosa) y la interacción entre ambos factores sobre los patrones de actividad del mono araña.
3) Discutir los resultados en relación con las variaciones en la dieta de estos mismos grupos de monos descrita en el capítulo I, así como las implicaciones que podría tener la flexibilidad conductual de esta especie para la conservación.

Capítulo IV

1) Someter a prueba la hipótesis de que la desaparición de monos araña en fragmentos altera la composición de plántulas, limitando el reclutamiento de las especies con semilla grande (>1.5 cm de diámetro).
2) Comparar la abundancia, riqueza, y diversidad de plántulas de acuerdo con su mecanismo de dispersión (i.e., si son dispersadas por primates, por mamíferos pequeños, o por medios abióticos) en bosque continuo, fragmentos con monos y fragmentos sin monos.
3) Determinar el efecto relativo de la abundancia de monos araña, la riqueza de frugívoros grandes, la composición de árboles adultos y las características de los fragmentos sobre los patrones observados.

Predicciones

Capítulo I

1) Debido a que en los fragmentos existe una menor disponibilidad de árboles grandes que producen frutos importantes en la dieta de *A. geoffroyi* en comparación con el bosque continuo, los monos se verán obligados a diversificar su dieta y a consumir más material foliar.
2) En ambos hábitats, la mayor parte del tiempo de alimentación estará enfocado en un pequeño grupo de especies pertenecientes a las familias Anacardiacae, Fabaceae y Moraceae, entre otras, tal y como se ha reportado para otras comunidades de monos araña en Mesoamérica (González-Zamora *et al.* 2009).

Capítulo II

1) Debido a los hábitos frugívoros del mono araña, a su capacidad para tragar semillas grandes, a su alta movilidad, y a su patrón de defecación espaciado (Peres 1994, Russo *et al.* 2005, Di Fiore *et al*. 2008), se espera que sean dispersores eficientes en términos cuantitativos y cualitativos en boque continuo y en fragmentos.
2) Debido a que en fragmentos la disponibilidad de frutos para los monos frecuentemente es menor que en bosque continuo (Arroyo-Rodríguez *et al.* 2007), se espera que en fragmentos los monos traguen menos semillas, y que sea menor el número de especies de semillas defecadas y el número de excretas sin semillas.

Capítulo III

1) Para compensar la menor abundancia y calidad de alimento en los fragmentos y durante la estación seca en comparación en el bosque continuo y en la estación lluviosa, los monos dedicarán más tiempo a la alimentación.
2) Debido a que en fragmentos y durante la estación seca muchos primates optan por aumentar el consumo de material foliar (Onderdonk & Chapman 2000, Hemingway & Bynum 2005), los monos araña invertirán más tiempo en descanso para poder digerir este material.
3) Los monos araña invertirán menos tiempo en actividades energéticamente costosas como la alimentación y la locomoción (Suarez 2006, Campos & Fedigan 2009) en la época seca que en la época lluviosa.

Capítulo IV

1) En fragmentos sin monos araña, la composición de plántulas será distinta a la de los fragmentos con monos y el bosque continuo. Específicamente, en fragmentos sin monos serán más abundantes las especies dispersadas por medios abióticos y menos abundantes las especies dispersadas por primates, en comparación con los otros dos hábitats.
2) Las especies más afectadas por la ausencia del mono araña serán las de semilla grande (>1.5 cm de largo), ya que como se mencionó arriba, entre más grande es la semilla, más reducido es el gremio de dispersores potenciales que pueden ingerirlas (Jordano 2000).
3) La composición de plántulas en cada hábitat estará explicada principalmente por la presencia de monos araña.

Área de estudio

Esta investigación se llevó a cabo durante un período de 17 meses (enero-junio y agosto-noviembre del 2007, y febrero-mayo y julio-septiembre de 2008) en la región de la Selva Lacandona, Chiapas, México (16°05'58" N, 90º52'36" W; elevación 10-50 m snm). Esta zona contiene el bosque tropical lluvioso más grande de Mesoamérica (ca. 300,000 ha) y comprende bosques de México, Guatemala y Belice (Dirzo 1994). La región es altamente estacional, y se pueden diferenciar con claridad una estación lluviosa (junio-diciembre) y una estación seca (enero-mayo). La precipitación promedio anual es 2881mm, la mayor parte de la cual se concentra en los meses de junio a septiembre (variando de 423 a 511 mm mes^{-1}). La temperatura promedio anual es 24 °C, variando de 20 a 25 °C/mes en la estación lluviosa y de 22 a 28 °C/mes durante en la estación seca (Comisión Federal de Electricidad, México, http://app.cfe.gob.mx/Aplicaciones/QCFE/Meteorologico /WebForms/Bol_Matutino.aspx). La vegetación original está representada por el bosque lluvioso y el bosque lluvioso semideciduo, con un gradiente altitudinal que varía entre 60 y 2450 msnm (Mendoza & Dirzo 1999).

Desde su colonización en los años 1960, la cobertura forestal original (aproximadamente 500,000 ha) de la región de la Selva Lacandona en México se ha reducido en una tercera parte, y actualmente la mayoría de bosques remantes se encuentra en la Reserva de la Biósfera Montes Azules (Mendoza & Dirzo 1999). En esta zona el bosque está dominado por plantas perennifolias de bosque lluvioso como *Brosimum alicastrum*, *Swietenia macrophylla*, y *Pouteria campechiana*. También existen zonas de bosque ripario con especies como *Spondias radlkoferi*, *Ficus glabrata*, y *Lonchocarpus guatemalensis*. Además, esta región es de una importancia clave para la conservación, ya que alberga la mayor diversidad biológica de México, con alrededor del 25% del total de especies de plantas y animales reportadas hasta la fecha en un área inferior al 1% de la superficie del país (Medellín 1996). Por ejemplo, existen al menos 4300 especies de plantas vasculares (Martínez *et al.* 1994), 112 especies de mamíferos (Medellín 1994), 340 especies de aves y 800 especies de mariposas diurnas (De la Maza & De la Maza 1991).

Sitios de estudio

El estudio se concentró en tres sitios de bosque continuo de la Reserva de la Biósfera Montes Azules (REBIMA), en tres fragmentos de bosque con *A. geoffroyi* y en tres fragmentos de bosque sin *A. geoffroyi* ubicados en el municipio de Marqués de Comillas (Fig. 1). Esta última región ha estado sometida a una considerable deforestación desde que fue colonizada por el ser humano a inicio de los años sesentas (Marquez-Rosano 2006). En general, el tamaño de los grupos de estudio varió entre 35 y 44 individuos. Todos los fragmentos con y sin monos fueron aislados hace al menos17 años y sus tamaños varían de 6.4 a 1125 ha (Cuadro 1). Tanto en los fragmentos con monos con los fragmentos sin monos, la distancia al parche boscoso más cercano varía entre 100 m y 450 m (Cuadro 1), y en la mayoría de los casos están rodeados por una matriz antropogénica mixta, constituida principalmente por pastizales, plantaciones de cacao y/o especies forestales (e.g., *Cedrella odorata* y *Swietenia humilis*), y por acahuales o bosques secundarios de diferentes edades. Además, en contraste con el bosque continuo y los fragmentos con monos, en los fragmentos sin monos la mayoría de frugívoros grandes están ausentes (ver capítulo IV).

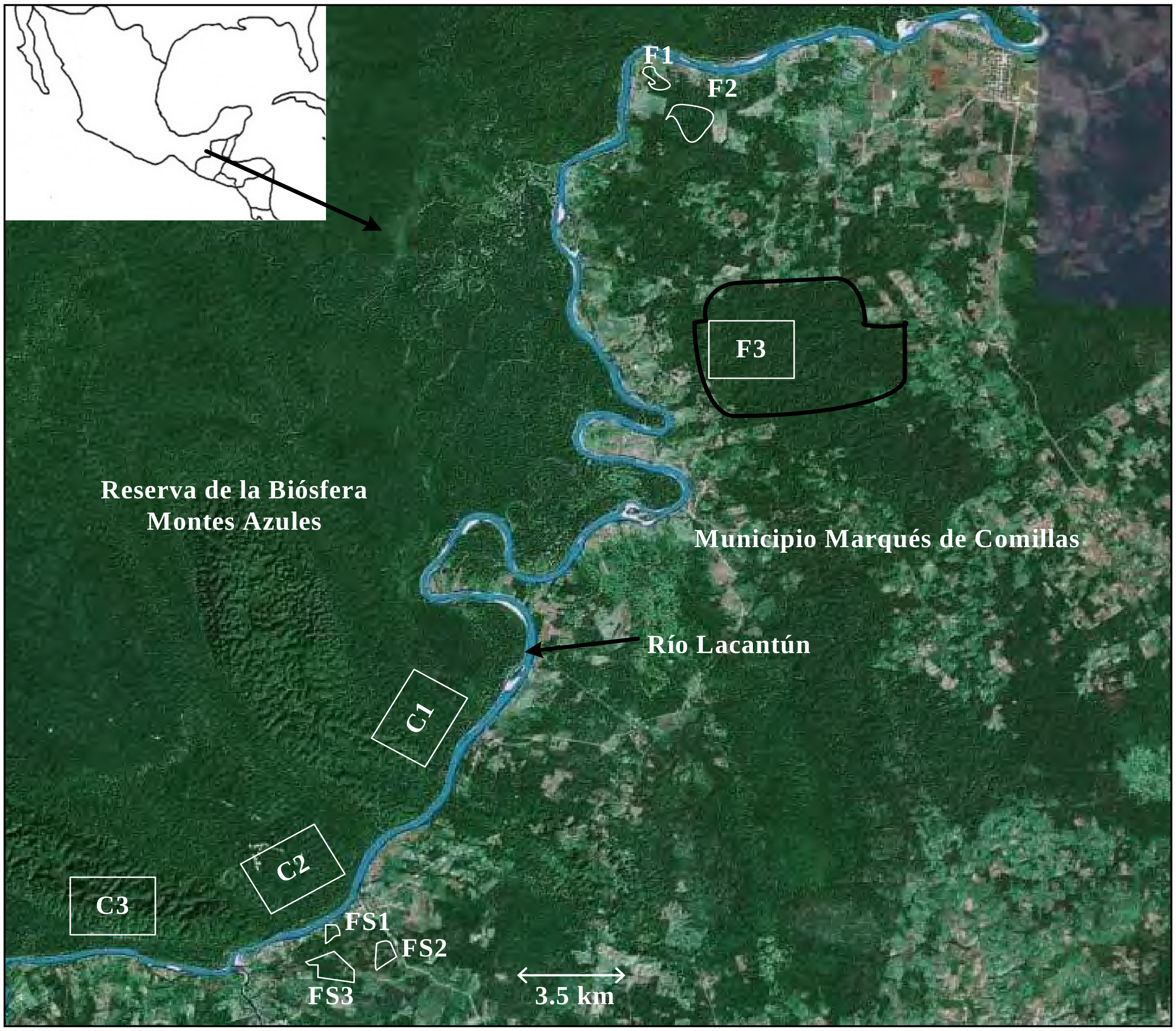

Fig. 1. Distribución espacial de los sitios de bosque continuo (C1, C2, C3), los fragmentos con monos (F1, F2, F3) y los fragmentos sin monos (FS1, FS2, FS3). En el Cuadro 1 se indican las principales características de cada sitio.

Cuadro 1. Descripción de los sitios de estudio en la Selva Lacandona, Chiapas, México.

Sitio	Tamaño (ha)	Localización	DF (m)[a]	DB (m)[b]	AF[c]	Grupo[d]	TD[e]
Bosque Continuo	331,000	Montes Azules					
CF1	–	16°06'58.2"N, 90°56'18.4"W	–	–	–	40	–
CF2	–	16°09'32.0"N, 90°54'06.6"W	–	–	–	36	–
CF3	–	16°09'40.0"N, 90°54'04.5"W	–	–	–	44	–
Fragmentos con monos		Marqués de Comillas					
F1	14.4	ejido Zamora Pico de Oro (16°19'52.0"N, 90°51'06.1"W)	450	200	29	35	–
F2	31	ejido Zamora Pico de Oro (16°19'24.5"N, 90°50'43.7"W)	150	1200	24	39	–
F3	1125	ejido Reforma Agraria (16°15'12.2"N, 90°49'59.5"W)	100	1100	26	41	–
Fragmentos sin monos		Marqués de Comillas					
FS1	6.4	ejido Boca de Chajul (16°06'39.5"N, 90°56'04.6"W)	200	150	25	0	15
FS2	11.4	ejido Boca de Chajul (16°06'15.7"N, 90°55'34.9"W)	160	1400	25	0	22
FS3	28	ejido Boca de Chajul (16°06'02.0"N, 90°56'03.7"W)	125	990	17	0	16

[a] Distancia al fragmento más cercano

[b] Distancia al bosque continuo

[c] Años de haber sido fragmentado

[d] Número de individuos en cada grupo de monos araña (incluyendo adultos, juveniles e infantes)

[e] Tiempo de desaparición de los monos araña (en años)

Especies de primates en el área de estudio

En la Selva Lacandona existen dos especies de primates: el mono araña (*Ateles geoffroyi vellerosus* Kuhl 1820) y el mono aullador negro (*Alouatta pigra*). *Ateles geoffroyi* está distribuido en bosques continuos y remanentes boscosos de diversos tamaños, desde el estado de Veracruz, en México, hasta el extremo norte del Chocó, Colombia (Rylands *et al.* 2006). En México se presentan las subespecies *A.g. vellerosus* y *A.g. yucatanensis* (Estrada *et al.* 2004a), la primera de las cuales está distribuida en el sureste del país y la segunda se encuentra restringida a la península de Yucatán (Watts & Rico-Gray 1987). Por su parte, *Alouatta pigra* Lawrence 1933 es una especie endémica del sureste de México, Belice y Guatemala (Rylands *et al.* 2006). En Montes Azules la densidad poblacional de *A. geoffroyi* se ha estimado en 2.9 ind/km^2, y para *A. pigra* ésta se ha estimado en 14.4 ind/km^2, mientras que una estimación cruda de las poblaciones de estas dos especies en un fragmento grande de Marqués de Comillas (fragmento F3, ver Cuadro 1), indica que en estos hábitats la densidad es 9.3 y13.3 ind/km^2, respectivamente (Estrada *et al*. 2004b). En general, los monos aulladores se caracterizan por tener un ámbito hogareño pequeño (1–62 ha: Ostro *et al.* 1999), una dieta fundamentalmente folívora, y por ser relativamente tolerantes a la fragmentación (Di Fiore & Campbell 2007). En contraste, los monos araña presentan un ámbito hogareño más amplio (37–98 ha: Fedigan *et al*. 1988) y una dieta especializada en frutos maduros (39 a 82% del tiempo total de alimentación) que combina con hojas, flores, y madera podrida (González-Zamora *et al*. 2009). Además, debido a su preferencia por el bosque conservado, sus amplios requerimientos espaciales, la cacería, y la pérdida de su hábitat natural, actualmente se encuentran clasificados en la lista roja de IUCN como especie críticamente amenazada (Ramos-Fernández & Wallace 2008). Debido a las anteriores características, las poblaciones de monos araña son más vulnerables a la pérdida de hábitat y la fragmentación del bosque que los monos aulladores (Boyle 2008, Ramos-Fernández & Wallace 2008).

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CAPÍTULO I

Differences in Diet between Spider Monkey Groups Living in Forest Fragments and Continuous Forest in Lacandona, Mexico

(accepted with minor corrections 10 March 2010, Biotropica, IF=2.17)

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Received______; revision accepted______.

ABSTRACT

Fragmentation can lead to an important reduction in food availability, especially for some large-bodied tropical mammals such as spider monkeys. Information on species' behavioral responses to these changes is critical for species conservation; however, little is known about this topic. During a 15-mo period, we assessed the diet of the largest Mesoamerican primate species – the spider monkey– in continuous forest and forest fragments in the Lacandona region of Chiapas, southern Mexico, and related differences in diet to differences in composition and vegetation structure between forest types. Compared with the continuous forest, spider monkeys in fragments: (1) diversified their overall diet, (2) increased consumption of immature and mature leaves, and (3) reduced time feeding on trees with a consequent increase in time feeding on hemiepiphytes (particularly *Ficus* spp.) and palms, both of which were common in fragments. We attribute these differences in diet to a probable response to food scarcity in fragments, as both the sum of the importance value index of top food species and the density of large trees were lower in fragments than in continuous forest. Overall, our findings suggest that spider monkeys are able to adjust their diet according to food availability in fragments, and thus persist in many small and medium-sized fragments. We show that some forest fragments harbor high plant diversity, providing important food sources for spider monkeys. We suggest that these fragments may function as stepping stones that increase the landscape's connectivity facilitating inter-fragment movements and ultimately enhancing seed dispersal.

*Key words***:** food availability; forest fragmentation; dietary flexibility; Neotropical primates.

ACCELERATED DEFORESTATION, FRAGMENTATION AND TRANSFORMATION of tropical rainforests around the world are considered to be the main reasons for the global decline in animal populations (*e.g.*, butterflies, fish, and mammals: Brook *et al.* 2003, birds: Sehgal 2010). These threats are particularly important in tropical primates (Cowlishaw & Dunbar 2000, Marsh 2003a), including spider monkeys (*Ateles* spp.). Owing to their large body, their large home range requirements (Fedigan *et al.* 1988), their low fecundity (Campbell & Gibson 2008), high hunting pressure (Duarte-Quiroga & Estrada 2003) and the drastic human alteration of their natural habitats (Ramos-Fernández & Wallace 2008), *Ateles geoffroyi* could be one of the first Mesoamerican primates to become locally extinct in the coming decades (Garber *et al.* 2006). Indeed, as a probable consequence of habitat fragmentation and disturbance, from the seven subspecies of *A. geoffroyi* recognized by Collins & Dubach (2000), six are currently included in the IUCN red list (Vulnerable: *A. g. frontatus*; Endangered: *A. g. ornatus, A. g. yucatanensis*; Critically Endangered: *A. g. panamensis*, *A. g. geoffroyi*, *A. g. vellerosus*; Cuarón *et al.* 2008).

One of the most frequent threats posed by forest fragmentation is the reduction in the food supply for different animal taxa (*e.g.*, birds: Robinson 1998; primates: Arroyo-Rodríguez *et al.* 2007). For instance, primates in fragments may face a loss of important food resources (see Marsh 2003a, Arroyo-Rodríguez & Dias 2009). In smaller fragments, home range size is usually smaller, limiting the amount of resources available to each group (*e.g.*, Bicca-Marques 2003, Chapman *et al*. 2007, Cristóbal-Azkarate & Arroyo-Rodríguez 2007). Additionally, as fragments become smaller, more irregularly shaped, and more isolated, their floristic composition, plant species diversity, and vegetation structure are increasingly modified (Hill & Curran 2003, Arroyo-Rodríguez & Mandujano 2009). Changes in vegetation structure that can reduce food availability to primates in fragments include the loss of large food trees (Arroyo-Rodríguez & Mandujano 2006, Dunn *et al.* 2009) and the reduction of plant species richness (Norconk & Grafton 2003, Arroyo-Rodríguez & Mandujano 2009). Since larger trees produce more fruits than smaller ones (Chapman *et al.* 1992), the reduction in richness and abundance of large trees could negatively affect the survival of many tropical primates (*e.g*., *A. palliata*: Arroyo-Rodríguez *et al*. 2007; *Protocolobus pennantii*, *Colobus guereza*: Onderdonk & Chapman 2000), especially in the case of highly frugivoruous monkeys such as *Ateles* spp. (Di Fiore *et al.* 2008, González-Zamora *et al.* 2009).

Under this scenario, the persistence of primate populations/species in fragments largely depends on their ability to adjust their diet to food shortage (*e.g.*, *Alouatta pigra*: Rivera & Calmé 2006, *A. palliata*: Dunn *et al*. 2009, *A. seniculus*, *Ateles paniscus*, *Cebus apella*: Boyle 2008). Evidence suggests that the success of primates in coping with habitat fragmentation is related to their capacity to: (1) diversify their diet by feeding from many different plant species/items, and adjust their diet to the species available in their habitat (Silver & Marsh 2003, Cristóbal-Azkarate & Arroyo-Rodríguez 2007, González-Zamora *et al*. 2009), (2) consume exotic and secondary successional species frequent in disturbed habitats (Onderdonk & Chapman 2000, Cristóbal-Azkarate & Arroyo-Rodríguez 2007), and/or (3) rely on some keystone food resources (*e.g.*, *Ficus* spp.: Cristóbal-Azkarate & Arroyo-Rodríguez 2007). Without these important feeding adjustments, primates may face episodes of generalized famine, which can affect their long-term persistence (Milton 1990, Hanya *et al.* 2004).

Studies about diet and feeding behavior of atelids are largely focused on more folivorous species such as howler monkeys (*Alouatta* spp.) and biased toward continuous forests (reviewed by Di Fiore & Campbell 2007). Although recent papers have reviewed the diet of spider monkeys throughout their range (Di Fiore *et al.* 2008, González-Zamora *et al.* 2009), little is known about their ability to adjust their diet to food shortage in fragments. The little available data show that spider monkeys increase the consumption of leaves in small unprotected forest fragments compared to large protected forests (González-Zamora *et al.* 2009), but the potential relationship between their diet shifts and local structure of vegetation remain unexplored.

We evaluate differences in diet of *A. geoffroyi* between continuous forest and forest fragments in the Lacandona rainforest, southeastern Mexico, and relate these differences to the composition and structure of vegetation within both forest types. In particular, we evaluate differences in: (1) dietary diversity; (2) top food plant species (*i.e.*, those comprising > 80% of total feeding time); (3) relative contribution of different plant items and plant growth forms to the diet; and (4) overlap of plant species in the diet between habitats. We hypothesized that the changes in food availability for spider monkeys between fragments and continuous forest result in dietary differences between monkey groups living in both forest types. We expect that lower structural and compositional diversity of vegetation in forest fragments will result in a more diverse diet including less nutritious food items. Assessing the changes in diet of spider monkeys in continuous and fragmented forests will be critical for the design and establishment of appropriate management strategies for the conservation of this and many other frugivorous species (Di Fiore *et al.* 2008)

METHODS

STUDY SPECIES.—The black-handed spider monkey (*Ateles geoffroyi* Kuhl, 1820) is the largest Mesoamerican primate species, and is distributed from Mexico, throughout most of Central America to the border of Panama and Colombia (Rylands *et al.* 2006). Spider monkeys are characterized by having a highly frugivoruous diet, large home range requirements, rapid speed of travel, and a fission-fusion social organization in which the multi-male/multi-female community regularly divides into subgroups of fluctuating size and composition for foraging (Di Fiore & Campbell 2007).

STUDY AREA AND STUDY SITES.—Fieldwork was conducted in the Lacandona rainforest, southern Chiapas, Mexico (16°05'58" N, 90º52'36" W; elevation 10–50 m a.s.l.). The study was conducted in two areas separated by the Lacantún river: the Marqués de Comillas region (MCR, eastern side of the river), and the Montes Azules Biosphere Reserve (MABR, western side). Covering parts of Mexico, Guatemala, and Belize, this region encompasses the largest portion of tropical rainforest in Mesoamerica and one of the most important in the Neotropics (Dirzo 1994). The original vegetation in the area is tropical wet forest and semideciduous rainforest. The climate in the region is hot and humid with 24 °C average temperature and 2881 mm average annual rainfall. The greatest rainfall concentration is found in June-September (range: 423–511 mm/month), and the lowest in February-April (46–61 mm/month) (Comisión Federal de Electricidad, Mexico, unpubl. data).

Human colonization of MCR began in the 1960s and 1970s and cattle ranching resulted in the rapid disappearance and fragmentation of the forest (Mendoza & Dirzo 1999). Approximately 50% of the land surface of MCR is nowadays used for agricultural purposes, but small (0.5–30 ha) and large (850–1500 ha) fragments still remain in the area. The protected area of MABR was created in 1978 and consists of approximately 300,000 ha of undisturbed forest.

STUDY SITES AND MONKEY GROUPS.—We studied the diet of six groups of spider monkeys: three independent groups in three different areas of the MABR separated by at least 4 km, and three groups in three different fragments located in MCR. All fragments in MCR were isolated ≥ 24 years ago, and their sizes were 14, 31, and 1125 ha (Table S1). Distances among fragments were ≥ 100 m, and distances from fragments to MABR ranged from 200 to 1400 m. Spider monkeys' group size ranged from 35 to 44 individuals (Table S1). For the three study sites of MABR and for the largest fragment, we restricted our data collection of spider monkey groups to an area of 30–90 ha (according to the home range recognized a posteriori for each focal group, see *Supporting information*), whereas for the other two smaller fragments the entire area was sampled.

DIET.—Diet of spider monkeys was studied during a 15-mo period (6 mo in the dry season: February-April 2007 and 2008; and 9 mo in the rainy season: May-October 2007, and August-October 2008). Diet was documented for each of the six focal groups during three consecutive days once every three weeks, using 5-min focal animal sampling (Altmann 1974). During the follows, spider monkeys were sighted with the aid of visual and auditory cues (*e.g.*, vocalizations, rustling tree crowns, and dropping branches or fruits) and high resolution binoculars (Swarovski SLC 10 x 42). Individuals were identified through unique marks found in skin pigmentation, hair, and other distinguishing marks (*i.e.*, scars). Focal animals were randomly changed at 5-min intervals or when animals moved out of sight.

Data were collected from 0700 h to 1730 h, totaling 1010 h of focal observations (496 h in continuous forest and 514 h in fragments), from which 448 h (44%) were feeding observations (205 h in continuous forest and 243 h in fragments).

During feeding we recorded the plant species used (hereafter "food plant species") and food item consumed: fruits (mature and immature), leaves (mature and immature), flowers, young branch piths, decayed wood and other plant items (*e.g.*, terminal stipules, roots, bulb, and secretions). Plant growth forms were classified as: trees, shrubs, palms, climbers (vines and lianas), epiphytes, and hemiepiphytes. We report the consumption of plant species, food items and plant growth forms in terms of percentage of total feeding time (TFT), that is, time spent consuming each plant species/item/growth form in relation to the total time spent consuming all plant species/items/growth forms.

DIET OVERLAP.—The annual overlap of fruit and leaves in diet between continuous forest and fragments was calculated using the Morisita-Horn index: $C = 2\sum x_i y_i/(\sum x_i^2 + y_i^2)$, where x_i is the proportion of the fruit/leaves i in the diet of spider monkeys in continuous forest, and y_i is the proportion of the same fruit/leaves in the diet of spider monkeys in fragments. This index ranges from 0 (no diet overlap) to 1 (complete diet overlap) (Krebs 1999).

VEGETATION ATTRIBUTES AND INDICATORS OF FOOD AVAILABILITY.—A posteriori, we sampled vegetation within the home range of each group (see *Supporting Information*) following the Gentry (1982) protocol. Throughout these areas, we randomly located ten 50 x 2 m transects and identified and measured the diameter at breast height (dbh) of all trees, shrubs, and palm species (and woody hemiepiphytes whenever possible) with dbh ≥ 10 cm. We chose this method because it is logistically simple, it is economical (in both time and money), and it is appropriate for the analysis of species diversity in tropical forests (Gentry 1982). Furthermore, since this method has been used to characterize vegetation in several Neotropical forests, and also to characterize the habitat of other Neotropical primates (*e.g.*, *Alouatta palliata*: Arroyo-Rodríguez & Mandujano 2006, Arroyo-Rodríguez *et al.* 2007, Dunn *et al.* 2009), it is possible to compare our data with other Mexican sites. Plant species not identified in the field were collected for later identification using the Lacandona seed reference collection located at the Centro de Investigaciones en Ecosistemas (CIEco, UNAM, Morelia, Mexico). Plant nomenclature followed the Missouri Botanical Garden nomenclatural update database (http://mobot.org/W3T/search/vast.html).

We pooled the transect data for each of the 6 sites and treated each one as a unit for all subsequent analyses. For each site, we quantified species richness, density and basal area for all plant species. Using data from a recent review of spider monkey diet in Mesoamerica (González-Zamora *et al.* 2009), we identified all plant species that constituted > 80 percent of total feeding time in this review paper and that were present in our study plots. We considered these species as potential top food species (Table S2) contributing to resource abundance. Using this information we calculated three indicators of food availability in continuous and fragmented forests: the total number of food plant species (excluding lianas and climbers, which were not sampled in the plots), the density of large trees (> 60 cm in dbh) from top food species, and the sum of the importance value index (IVI) of top food species. In both continuous and fragmented forests, the IVI was calculated for each of the top food plant species based on the sum of density (trees/3000 m^2), frequency (number of transects in which each species appeared/30 transects), and dominance (total basal area for each species in the 3000 m^2) (see Arroyo-Rodríguez *et al.* 2007).

STATISTICAL ANALYSIS.— We used generalized linear models (GLM; Crawley 1993) to test the effect of forest type (continuous or fragmented) on proportion of time consuming each plant item and each growth form. We constructed the following models: PROPORTION OF TIME = PLANT ITEM (or PLANT GROWTH FORM) nested in FOREST TYPE + FOREST TYPE. Proportion data were first arcsine transformed, and we selected a normal distribution with an identity link-function to the response variable (Crawley 1993). To identify which treatments were statistically different between each other we used post-hoc analyses with contrasts (Crawley 1993). To compare the number of food plant species between forest types (continuous and fragmented) we also used GLM. As suggested for count dependent variables, we fixed a Poisson distribution and a log-link function to the response variable (Crawley 1993). We considered each of the three sites per forest type as replicates. The same procedure also was used to compare the number of food plant species and the density of large trees (> 60 cm in dbh) from top food species present in each forest type. In the former case, we previously standardized the sampling effort in each study site to control for differences in species density using the rarefaction approach. All tests were performed with JMP software (version 7.0, SAS Institute Inc., Cary, N.C.).

RESULTS

DIET DIVERSITY.—Overall, spider monkeys fed from a total of 121 plant species (and 53 morphospecies) belonging to 96 genera and 39 families. Diet diversity was higher in fragments (65.7 ± 3.1 species) than in continuous forests (50.3 ± 3.2 species; $\chi^2 = 6.1$, df = 1, $P = 0.01$). This pattern also was observed when comparing the number of top food species: spider monkeys fed from almost twice as many top food species in fragments (11.7

± 2.1 species) than in continuous forest (6.7 ± 0.6 species; $\chi^2 = 4.1$, df = 1, $P = 0.04$) (Table 1).

In both forest types, most top food species were large tree species with fleshy fruits (Table 1). The families that were most used as food sources in both forest types were Moraceae, Anacardiaceae, Fabaceae, and Chrysobalanaceae, together representing ca. 77% of total feeding time (Table 1). Interestingly, monkeys in fragments used more Moraceae species (7 species) and devoted more time foraging on species from this family (39.1% of TFT) than in continuous forest (3 species, 11.5% of TFT). In fragments, spider monkeys exploited more top food species of *Ficus* (4 species, 25.8% of TFT) than in continuous forest (2 species, 7.1% of TFT; Table 1). *Dialum guianense* also was consumed more in fragments (18.3% of TFT) than in continuous forest (3.8% of TFT). However, *Spondias* spp. and *Licania platypus* were consumed notably more in continuous forest (28.7% and 31.2% of TFT, respectively) than in fragments (12.7% and 4.9%, respectively).

CONSUMPTION OF PLANT ITEMS.—Overall, fruit was the most eaten item (55.6% of TFT, 88 species), followed by leaves (18.5%, 66 species), decayed wood (15.7%, 3 species), branches (7.3%, 20 species), flowers (1.2%, 18 species), and other plant items (1.7%, 32 species). However, the proportion of different plant items in the diet of spider monkeys differed significantly between forest types ($\chi^2 = 69.5$, df = 14, $P < 0.0001$), with the consumption of mature and immature leaves being higher in fragments than in continuous forest (contrast tests, $P < 0.05$ in both cases, Fig. 1A).

In general, we found a high overlap between forest types in the plant species used as fruit sources (Morisita-Horn’s index = 0.84). In continuous forest the consumption of mature fruits was focused on *Spondias radlkoferi* (29.6% of the time spent eating mature fruits), *S. mombin* (11.2%), and *Ficus tecolutensis* (10.9%), whereas in fragments it was focused on three *Ficus* species (35.3%), *S. radlkoferi* (13.3%), and *Calatola laevigata* (5.9%). Similarly, the consumption of immature fruits in continuous forest was focused on *S. radlkoferi* (69.3% of the time spent eating immature fruits), whereas in fragments it was focused on *S. radlkoferi* (32.1%), and *Brosimum alicastrum* (27.0%).

We also found a high overlap between forest types in the plant species used as leaf sources (Morisita-Horn's index = 0.82). For example, the consumption of immature leaves was focused on *D. guianense* and *B. alicastrum* in both continuous forests (39.5% and 25.2% of the time spent eating immature leaves, respectively) and fragments (62.5% and 10.2%, respectively). However, in continuous forest consumption of mature leaves was focused on *Machaerium* sp. (43.7% of the time spent eating mature leaves) and *Bravaisia integerrima* (14.1%), while in fragments it was focused on *Ficus* sp. (63.9%).

CONSUMPTION OF GROWTH FORMS.—Overall, in terms of total feeding time, trees were the most consumed plant growth form in terms of total feeding time (73% of TFT, 70 species), followed by hemiepiphytes (17.0%, 11 species), climbers (4.7%, 18 species), epiphytes (2.3%, 11 species), palms (2.1%, 4 species), and shrubs (0.7%, 7 species). The proportion of different growth forms in the diet of spider monkeys differed between forest types (χ^2 = 127.3, df = 14, $P < 0.0001$), with the consumption of trees being higher in continuous forest than in fragments (contrast test, $P < 0.0001$; Fig. 1B), whereas the opposite pattern was found when analyzing hemiepiphytes and palms (contrast tests, $P < 0.05$ in both cases, Fig. 1B). Spider monkeys exploited more hemiepiphytes in fragments (11 *Ficus* species: 29.5% of TFT, and 2 *Philodendron* species: 0.8% of TFT) than in continuous forest (7 *Ficus* species: 9.6% of TFT, and 3 *Philodendron* species: 1.5% of TFT). Similarly, in fragments spider monkeys exploited more palm species (*Attalea butyracea*, *Bactris balanoidea*, *B. mexicana* and *Sabal mexicana*: 3.7% of TFT) than in continuous forest (*Attalea butyracea* and *B. balanoidea*: 0.6% of TFT).

COMPOSITION AND STRUCTURE OF VEGETATION.—We recorded a total of 1774 plants, from 96 species (and 36 morphospecies) belonging to 78 genera and 34 families within the foraging areas. In general, the families with the highest number of individuals were Meliaceae (18%), Malvaceae (17%), Fabaceae (12%), and Moraceae (10%). Both continuous forest and fragments presented top food species for spider monkeys (recognized based on review of spider monkey diet; see methods), and 5 of them (*B. alicastrum*, *D. guianense*, *Guarea glabra*, *L. platypus*, and *S. radlkoferi*) were among the ten species with the highest IVI in both forest types (Table 2). However, the sum of the IVI of top food species was notably greater in continuous forest (IVI = 217) than in fragments (IVI = 149; Table S2). The number of food plant species was similar in both forest types (mean ± SD; 67.5 ± 7.2 species in continuous forest; 64.1 ± 2.1 species in fragments; $\chi^2 = 0.4$, df = 1, $P = 0.5$). However, the density of large trees (> 60 cm in dbh) from top food species was higher in continuous forest (4 ± 1 stems/1000 m^2) than in fragments (1.3 ± 1.1 stems/1000 m^2; $\chi^2 = 4.2$, df = 1, $P = 0.04$).

DISCUSSION

As in most vertebrates, in primates the ability to make shifts in diet in response to environmental pressures influences the costs and benefits of different foraging strategies, affecting nutrient acquisition, survival and reproduction (Felton *et al*. 2009a, MacArthur & Pianka 1966, Harrison 1984, Garber 1987). Our results suggest that, as a probable response to fruit shortage in fragments (*e.g.*, lower IVI of top food species and lower density of large top food trees), spider monkeys in the Lacandona rainforest are able to carry out notable adjustments in their diet. Spider monkeys in fragments: (1) diversified their overall diet; (2) increased consumption of immature and mature leaves; and (3) increased time feeding on non-tree growth forms (*e.g.*, hemiepiphytes and palms).

Based on optimal foraging theory (MacArthur & Pianka 1966), we would expect that the diet becomes less selective when profitable items are less common. Therefore, when and where fruit and top food species are less available (*i.e.*, in fragments), primates should diversify their diets. Other studies also have found that the diet of primates is more diverse in forest fragments than in large forest reserves (*e.g.*, *Alouatta pigra*: Rivera & Calmé 2006, *A. palliata*: Cristóbal-Azkarate & Arroyo-Rodríguez 2007). Also, fruit shortage in fragments could 'force' primates to use foods of lower energetic content and with higher concentration of secondary compounds, such as leaves (Milton 1980, Peres 1994, Cristóbal-Azkarate & Arroyo-Rodríguez 2007, Felton *et al.* 2009a, present study). Therefore, to avoid potential negative health problems (Freeland & Janzen 1974, Glander 1982) and obtain the macronutrients, vitamins and minerals that a primate requires to meet its nutritional needs (Lambert 2007, Felton *et al*. 2009a, 2009b) primates tend to increase the number of plant species when consuming more leaves.

Although we found that spider monkeys are able to switch to a more folivorous diet when necessary (see also Wallace 2005, González-Zamora *et al*. 2009), we do not know if this dietary adjustment may favor their persistence in altered landscapes. This behavior could in fact have negative consequences not only for spider monkeys (Karesh *et al.* 1998, Wallace 2005), but also for the plant assemblage (*e.g.*, reduced seed dispersal efficiency; Chaves *et al.* in press). As the digestive system of spider monkeys appears to be designed essentially for a diet mainly composed of easily digestible food items like fleshly fruits (*e.g.*, they have fast gut passage rates and relatively small hind-gut: Milton 1981, Lambert 1998), this species is apparently constrained in how much folivorous material they are able to digest (Rosenberger & Strier 1989). Karesh *et al.* (1998) and Wallace (2005) found that body condition of spider monkeys dropped dramatically during periods in which their diet was more folivorous. Similarly, Rangel-Negrín *et al.* (2009) argued that food scarcity in fragments could explain the increment of physiological stress of spider monkey in these areas. Primate socio-ecological models indicate that an increase in folivory results in an increase in the enforced resting time (*i.e.*, resting needed for digestive and/or thermoregulatory purposes), which may limit noticeably the time available for other vital activities, and hence affect the survival of the primates (Kortjents *et al.* 2010). Future studies are necessary to quantify changes in foraging strategies in fragmented habitats and their potential effects on health of individuals and population sizes.

Since top food species are not as common in fragments, spider monkeys are likely ‘forced’ to use non-tree growth forms more common in fragments such as palms and hemiepiphytes (Fig. 1B). The higher consumption of hemiepiphytes in fragments is explained by the exploitation of hemiepiphytic *Ficus* spp., which are commonly found in fragmented habitats. Although we only could determine the IVI of two *Ficus* species in the region (Table S2), it is probable that some characteristics of this light demanding genus (*e.g.*, fast growing, high ability to proliferate in disturbed and open habitats, large number of potential dispersers: Shanahan *et al*. 2001, Serrato *et al*. 2004) result in a greater abundance of these species in fragments than in continuous forest. The palms used as food sources also were very common in fragments (*e.g.*, *Sabal mexicana*; see Table S2).

Despite the capacity to feed from many different species, spider monkeys in Lacandona spent most of their time feeding on *Ficus* spp., *Spondias* spp., *Brosimum* spp., *Dialium guianense*, and *Licania platypus*. These top food species also have been reported as top food species throughout the distribution range of *A. geoffroyi* in Mesoamerica (González-Zamora *et al*. 2009), and the three former ones are top food species for *Ateles* spp. in different forests in Central and South America (see Di Fiore *et al.* 2008). The fact that spider monkeys concentrate their feeding time on these plant taxa in both forest types (continuous and fragmented) is likely related to several characteristics of these species including: (1) their high abundance in the study sites (Table 2), (2) their large size and consequent large fruit and leaf production, and (3) in the particular case of *Ficus* spp., their asynchronous fruit phenology with more than one fruit crop per year (Milton 1991, Shanahan *et al*. 2001). The marked and continued use of *Ficus* suggests that figs represent a staple food resource for spider monkeys (Weghorst 2007, Felton *et al*. 2008). As it has been widely demonstrated that presence and abundance of primates in their habitats are strongly associated with the abundance of important food resources (*e.g.*, *Pan troglodytes*: Balcomb *et al.* 2000, Neotropical primates: Stevenson 2001, *Cercopithecus mitis*: Worman & Chapman 2006, *Alouatta palliata*: Arroyo-Rodríguez *et al*. 2007), it is crucial to consider these top food species as a priority for conservation to develop effective management and restoration plans for *Ateles* spp.

Since spider monkeys have large home range requirements (37–98 ha: Fedigan *et al*. 1988), it is unlikely that the small size of two of the three study fragments (14 and 31 ha, Table S1) can maintain viable populations of spider monkeys in the long-term. Small forest fragments by themselves cannot provide sufficient habitat for viable populations of many animal species (Zuidema *et al*. 1996, Arroyo-Rodríguez *et al*. 2007, Chapman *et al*. 2007), especially in the case of large-bodied mammal species such as spider monkeys. Despite the fact that our study contained extremely variable sized fragments, our data support the idea that even small fragments (< 30 ha) are undoubtedly valuable for primate conservation as they may function as stepping stones that increase the landscape's connectivity facilitating inter-fragment movements (Marsh 2003b, Arroyo-Rodríguez *et al*. 2007). Thus, although the urgent need to conserve the most extensive areas of well-protected rainforest cannot be forgotten, in highly deforested and fragmented regions, such as the Marqués de Comillas region, primate persistence requires the preservation and restoration of small- and intermediate-sized forest remnants. By increasing the size and connectivity of small fragments, it is reasonable to expect the reduction of some important environmental pressures (*e.g.*, selective logging, hunting, vulnerability to predation, edge effects) constraining the survival of primates and many other mammals in these habitats (Michalski & Peres 2007, Stoner *et al.* 2007, Asensio *et al*. 2009). Finally, we suggest that future long-term studies evaluating the temporal and spatial variability of diet as well as the nutritional ecology of spider monkeys (and other atelids) in contrasting habitats (*e.g.*, fragmented and continuous forests, logged and unlogged forests) could be crucial to a better understanding of the ability of these primates to cope with stressful environmental conditions.

ACKNOWLEDGEMENTS

This research was supported by grants from the Consejo Nacional de Ciencia y Tecnología, Mexico (CONACyT Grant CB-2005-51043 and CB-2006-56799). The Instituto para la Conservación y el Desarrollo Sostenible, Costa Rica (INCODESO) provided logistical support. OMC obtained a scholarship from the Dirección General de Estudios de Posgrado, UNAM, and from the Secretaría de Relaciones Exteriores (SRE) of Mexico. A postdoctoral fellowship was given to VAR by the Consejo Técnico de la Investigación Científica (UNAM). A. Estrada and J. Benítez-Malvido provided useful comments and suggestions in the development of this research. This study would not have been possible without the collaboration of the local people in Loma Bonita, Chajul, Reforma Agraria and Zamora Pico de Oro ejidos. We thank C. Balderas, C. Hauglustaine, J. Herrera, R. Lombera and S. Martínez, for field assistance and J. M. Lobato and G. Sánchez for technical support. We finally thank J.C. Dunn and one anonymous reviewer for valuable criticisms and suggestions that improved the manuscript.

SUPPORTING INFORMATION

TABLE S1**.** *Characteristics of the sites and groups of spider monkeys studied in Lacandona, Chiapas, Mexico.*

TABLE S2. *Importance value index (IVI) of the top food species for spider monkeys in 6 study sites: Three sites within the continuous forest of the Montes Azules Biosphere Reserve, and 3 forest fragments within the Marqués de Comillas region, Lacandona, Chiapas, Mexico.*

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TABLE 1. *Species contributing to 80% of feeding time of* A. geoffroyi *in continuous and fragmented forests in Lacandona, Chiapas, Mexico. Species are ordered based on the percentage of feeding time. Plant growth form (GF), relative percentage of frugivory (%FR), percentage of total feeding time (%TFT), and percentage of tree abundance (%TA). (HE) Hemiepiphyte. (—) Undetermined data.*

Species	Family	GF	PI[a]	%FR	%TFT	%TA	Top food[b]
Continuous forest							
Licania platypus	Chrysobalanaceae	Tree	1,4,5,6	0.9 (0–1)	31.2 (0.4–45)	1.73	Yes
Spondias radlkoferi	Anacardiaceae	Tree	1,2,4	96.7 (91–100)	22.5 (7.4–46)	1.09	Yes
Spondias mombin	Anacardiaceae	Tree	1,2	100 (0–100)	6.2 (0–10)	0.01	Yes
Ficus tecolutensis	Moraceae	HE	1,2,4	99.8 (99–100)	4.6 (4–6)	0.27	Yes
Brosimum alicastrum	Moraceae	Tree	1,2,4	50.7 (33–63)	4.4 (3–6)	3.9	Yes
Dialium guianense	Fabaceae	Tree	1,2,4	16.2 (7–25)	3.8 (3–6)	5.2	Yes
Ampelocera hottlei	Ulmaceae	Tree	1,5	98.2 (68–100)	3.6 (0.3–7)	6	Yes
Ficus obtusifolia	Moraceae	HE	1	100	2.5 (0–9)	—	Yes
Strychnos tabascana	Loganiaceae	Vine	1,5	33.8 (19–82)	1.9 (0–4)	—	
Forest fragments							
Dialium guianense	Fabaceae	Tree	1,2,4	21.9 (17–27)	18.3 (12–27)	4.05	Yes
Ficus tecolutensis	Moraceae	HE	1,2,4	98.8 (99–100)	12.2 (7–23)	0.18	Yes
Spondias radlkoferi	Anacardiaceae	Tree	1,2,4	99.5 (99–100)	10.7 (8–19)	1.06	Yes
Brosimum alicastrum	Moraceae	Tree	1,2,4	70.6 (0–83)	10 (4–16)	4.05	Yes
Ficus sp1	Moraceae	HE	1,4,6	58.7 (42–97)	8.2 (1–15)	—	Yes
Licania platypus	Chrysobalanaceae	Tree	1,4,5,6	8.3 (0–9)	4.9 (2–9)	0.7	Yes

Ficus insipida	Moraceae	Tree	1,6	9.7 (0–12)	3.2 (0.7–6)	0.01	Yes
Sabal mexicana	Arecaceae	Palm	1,2	100 (0–100)	2.2 (0–8)	1.06	Yes
Calatola laevigata	Icacinaceae	Tree	1,2	100 (0–100)	2.2 (0–3.2)	0.7	
Ficus sp2	Moraceae	HE	1,4,7	98.7 (0–100)	2.2 (0.2–7)	–	Yes
Spondias mombin	Anacardiaceae	Tree	1,2	100	2.0 (1–3)	0.18	Yes
Maclura tinctoria	Moraceae	Tree	1,2,4	88.1 (0–88)	1.7 (0–3)	0	
Poulsenia armata	Moraceae	Tree	1,2,7	5.9 (0–6)	1.6 (0–3)	1.76	Yes
Guarea glabra	Meliaceae	Tree	1,2,4	77.3 (43–100)	1.3 (0.8–2)	13.6	Yes

[a] Plant items: 1, mature fruits; 2, immature fruits; 3, mature leaves; 4, immature leaves; 5, young branch piths; 6, decayed wood; 7, others.

[b] Plant species representing > 80% of feeding time of spider monkeys throughout Mesoamerica (González-Zamora *et al*. 2009).

TABLE 2**.** *The ten plant species with the highest importance value indices (IVI) for trees ≥ 10 dbh within continuous and fragmented rainforests in Lacandona, Chiapas, Mexico.*

Species	Family	Density (stems/3000 m^2)	Basal area (m^2)	IVI	Top food[a]
Continuous forest					
Guarea glabra	Meliaceae	27	28.9	74.6	Yes
Dialium guianense	Fabaceae	13	10.9	33.9	Yes
Ampelocera hottlei	Ulmaceae	15	8.0	32.3	Yes
Quararibea funebris	Malvaceae	18	8.4	29.5	Yes
Spondias radlkoferi	Anacardiaceae	5	4.6	14.2	Yes
Pouteria campechiana	Sapotaceae	7	1.8	12.8	Yes
Brosimum alicastrum	Moraceae	5	1.6	17.0	Yes
Bravaisia integerrima	Acanthaceae	8	1.5	2.8	
Nectandra reticulata	Lauraceae	4	0.4	6.1	Yes
Licania platypus	Chrysobalanaceae	2	1.8	5.6	Yes
Forest fragments					
Guarea glabra	Meliaceae	27	16.5	54.1	Yes
Theobroma cacao	Malvaceae	23	10.1	11.2	
Dialium guianense	Fabaceae	12	8.4	28.4	Yes
Bravaisia integerrima	Acanthaceae	11	9.0	8.8	
Brosimum alicastrum	Moraceae	7	5.5	10.2	Yes
Brosimum lactescens	Moraceae	9	1.5	12.3	Yes
Spondias radlkoferi	Anacardiaceae	5	2.9	10.8	Yes
Licania platypus	Chrysobalanaceae	6	2.2	7.6	Yes
Cojoba arborea	Fabaceae	4	1.2	2.5	Yes
Poulsenia armata	Moraceae	5	0.6	2.4	Yes

[a] See Table 1 legend.

Figure legend

FIGURE 1**.** Diet composition in continuous and fragmented forests according to percentage of total feeding time (mean ± SD) consuming different plant items (A) and different growth forms (B). Different letters above bars indicate significant differences between continuous forest and fragments ($P < 0.05$). Plant items: mature fruits (MF), immature fruits (IF), immature leaves (IL), mature leaves (ML), young branches (BR), flowers (FL), decayed wood (DW), and other plant items (OT). Growth forms: trees (T), hemiepiphytes (H), climbers (C), palms (P), epiphytes (E), and shrubs (S).

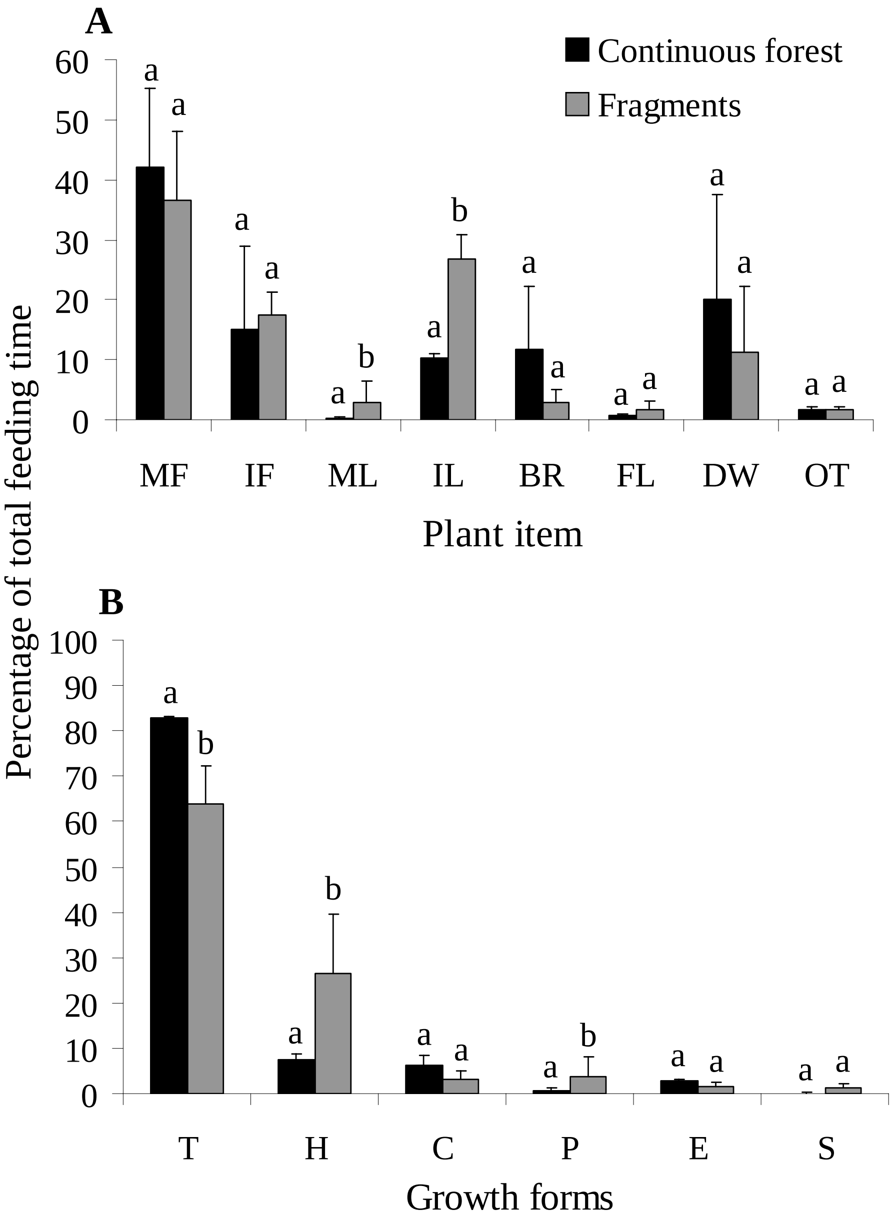

FIGURE 1. O. M. Chaves, K.E. Stoner and V. Arroyo-Rodríguez.

SUPPORTING INFORMATION

HOME RANGE OF THE MONKEY GROUPS.— From February-Jun and August-October 2008, we daily recorded with GPS the location of each focal group foraging in continuous forest and in the fragment F3 during the morning and the afternoon. Following Spehar *et al.* (2010), for each focal group a map of the home range was created in Arc View GIS 3.3 (Environmental System Research Institute Inc., USA) using all GPS coordinates. A set of 100 m x100 m (1 ha) grid squares was then superimposed over these maps, and a representation of the monkey group's home range was created by calculating the number of 100 m x 100 m grid squares into which monkey group ranged as well as the minimum convex polygon (MCP) encompassing all of the location points. We preferred MCP method rather than adaptive kernel (AK) or fixed kernel (FK) because it allow a more accurate estimation of home range when sample size is small (see Boyle *et al*. 2009).

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TABLE S1. *Characteristics of the sites and groups of spider monkeys studied in Lacandona, Chiapas, México. DNF, distance to nearest forest fragments; DCF, distance to the continuous forest; YFF, year since fragmentation.*

Sites	Size (ha)	Location	DNF (m)	DCF (m)	YFF	Group size	Home range (ha)[b]
Continuous forest	300,000	Montes Azules Biosphera Reserve					
C1	–	16°06'58.2"N, 90°56'18.4"W	–	–	–	40	29.7
C2	–	16°09'32.0"N, 90°54'06.6"W	–	–	–	36	47.3
C3	–	16°09'40.0"N, 90°54'04.5"W	–	–	–	44	89.6
Forest fragments							
F1	31	Zamora Pico de Oro (16°19'24.5"N, 90°50'43.7"W)	150	1200	24	39	31
F2	14.4	Zamora Pico de Oro (16°19'52.0"N, 90°51'06.1"W)	450	200	29	35	14.4
F3	1125[a]	Reforma Agraria (16°15'12.2"N, 90°49'59.5"W)	100	1100	26	41	63.1

[a] Total size of this fragment is 1450 ha, but due to the presence of many wide trails along and within of the fragment, the presence of cocoa (*Teobroma cacao*) and pita (*Aechmea magdalenae*) plantations, and the different reserve restructuring, the potential successful habitat for spider monkeys is restricted to ca. 1125 ha of disturbed tropical rainforest.

TABLE S2. *Importance value index (IVI) of the top food species for spider monkeys in 6 study sites: Three sites within the continuous forest of the Montes Azules Biosphere Reserve, and 3 forest fragments within the Marques de Comillas region, Lacandona, Chiapas, Mexico. Asterisks indicate the cases in which IVI was greater in continuous forest than in fragments.*

		IVI	
Species	Family	Continuous forest	Fragments
Ampelocera hottlei	Ulmaceae	32.3	7.2*
Brosimum alicastrum	Moraceae	17.0	10.2*
Bursera simaruba	Burseraceae	2.1	1.6*
Castilla elastica	Moraceae	4.1	6
Cupania spp. (2)	Meliaceae	3.8	0.5*
Dialium guianense	Fabaceae	33.9	28.4*
Ficus insipida	Moraceae	0	0.7
Ficus tecolutensis	Moraceae	0.6	0.5*
Guarea glabra	Meliaceae	74.6	54.1*
Licania platypus	Chrysobalanaceae	5.6	7.6
Poulsenia armata	Moraceae	0	7.2
Pouteria campechiana	Sapotaceae	12.8	3*
P. sapota	Sapotaceae	1.9	1.5*
Protium copal	Burseraceae	3.3	1.5*
Mortoniodendron	Malvaceae	1.8	0*
Nectandra reticulata	Lauraceae	6.1	1.5*
Sabal mexicana	Arecaceae	0	4.9
Spondias radlkoferi	Anacardiaceae	14.2	10.8*
S. mombin	Anacardiaceae	0	1.5
Virola guatemalensis	Myristicaceae	2.9	0*
Total		217	148.7

*Indicates the cases in which IVI was greater in continuous forest than in fragments.

CAPÍTULO II

Running title: Spider Monkey Seed Dispersal Effectiveness

Effectiveness of Spider Monkeys (*Ateles geoffroyi vellerosus*) as Seed Dispersers in Continuous and Fragmented Rainforests in Southern Mexico

(accepted 24 May 2010, International Journal of Primatology, IF=1.78)

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Received:__ /Revised:__/Accepted:__

Abstract Seed dispersal is considered a key process determining spatial structure and dynamics of plant populations, and has crucial implications for forest regeneration. We evaluated the effectiveness of spider monkeys (*Ateles geoffroyi*) as seed dispersers in continuous and fragmented habitats to test if this interaction is altered in forest fragments. We documented fruit and seed handling, defecation patterns, diversity and composition of seeds in feces, and seed germination of defecated and control seeds in the Lacandona rainforest, Mexico. For most species contributing to 80% of total fruit feeding time, monkeys swallowed and spat seeds, but swallowing was the most frequent seed handling category in continuous and fragmented forests. However, the proportion of feeding records of swallowed seeds was higher in continuous forest (0.59) than in fragments (0.46), whilst the opposite was true for proportion of dropped seeds (0.16 versus 0.31). This pattern was reflected in the number of fecal samples containing seeds, which was greater in continuous (95.5%) than fragmented forests (82.5%). Seeds in fecal samples included a total of 71 species from 23 plant families. The number of defecated seed species was similar between forest conditions and in both cases most seeds (> 86%) were undamaged. Defecated seeds showed greater germination percentages than control seeds in all of the five species evaluated. Although we identified some differences in seed handling and the percentage of feces with seeds between continuous forest and fragments, our results indicate that, in general terms, spider monkeys are efficient seed dispersers in both forest conditions.

Keywords forest regeneration; fragmentation; frugivorous primates; seed dispersal

Introduction

Plant recruitment, distribution and regeneration of tropical forest species largely depend on the effectiveness of animals as seed dispersers (Cordeiro *et al*. 2009). Disperser effectiveness is defined in terms of the contribution a disperser makes to the future reproduction of a plant or to plant fitness, and may be considered from the perspective of both the dispersal agents and the dispersed plants at a variety of scales from individuals to communities (Jordano and Schupp 2000; Schupp 1993).

From the plant perspective, seed dispersal effectiveness depends on two main components (1) the quantity of dispersed seeds, and (2) the quality of seed dispersal (i.e., the probability that seeds are deposited intact in sites with high prospects for establishment) (Muller-Landau and Hardesty 2005; Schupp 1993). According to Schupp (1993), the first component is a function of the number of visits made to the plant by a disperser and the number of seeds dispersed per visit, which depends on the abundance of the disperser, its feeding behavior, the fruit/seed handling strategies, and the reliability of visitation. The second component is a function of the quality of treatment given a seed in the mouth and in the gut (i.e., percentage of handled seeds destroyed, and percentage of germination of defecated seeds) and the quality of seed deposition (i.e., defecation pattern, predator pressures, and probability of establishment). In sum, both the quantity and quality of seed dispersal determine the final fate of a seed and in turn, the relative impact dispersers have on plant community structure and composition (Jordano and Schupp 2000; Schupp 1993).

Seed dispersal effectiveness may be particularly critical in forest fragments, in which some fruit-eating animal species disappear (e.g., birds: Martensen *et al*. 2008; bats: Cosson *et al.* 1999; large birds and mammals: Melo *et al.* 2010; primates: Arroyo-

Rodríguez *et al*. 2008), affecting plant species diversity and vegetation structure (Moran *et al*. 2009). This threat is higher for large-seeded tree species because their dispersal agents are often large-bodied and hence, at greater risk of local extinction in fragments (i.e. with greater hunting pressures, lower reproductive rates, smaller population sizes, and in many cases, with larger home range requirements: Stoner *et al*. 2007). This is the case for primates, which constitute 25–40% of the frugivore biomass in tropical forests (Chapman 1995), and are important seed dispersers for many tree species (Link and Di Fiore 2006). Overall, ecological services provided by primates through seed dispersal are critical for the recruitment of many medium- and large-seeded plant species in both continuous and fragmented forests (Stevenson and Aldana 2008).

In Neotropical primates seed dispersal effectiveness has been evaluated only in a few species, and mainly in continuous forests (e.g., *Lagothrix lagotricha*: Stevenson 2000; *Alouatta seniculus*: Julliot 1996; *Cebus capucinus*: Valenta and Fedigan 2009). These studies have assessed only isolated aspects of dispersal effectiveness (e.g., dispersal distance and germination rates: Stevenson 2000; fruit choice: Stevenson 2004; dispersal quantity: Link and Di Fiore 2006; Stevenson 2007) and did not consider the potential effect of the site-specific vegetation structure (e.g. abundance and diversity of food species for primates) on the aspects evaluated. Thus, for a given primate species, observed patterns of seed dispersal may be more related to differences in inter-site plant species composition and abundance (which result in differential fruit availability at each site), than only to differences in the behavior of the disperser among habitats (e.g., *Ateles* spp.: Russo *et al*. 2005). Despite these facts, evidence suggests that effectiveness of primates as seed dispersers is highly variable in terms of proportion of fruit in the diet, number of seed species in feces, size of swallowed seeds, percentage of fecal samples without seeds, and effect of gut passage on seed germination (Table S1). For example, fruit in the diet for some sympatric primates may range from 2% (*Alouatta seniculus*: Orihuela-López *et al*. 2005) to 87% (*Ateles belzebuth*: Dew 2008). The number of seed species in feces may range from 9 (*A. palliata*: Wehncke *et al*. 2004) to 133 species (*Ateles belzebuth*: Link and Di Fiore 2006). Contrasting defecation patterns have been reported for different primates (e.g., scattered in *Cebus capucinus*: Wehncke *et al*. 2004; clumped in *Alouatta seniculus*: Andresen 2002), which may differentially affect the probability of seed and seedling survival (see Howe 1989). Similarly, positive, neutral and negative net effects of primate gut passage on seed germination have been reported; nevertheless, positive effects are more frequent (Table S1).

Finally, post-dispersal seed fate including the effect of secondary seed dispersers and predators (e.g., dung beetles and scatter hoarding rodents) represent additional elements influencing the effect of primary seed dispersers on plant fitness (Schupp and Fuentes 1995). Although most secondary dispersers move seeds short distances and frequently bury them close to the original deposition microsite (e.g., < 1 m in dung beetles: Andresen 2002), the cached seeds often have a higher survival than the uncached seeds (Andresen and Levey 2004; Forget and Cuijpers 2008). However, secondary dispersal is less likely to occur when highly frugivorous and mobile primates, such as spider monkeys, are the primary seed dispersers than when they are not (Forget and Cuijpers 2008).

In continuous forests evidence suggests that spider monkeys are legitimate seed dispersers for a large number of plant species because they swallow large quantities of seeds and defecate them intact (Di Fiore *et al*. 2008), and they transport seeds far away from parent trees (> 100 m) to sites with higher probability of seedling establishment (Link and Di Fiore 2006). Nevertheless, no study to date has examined simultaneously different quantitative and qualitative aspects of *Ateles*' seed dispersal effectiveness and how these attributes are modified in forest fragments. In spite of this fact, evidence suggests that primate-plant interactions may be negatively affected in forest fragments because these habitats often present less availability of fruit resources for primates in comparison with continuous forests (Arroyo-Rodríguez and Mandujano 2006; Dunn *et al*. 2009), forcing frugivorous primates to adjust their feeding behavior (e.g., exploiting alternative plant items: González-Zamora *et al*. 2009; Onderdonk and Chapman 2000).

We aimed to determine the effectiveness of spider monkeys (*Ateles geoffroyi vellerosus*) as primary seed dispersers in quantitative and qualitative terms and to assess if this interaction is altered in forest fragments. Seed dispersal effectiveness was estimated in areas of continuous and fragmented forest in Lacandona, Chiapas, Mexico, by analyzing (1) seed handling of the top fruit plant species and its relationship with seed size; (2) defecation patterns; (3) diversity and composition of defecated seed species, and percentage of undamaged seeds; and (4) germination of defecated versus control seeds. Since spider monkeys are highly frugivorous and commonly defecated in a scattered pattern (Di Fiore *et al*. 2008; Howe 1989; Russo 2005) we predict that they will be efficient seed dispersers in terms of number of defecated seeds, defecation pattern, and the effect of gut passage on the germination in continuous forest and fragments. However, since fragmentation often reduces fruit availability and promotes shifts in feeding behavior (see above), we also predict that fragments will experience a decrease in the proportion of seeds ingested, the number of seed species defecated, and the proportion of feces with seeds. This is the first study that documents the importance of a Neotropical monkey on seed dispersal effectiveness in forest fragments (but see González-Di Pierro *et al.* in press).

Methods

Study Sites and Spider Monkey Communities

We studied the fruit-eating behavior of six communities of spider monkeys: three independent communities in three different areas of the Montes Azules Biosphere Reserve (MABR, > 3000 km^2) separated by at least 4 km (i.e., the closest distance among home range perimeters), and three communities in three different fragments located in the Marqués de Comillas Region (MCR), Chiapas, Mexico (for further details see Electronic supplementary material). All fragments in MCR were isolated ≥ 24 years ago, and their sizes were 14, 31, and 1125 ha (Table S2). For the three study sites of MABR and for the largest fragment, we restricted spider monkey follows to an area of 30–100 ha (depending on the movements of focal communities), whereas for the other two fragments the entire area was sampled. Finally, although there are differences in size and distance among sites, both forest conditions (continuous forest and fragments) had a similar adult tree composition (see Electronic supplementary material).

Primate Species in the Study Area

Two primate species are present in the study area: the black-handed spider monkey (*Ateles geoffroyi vellerosus*) and the black howler monkey (*Alouatta pigra*). In MABR population density of *A. geoffroyi* has been estimated as 2.9 ind/km^2, while that for *A. pigra* is 14.4 ind/km^2, whilst a gross estimate of these population densities in a large fragment at MCR are 9.3 and 13.3 ind/km^2, respectively (Estrada *et al*. 2004). Overall, howler monkeys are characterized by having a folivorous diet (Di Fiore and Campbell 2007). By contrast, *Ateles* spp. has been described as a fruit specialist (Di Fiore *et al*. 2008) that accounts for more than 70% (ranging from 39 to 82%) of their feeding time (González-Zamora *et al*. 2009).

Feeding Behavior and Seed Handling

Diet of spider monkeys was studied during a 15-mo period (6 months in the dry season: February-April 2007 and 2008; and 9 months in rainy season: May-October 2007, and August-October 2008). Feeding behavior was documented for each of the 6 focal communities during 3 consecutive days once every 3 weeks, using 5-min focal animal sampling (Altmann 1974). Follows were conducted from 7:00 h to 17:30 h, totaling 223 observation days and 1000 h of focal observations. Further details of feeding sampling are provided in Electronic supplementary material.

We recorded the feeding behavior to determine how much of the diet was devoted to consumption of different plant items (Chaves *et al.* in press) but here we focus on the fruit diet. When monkeys were feeding on fruits we identified whether they were consuming ripe or unripe pulp/aril and we recorded growth-form (trees, shrubs, epiphytes and climbers), species and seed handling behavior (see below). When fruit development could not be determined because of poor illumination, we simply recorded the food item as fruit. The relative importance of different fruit species in the diet was calculated as percent time spent consuming a particular fruit species in relation to total time feeding on fruits. We ranked the fruit species based on the percent of time spent consuming each fruit species in relation to the total time spent consuming all fruit species until the sum was 80% and hence recorded the seed handling only for these species (hereafter named top fruit species).We recognized three categories of seed handling: (1) swallowed—ingestion of the entire fruit swallowing pulp and seeds; (2) spat out—when monkeys ate the fruit pulp or aril and spat out the seeds under the parent tree while eating; and (3) dropped—when monkeys ingested only fruit pulp and dropped seeds under the parent tree. Finally, because the top fruit species were not the same in continuous forest and fragments, we restrict the statistical analysis to the five top fruit species present in both forest conditions (*Brosimum alicastrum*, *Ficus tecolutensis*, *Ficus* sp1., *Spondias mombin* and *S. radlkoferi*) in order to control for seed handling effects at the species level.

Defecation Pattern, Defecated Species, and Germination Trials

Following Wehncke *et al*. (2004), we classified deposition or defecation pattern as scattered (i.e., when monkeys defecated individually in space and time creating a scatter of small defecations) or clumped (i.e., when a monkey community or subgroup defecated simultaneously in a particular place producing large areas of clumped defecations). In contrast to Russo and Augspurger (2004), we did not discriminate between sleeping sites and in-transit sites because in Lacandona the location of sleeping sites (both diurnal resting trees and nocturnal sleeping trees) varied constantly over time. Furthermore, we did not sample at dawn or dusk when the entire community was found together, but rather sampled from subgroups while foraging and moving throughout the day.

Fecal samples were collected from individual monkeys immediately after defecation, and placed individually in labeled plastic bags and later processed in the field laboratory. Each sample was thoroughly rinsed with water in a sieve using successively decreasing mesh size (3 mm and 1 mm mesh, respectively). The number, composition, and damage level of seed species in each sample was recorded using a stereoscope (10–40X magnification). Seeds were classified as: (1) undamaged—intact seeds or with ≤ 5% of the testa damaged; (2) moderate damage—seeds with > 5% to ≤ 25% of the testa damaged; and (3) heavy damage—> 25% of the testa damaged. In both forest conditions, we ranked the defecated seed species based on the percent of fecal records containing each seed species in relation to the total fecal records for all seed species until the sum was 80% (hereafter named top defecated seed species). To identify seed species we used the Lacandona seed reference collection located at the Centro de Investigaciones en Ecosistemas (UNAM, Morelia, Mexico). Plant nomenclature followed the Missouri Botanical Garden nomenclatural update database (http://mobot.org/W3T/search/vast.html).

To examine the effect of seed passage through spider monkeys´ digestive tract, we performed a series of germination trials in four tree species (*S. radlkoferi*, *Ampelocera hottlei*, *Brosimum lactescens*, and *Faramea occidentalis*), and one vine (*Cissus verticilata*) with large seeds (1.4–4.5 cm in length) . These species were selected because they represent important fruit sources for spider monkeys in the study area (comprising 6–40% of their fruit feeding time for the first three species and ca. 2% for the latter two species: Chaves *et al*. in press), and because their size limits potential dispersers to primates and a few large-bodied birds (Jordano 1995). Seeds for germination trials were collected from fresh feces just after defecation and from mature fruits (control seeds). Mature fruits were collected under the crowns of 5–14 parent trees where the monkeys fed. Pulp or aril was manually removed and all seeds were observed with a stereoscope (10–40X magnification) in order to select only intact seeds (i.e., seeds without holes, malformations or other damage to the testa). For each species, we used 14–40 seeds from

12–36 mature fruits (control seeds) and 15–30 seeds from 10–20 fecal samples. Defecated and control seeds were similar in size and weight and were collected from continuous forest. Seeds were placed in 10 x 20 cm plastic boxes containing river sand and placed in a greenhouse (*ca.* 40% full sun) located in a 1-ha fragment at 150 m from MABR. Seeds were watered daily for 12 weeks and germination (i.e., radicle emergence) was recorded daily.

Data Analysis

To evaluate if seed handling differed between continuous forest and fragments we used generalized linear models (GLM: Crawley 1993). We estimated the proportion of records devoted to each category of seed handling per study site considering each of the three sites as replicates within each forest condition. As different seed handling occurs within each forest condition (Fig. 1), we nested seed handling within forest condition, with the whole model being: PROPORTION OF RECORDS = SEED HANDLING nested within FOREST CONDITION + SEED HANDLING*SPECIES nested within FOREST CONDITION + FOREST CONDITION. Proportion data were first arcsine transformed, and tested for a normal distribution with a Shapiro Wilk test (passed, $p>0.1$). We then selected Normal distribution with an identity link-function to the response variable. To identify which seed handling categories were statistically different among each other we used post-hoc analyses with contrasts (Crawley 1993). We also explored the relationship between percentage of swallowed seeds and seed size in each forest condition with a linear regression of arcsine transformed proportions. To compare the defecation pattern in continuous and fragmented forest we used a GLM, fixing a Poisson distribution and log-link function to the response variable (i.e., number of defecation records) (Crawley 1993). Previously, we standardized the number of defecation records in each forest condition to control for differences in sample size. Additionally, to test for consistency between fruit diet data obtained from foraging observations and defecated seeds, we estimated the species overlap between these two techniques with the Morisita-Horn index.

To test for differences in the number of defecated seed species per site and in the number of seed species per fecal sample between continuous and fragmented forests, we used analyses of deviance with GLM. As suggested for count response variables, we fixed a Poisson distribution to a log-link function (Crawley 1993). First, we standardized the number of fecal samples to control for differences in species density using the rarefaction approach (EcoSim: Gotelli and Entsminger 2001). The number of fecal samples that contained no seeds was compared with GLM, fixing a Poisson distribution and log-link function to the response variable. Finally, to compare the number of seeds that germinated from defecated versus control seeds we constructed a 2 x 2 contingency table for each species and tested differences with *G*-tests. All statistical analyses were performed using JMP software (version 7.0, SAS Institute, Cary, N.C.).

Results

Feeding Behavior and Seed Handling

Overall, fruit made up 55.6 ± 18.9% (mean ± SD) of the spider monkeys' diet (57.0 ± 27.1% in continuous forest and 54.1 ± 12.5% in fragments). The monkeys consumed fruits from 73 species in continuous forest and 61 species in fragments. In general, for most top fruit species (*ca*. 90%) spider monkeys showed more than one category of seed handling, with swallowed being the most frequent category in both continuous (55.6% of species) and fragmented forests (60% of species; Table I). The number of feeding records did not differ between forest conditions ($\chi^2 = 0.28$, df = 1, $p = 0.9$). However, it was significantly different among categories of seed handling nested within forest condition ($\chi^2 = 68$, df = 4, $p < 0.0001$), with the proportion of swallowed seeds being greater than spat out and dropped seeds in both forest conditions (contrast tests, $p < 0.05$ in all cases; Fig. 1). The proportion of swallowed seeds was higher in continuous forest than in fragments (0.59 versus 0.46, contrast test: $p = 0.01$), while the opposite was true for the proportion of dropped seeds (0.16 versus 0.31, contrast test: $p = 0.03$; Fig. 1). Furthermore, we found significant differences among categories of seed handling by species nested within forest condition ($\chi^2 = 155$, df = 16, $p < 0.0001$), with seeds of *Spondias mombin* swallowed more in continuous forest than in fragments (mean ± SD, 24 ± 27% and 5 ± 4.5% respectively; contrast test: $p = 0.001$), while the opposite pattern occurred with the proportion of dropped seeds (28 ± 25% and 73 ± 6% respectively; contrast test: $p < 0.004$). No other significant differences were detected in the remaining four species (contrast tests: $p > 0.05$ in all cases). Finally, the percentage of seeds swallowed was inversely related to seed size in both continuous ($r = -0.84$, $p = 0.005$) and fragmented forests ($r = -0.71$, $p = 0.02$; Table I).

Defecation Pattern, Defecated Species, and Germination Trials

Scattered defecations were significantly more common than clumped defecations in continuous forest (94%, $n = 523$) and fragments (89.4%, $n = 496$, $\chi^2 = 912$, df = 2, $p <$

0.0001). However, the number of scattered and clumped defecations did not differ between forest conditions (contrast tests: $p = 0.1$ in both cases).

We collected a total of 957 fecal samples (519 in continuous forest and 438 in fragments) and found seeds from 71 species (of which 52 were identified to species and 19 to morphospecies), 39 genera, and 23 families. The number of defecated seed species was similar between continuous forest (37 species and 9 morphospecies, range = 18–27 species) and fragments (38 species and 13 morphospecies, range = 18–24 species, $\chi^2 = 0.03$, df = 1, $p = 0.86$). Although species composition was similar between forest conditions (Electronic supplementary material), only 21 out of 52 defecated seed species were shared between continuous forests and fragments, resulting in a moderate species overlap between forest conditions (Morisita-Horn's index = 0.62).

The mean (± SD) number of seed species per fecal sample was 1.3 ± 0.8 species, ranging from 0 to 6 species, and no significant differences were detected between continuous forest and fragments (1.3 ± 0.8 and 1.3 ± 1.0 species, respectively; $\chi^2 = 0.64$, df = 1, $p = 0.42$). More than 90% of the fecal samples contained seeds, but the average percentage of feces without seeds was greater in fragments (17.5 ± 10%) than in continuous forest (4.5 ± 3.7%, $\chi^2 = 26.5$, df = 1, $p < 0.0001$). Finally, the overlap in the composition of fruit species in the diet based on direct observations from foraging data and seed species in feces was relatively high (Morisita-Horn's index = 0.75), indicating that seeds collected from fecal samples reflect approximately 75% of what monkeys are feeding on.

In general, seed size in feces ranged from < 0.1 cm in length and width (e.g., *Ficus* spp.) to 3.7–4.5 cm in length and 2.1–2.7 cm in width (e.g., *Spondias radlkoferi* and *Attalea butyracea*). However, spider monkeys also ate the fruit pulp and dropped the seeds of *Licania platypus* (ca. 10 x 7 cm) in both forest conditions. Considering the top defecated seed species for all samples, spider monkeys defecated seeds of 12 species belonging to 9 genera, and 7 families, with *Ficus* spp. (Moraceae) and *Spondias radlkoferi* (Anacardiaceae) being the most frequent in fecal samples (18.3% and 17.5% of fecal records, respectively). However, the number of species constituting the top defecated seed species was higher in fragments than in continuous forest (20 and 10 species, respectively; Table II). Seven out of 16 top defecated seed species were the same in both forest conditions (*Celtis iguanaea*, *Dialium guianense*, *Ficus tecolutensis*, *Ficus* sp1., *Guarea glabra*, *S. radlkoferi*, and *S. mombin*, Table II). Of these species, *S. radlkoferi* and *F. tecolutensis* were the most frequent seed species in continuous forest, and *F. tecolutensis* and *Sabal mexicana* the most frequent in fragments (Table II). Overall, the percentage of undamaged seeds was greater than 86% for most seed species in both forest conditions (Table II).

Finally, in the five studied species, the number of seeds that successfully germinated was significantly higher for defecated than for control seeds, indicating a positive effect in all cases (Table III).

Discussion

As predicted, spider monkeys were efficient seed dispersers in quantitative and qualitative terms. In both continuous forest and fragments they fed on a large number of fruit species and swallowed seeds of most of them, most feces contained seeds, a scattered deposition pattern was the most common, and the majority of defecated seeds were undamaged. Furthermore, defecated seeds showed greater germination percentages than control seeds in all of the five plant species evaluated. Our results concur with previous studies on spider monkeys, which have shown that they are efficient in terms of fruit diet diversity, seed handling, richness of seeds dispersed and defecation pattern (e.g., *Ateles* spp.: Russo *et al*. 2005; *A. belzebuth*: Link and Di Fiore 2006; Dew 2008). Although we identified some differences in the seed handling and the percentage of feces with seeds between continuous forest and fragments, our study concurs with some recent studies showing that animal seed dispersal effectiveness is not notably affected by fragmentation (e.g., understory birds: Figueroa-Esquivel *et al*. 2009).

Seed Handling

Seed handling differed between forest conditions. Compared to communities in continuous forests, spider monkeys in fragments swallowed proportionally less seeds and dropped more seeds, which support our second prediction. Although we did not measure if seed handling is related to fruit shortage in fragments, there is some evidence that supports this possibility (e.g., Arroyo-Rodríguez and Mandujano 2006). Although overall adult tree composition was similar in continuous and fragmented forests (Electronic supplementary material), we found a greater abundance of larger trees (> 60 cm in DBH) of top fruit species in continuous forest compared to fragments (see Fig. S2). Since the abundance of large trees is a good indicator of fruit availability (Chapman *et al*. 1992), it is likely that less fruit was available for spider monkeys in the studied fragments. Lower fruit availability often results in primates eating alternative plant items and/or more species (e.g., *Ateles geoffroyi, Alouatta palliata* and *Cebus capucinus*: Chapman 1987; *Alouatta palliata*: Cristóbal-Azkarate and Arroyo-Rodríguez 2007). Indeed, this same pattern has been observed in our same studied monkey communities. Chaves *et al.* (in press) found that spider monkeys in fragments invest proportionally more time consuming leaves and immature fruits than in continuous forest.

Since immature fruits are less palatable and contain more secondary metabolites than mature fruits (Waterman 1984), primates that eat immature fruits frequently drop or spit out more seeds (Norconk *et al*. 1998). We observed that spider monkeys feeding on immature fruits usually ate a small portion of the fruit pulp or aril and dropped and/or spat out the seeds directly under the parent tree. This is particularly the case for *S. radlkoferi* and *S. mombin*, in which spider monkeys dropped a higher proportion of seeds in fragments than in continuous forest. Exploiting more immature fruits in fragments may influence the seed dispersal effectiveness in two ways. First, seeds from immature fruits may have lower germination success due to the presence of immature embryos and second, even if the seeds are viable and germinate, seeds dropped under parent trees commonly experience higher density-dependant mortality (Janzen 1970; Nathan and Casagrandi 2004). Finally, we found that the percentage of swallowed seeds decreased with seed size, which also has been reported in other primate studies (e.g., *Ateles geoffroyi*, *A. palliata*, and *C. capucinus*: Chapman 1989; *L. lagotricha*: Stevenson *et al*. 2005). Although from the animal's perspective spitting out (or dropping) medium (0.5–1.5 cm in length) to large (> 1.5 cm in length) seeds may be the most successful seed handling strategy, the ability of these primates to swallow large seeds certainly favors seed dispersal of large-seeded species in continuous and fragmented forests (e.g., *Attalea butyracea* and *Spondias* spp.). However, this does not necessarily imply that spider monkeys are more effective dispersers for small than for large-seeded species, but rather the amount of swallowed seeds for each fruit species is negatively affect by their seed size due to mechanical limitations related to fruit and seed handling (Jordano 1995). Further information about seed dispersal distance and seed fate is needed to clarify whether spider monkey seed dispersal effectiveness differs between seeds with contrasting sizes.

Defecation Pattern and Defecated Seed Assemblages

The effectiveness of primates as seed dispersers largely depends on the defecation pattern, and diversity of seeds in feces. The higher the number of scattered depositions, seeds dispersed, and seed species in feces, the higher the probability of successful seed dispersal and seedling recruitment due to a decrease in both the density and/or distance dependent mortality near parents (Howe 1989; Muller-Landau and Hardesty 2005) and sibling competition for resources (Cheplick 1992; Queenborough *et al.* 2007). Although, most defecations were scattered in both forest conditions, the proportion of feces without seeds was significantly higher in fragments than in continuous forest suggesting that some aspects of seed dispersal effectiveness may be negatively affected by fragmentation. Additionally, the greater proportion of feces without seeds, as well as the higher number of species contributing to the top defecated seed species is likely due to changes in foraging patterns in fragments (described above).

Fecal samples contained seeds from 71 plant species (46 in continuous and 51 in fragments), indicating that spider monkeys provide seed dispersal services for many fleshy fruit species in both forest conditions. The number of defecated seed species was notably higher than that reported for spider monkeys in tropical dry forests (Chapman 1989) and for most *Alouatta* species in many tropical forests (Table S1), however, we found fewer plant species than those reported for some South American primates (e.g., *Alouatta seniculus*: Julliot 1996, *Ateles belzebuth*: Link and Di Fiore 2006; Table S1). This result can be explained by the higher plant species diversity in South America in comparison with

Mesoamerica (Gentry 1982). Overall, dietary diversity in *Ateles* spp. is directly related with both proximity to the equator and mean annual rainfall (Di Fiore *et al*. 2008).

Despite the large number of seed species in feces, only a small number of species were abundant. This pattern is consistent with the selective foraging behavior characteristic of spider monkeys throughout their geographic range (Di Fiore *et al*. 2008; González-Zamora *et al*. 2009). In general, spider monkeys prefer to feed on species with large tree sizes, fleshy fruits, long fruiting periods and clumped distributions (Di Fiore *et al*. 2008). Our results concur with two recent reviews (Di Fiore *et al*. 2008; González-Zamora *et al*. 2009), showing that plant families such as Moraceae, Fabaceae and Anacardiaceae, and genera such as *Ficus*, *Brosimum*, *Spondias*, *Dialium* and *Inga* are keystone species for spider monkeys.

Effects of Gut Passage

In the five plant species evaluated, seed germination was significantly higher in defecated than in control seeds. This finding illustrates the positive effect that spider monkeys have on seed germination, a finding similar to that observed in other Neotropical primates (e.g., *Alouatta*, *Cebus* and *Lagothrix*; Table S1). Additionally, while some primates can negatively affect the germination of some plant species (see Table S1), in our study *A. geoffroyi* did not affect negatively the germination for any of the species studied, suggesting that it may be a more efficient seed disperser than some other highly frugivoruous species. For example, negative gut passage effect on seed germination ranges from 5% in *Lagothrix lagotricha* (Stevenson *et al*. 2002) to 28.6% in *Ateles belzebuth* (Link and Di Fiore 2006).

Although our study has some limitations that make it difficult to infer the effects of seed dispersal by these monkey communities on plant populations (e.g. we did not determine fruit availability in each study site, we did not provide a quantification of seed dispersal at the monkey population level, we restricted the germination tests to a small number of species, and we did not evaluate the final fate of defecated seeds), our findings clearly demonstrate that, at least for the aspects of effectiveness evaluated, spider monkeys are efficient seed dispersers in both continuous forest and fragments. Dispersal services provided by spider monkeys in Lacandona may be especially important for large-seeded species such as *Ampelocera hottlei* and *Spondias* spp. (Chaves *et al*., *unpublished data*), due to the limited number of animals that can swallow seeds of these large-seeded species (e.g. Stevenson and Aldana 2008). Although evidence suggests relationships among angiosperms and their animal dispersers are generally best described as diffuse networks rather than close coevolutionary relationships (see Herrera 1985), services provided by legitimate dispersers, such as spider monkeys, undoubtedly may favor gene flow, and recruitment of their top food plant species (Schupp and Fuentes 1995; Stevenson *et al*. 2002). We suggest that more long-term studies quantifying seed dispersal by spider monkeys at the population level, as well as the final fate of defecated seeds are critical to improve our understanding about the contribution of spider monkeys (and other Neotropical primates) to plant regeneration.

Acknowledgements This research was supported by grants from the Consejo Nacional de Ciencia y Tecnología, México (CONACyT Grant CB-2005-51043 and CB-2006-56799). This paper constitutes a partial fulfillment of the Graduate Program in Biological Sciences of the National Autonomous University of México (UNAM). The organization Idea Wild provided equipment. This study would not have been possible without the collaboration of the local people in Loma Bonita, Chajul, Reforma Agraria and Zamora Pico de Oro ejidos. V. Sork, D. Scofield, P. Thompson, and M. Quesada provided useful comments and suggestions in advanced drafts of this paper. We thank to C. Hauglustaine, C. Balderas, S. Martínez, J. Herrera, A. González-Di Pierro and R. Lombera for field assistance. J. Rodríguez collaborated in the identification of seeds, and J. M. Lobato, G. Sánchez, H. Ferreira, and A. Valencia provided technical support. We also thank J.M. Setchell, E.W. Shcupp and one anonymous reviewer for valuable criticisms and suggestions that improved the manuscript.

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Electronic supplementary material The online version of this article (doi:__) contains supplementary material which is available to authorized users.

Table I Seed handling and seed size of top fruit species in the diet of *A. geoffroyi* communities inhabiting continuous forest and forest fragments in Lacandona, Chiapas.

Forest condition/species	Family	Mean Seed size (cm.	%TFT[a]	*n*	% Seed handling		
					Swallowed	Spat out	Dropped
Continuous forest							
Spondias radlkoferi	Anacardiaceae	3.87	33.1	661	10.4	37.4	47.0
Ficus sp1	Moraceae	<0.1	10.3	27	100	0	0
Spondias mombin	Anacardiaceae	1.97	9.5	151	31.8	25.8	33.8
Ficus tecolutensis	Moraceae	<0.1	7.0	155	100	0	0
Calatola laevigata	Icacinaceae	1.20	5.6	35	100	0	0
Ampelocera hottlei	Ulmaceae	1.38	5.4	126	36.9	59.1	3.6
Ficus obtusifolia	Moraceae	<0.1	3.9	68	100	0	0
Brosimum alicastrum	Moraceae	1.58	3.4	85	14.2	61.2	24.6
Inga punctata	Fabaceae	1.32	2.1	27	75.9	24.1	0
Forest fragments							
Spondias radlkoferi	Anacardiaceae	3.87	20.5	358	7.1	32.5	59.6
Brosimum alicastrum	Moraceae	1.58	13.4	182	12.5	65	22.5
Ficus tecolutensis	Moraceae	<0.1	10.2	188	100	0	0
Ficus sp1	Moraceae	<0.1	9.3	194	99.0	1.0	0
Dialium guianense	Fabaceae	1.01	7.7	40	13.8	86.3	0
Sabal mexicana	Arecaceae	0.60	4.3	87	78.7	21.3	0
Ficus sp2	Moraceae	<0.1	4.2	77	100	0	0
Calatola laevigata	Icacinaceae	1.20	4.0	40	100	0	0
Spondias mombin	Anacardiaceae	1.97	3.8	64	6.3	17.2	76.6
Inga punctata	Fabaceae	1.32	2.5	40	100	0	0

The number of seed handling records for each plant species is indicated (*n*). All species are trees with the exception of the palm *Sabal mexicana*

[a] Species were ranked based on the percent of time spent consuming each fruit species in relation to the total time spent consuming all fruit species until the sum was 80%

Table II Top defecated seed species in *A. geoffroyi* communities inhabiting continuous forest and forest fragments in Lacandona, Chiapas

Forest condition/species	Family	GF	FR	%TFR[a]	*n*	%US
Continuous forest						
Spondias radlkoferi	Anacardiaceae	Tree	187	26.8	579	100
Ficus tecolutensis	Moraceae	Tree	85	12.2	>23300	–
Cissus verticillata	Vitaceae	Vine	57	8.2	250	100
Spondias mombin	Anacardiaceae	Tree	47	6.7	136	100
Guarea glabra	Meliaceae	Tree	40	5.7	142	100
Ampelocera hottlei	Ulmaceae	Tree	39	5.6	174	95.0
Dialium guianense	Fabaceae	Tree	39	5.6	202	97.5
Celtis iguanaea	Ulmaceae	Vine	29	4.2	216	100
Paullinia costata	Sapindaceae	Vine	18	2.6	59	100
Ficus sp1	Moraceae	Tree	18	2.5	>2800	–
Fragmented forest						
Ficus tecolutensis	Moraceae	Tree	140	22.3	>58800	–
Sabal mexicana	Arecaceae	Palm	50	8.0	293	100
Dialium guianense	Fabaceae	Tree	46	7.3	161	93.7
Guarea glabra	Meliaceae	Tree	46	7.3	120	100
Ficus sp1	Moraceae	Tree	32	5.1	>4450	–
Spondias radlkoferi	Anacardiaceae	Tree	28	4.5	154	96.4
Guarea grandifolia	Meliaceae	Tree	26	4.2	93	100
Inga sp1	Fabaceae	Tree	22	3.5	233	86.4

Castilla elastica	Moraceae	Tree	21	3.4	90	100
Spondias mombin	Anacardiaceae	Tree	19	3.0	77	100
Acacia farnesiana	Fabaceae	Shrub	14	2.2	64	92.3
Ficus sp2	Moraceae	Tree	14	2.2	>2000	—
Attalea butyracea	Arecaceae	Palm	10	1.6	15	100
Bactris balanoidea	Arecaceae	Palm	8	1.3	16	100
Inga sp2	Fabaceae	Tree	7	1.1	68	100
Sapium sp.	Euphorbiaceae	Tree	6	1.0	91	100
Celtis iguanaea	Ulmaceae	Vine	4	0.6	39	100
Faramea occidentalis	Rubiaceae	Shrub	4	0.6	27	100
Ficus sp3	Moraceae	Tree	4	0.6	>300	—
Nectandra sp.	Lauraceae	Tree	4	0.6	23	100

Column headings: GF = growth form; FR = number of fecal records; %TFR = percent of total fecal records; *n* = total number of seeds in feces; %US = percent undamaged seeds for each plant species; — = undetermined data. Species are ordered based on %TFR

[a] Species were ranked based on the percent of fecal records in which each seed were found in relation to the total fecal records for all seed species until the sum was 80%

Table III Germination success of defecated versus control seeds

Plant species	% Germination						
	Defecated	*n*	Control	*n*	*G*-test	*p*	Effect
Ampelocera hottlei	33	15	6.6	15	7.93	0.005	+
Brosimum lactescens	100	15	29	14	23.9	0.0008	+
Cissus verticilata	55	20	6.2	16	10.8	0.001	+
Faramea occidentalis	90	10	50	16	4.9	0.03	+
S. radlkoferi	38	24	2.5	40	14.6	0.001	+

Germination trials were 90 days except for *B. lactescens* which was 20 days.

Figure legend

Fig. 1 Seed handling in continuous and fragmented forest in Lacandona, Chiapas. Different capital letters indicate significant differences among forest conditions, while different lower case letters indicate differences among seed handling categories within each habitat (contrast tests, $p < 0.05$).

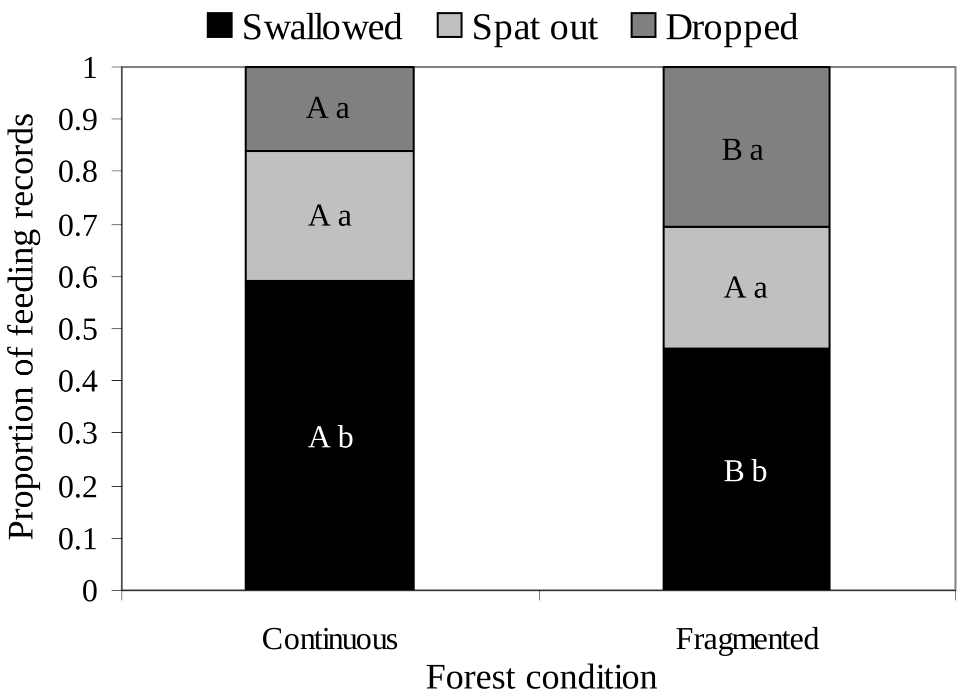
Swallowed
Spat out
Dropped
Proportion of feeding records
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
A a
A a
A b
B a
A a
B b
Continuous
Fragmented
Forest condition

Fig. 1

Electronic Supplementary Material

Effectiveness of Spider Monkeys (*Ateles geoffroyi vellerosus*) as Seed Dispersers in Continuous and Fragmented Rainforests in Southern Mexico

Journal: International Journal of Primatology

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Study Area

Fieldwork was conducted during a 15-mo period in 2007 and 2008 in the Lacandona rainforest, southern Chiapas, Mexico (16°05'58" N, 90º52'36" W; elevation 10–50 m a.s.l.). Covering parts of Mexico, Guatemala, and Belize, this region encompasses the largest portion of tropical rainforest in Mesoamerica and one of the most important in the Neotropics (Dirzo 1994). The original vegetation in the area is lowland tropical rainforest and semideciduous rainforest. The climate in the region is hot and humid with 24 °C average temperature and 2881 mm average annual rainfall. Greatest rainfall concentration is found in June–September (range: 423–511 mm/month), and lowest in February-April (46–61 mm/month) (Comisión Federal de Electricidad, Mexico, *unpublished data*).

The study was conducted in two adjacent areas separated by the Lacantún river: the Marqués de Comillas region (MCR, eastern side of the river), and the Montes Azules Biosphere Reserve (MABR, western side) (Table S2). Human colonization of MCR began in the 1960's (Mendoza and Dirzo 1999), and cattle ranching resulted in the rapid disappearance and fragmentation of the forest. Approximately 50% of the land surface of MCR is currently used for agricultural purposes, but small (0.5–30 ha) and large (850–1465 ha) fragments still remain in the area. The protected area of MABR was created in 1978 and consists of approximately 300 000 ha of continuous forest.

Methodological Details of Feeding Behavior

Focal animals were randomly changed at 5-min intervals or when animals moved out of sight. Since spider monkeys split into foraging subgroups, data were collected from more than one subgroup throughout the day whenever possible. We collected 116 observation days in continuous forest and 107 observation days in fragments. These observation days corresponded to 18923 5-min records in 1000 h of focal observations (496 h in continuous forest and 504 h in fragments), from which 442 h (44.2%) were feeding observations (204 h in continuous forest and 238 h in fragments).

Tree Composition, Statistical Analysis and Results

To determine the vegetation structure in continuous and fragmented forests, we fixed 10 50 × 2 m linear transects randomly (Gentry 1982) within each of the 6 sites, for a total of 60 transects. We recorded all trees and shrubs with diameter at breast height (DBH) ≥10 cm. To compare adult tree community structure among the six study sites, we used a Principal Component Analysis (PCA) and a nonparametric t-test (Mann-Whitney *U* test) to compare the PCA component scores between continuous and fragmented forests (for the first axis, which explained 59.4% of total variance, Table S3, Fig. S1). To compare the abundance of fruit trees exploited in four different DBH categories (10–30 cm, 30–50 cm, 50–70 cm and >70 cm) in each forest condition, we used generalized linear models (GLM) fixing a Poisson distribution and log-link function to the response variable (Crawley 1993). To identify which DBH categories were statistically different among each other we used post-hoc analyses with contrasts (Crawley 1993). All statistical analyses were performed using JMP software (version 7.0, SAS Institute, Cary, N.C.).

Tree composition between continuous and fragmented forests was not significantly different (Mann-Whitney $U = 6$, df. = 1, $p = 0.51$, Fig. S1). We found significant differences in the number of individuals among DBH categories ($\chi^2 = 106$, df = 6, $p <$

0.0001), being the number of individuals in the latter DBH category (>70 cm) greater in continuous than in disturbed forests (contrast test, $p = 0.04$). However, no other significant differences were detected in the other DBH categories ($p > 0.05$, Fig. S2).

Table S1 Seed dispersal by twelve Neotropical primates

Primate species	% FRU	DSS (no. feces)	Seed length (cm)	% FWS (no. feces)	Gut passage net effect				Site	Ref
					n	%Positive	%Negative	%Neutral		
Alouatta guariba	—	14 (—)	—	45 (66)	4	75	25	0	FBR	1
A. palliata	28	12 (53)	—	15.1 (—)	—	—	—	—	SRNP	2
A. palliata	—	15 (250)	<0.1–3.5	—	6	83.3	0	16.7	TUX	3
A. palliata	—	9 (—)	<0.1–2.4	46 (31)	—	—	—	—	PVNP	4
A. seniculus	—	80 (—)	—	—	7	57.1	14.3	28.6	TNP	5
A. seniculus	44	14 (27)	—	21 (—)	—	—	—	—	MNP	6
A. seniculus	—	86 (236)	<0.1–4	—	17	23.5	35.3	41.2	NS	7
Brachyteles arachnoides	—	18 (—)	—	21 (25)	6	50	16.7	33.3	FBR	1
Cebus capucinus	—	—	—	—	9	55.5	22.2	22.3	BCI	8
C. capucinus	81	14 (28)	—	0 (—)	—	—	—	—	SRNP	2
C. capucinus	—	30 (—)	<0.1–>1.5	2 (3)	—	—	—	—	PVNP	4
C. capucinus	53	67 (—)	0.1–3	7.5 (13)	—	—	—	—	BCI	9
Lagothrix lagotricha	—	76 (—)	—	—	16	50	6.2	43.7	TNP	5

Saguinus mystax	70	67 (1094)	0.06–2.3	5.2 (57)	—	—	—	—	EBQB	10
S. fuscicollis	60	81 (1376)	0.06–2.3	3.8 (52)	—	—	—	—	EBQB	10
S. midas	87.5	12 (—)	0.5–2.4	—	—	—	—	—	FVI	11
Ateles belzebuth	—	75 (—)	—	—	14	42.8	28.6	28.5	TNP	5
A. belzebuth	79	133 (916)	<0.1–4	—	—	—	—	—	YNP	12
A. belzebuth	87	27 (144)	<0.2–2.7	1 (176)	—	—	—	—	YNP	13
A. paniscus	80	71 (47)	—	0 (—)	—	—	—	—	MNP	6
A. geoffroyi	78	17 (39)	—	0 (—)	—	—	—	—	SRNP	2
A. geoffroyi	54	71 (957)[a]	<0.1–4.5	9.9 (95)	6	83.3	0	0	LAC	14

Abbreviations: DSS, number of defecated seed species; %FRU, percent of fruit in the diet; %FWS, percent fecal samples without seeds; SDD, seed dispersal distance (m); (—) data unavailable.

Site abbreviations: BCI, Barro Colorado Island, Panama; EBQB, Estación Biológica Quebrada Blanco, Perú; FBR, Fazenda Barreiro Rico, Brazil; FVI, Fazenda Vitória, Brazil; LAC, Lacandona, Chiapas, Mexico; MNP, Manú National Park, Peru; NS, Nouragues Station, French Guiana; PVNP, Palo Verde National Park, Costa Rica; SRNP, Santa Rosa National Park, Costa Rica; TNP, Tinigua National Park, Colombia; TUX, Los Tuxtlas Biological Station, Mexico; YNP, Yasuní National Park, Ecuador.

References: 1. Martins (2006); 2. Chapman (1989); 3. Estrada and Coates-Estrada (1984); 4. Wehncke *et al*. (2004); 5. Stevenson *et al*. (2002); 6. Andresen (1999); 7. Julliot (1996); 8. Wehncke and Dalling (2005); 9. Stevenson (2000); 10. Knogge and Heymann (2003); 11. Oliveira and Ferrari (2000); 12. Link and Di Fiore (2006); 13. Dew (2008); 14. present study.

Table S2 Study sites and groups of *Ateles geoffroyi* studied in the Montes Azules Biosphere Reserve (MABR) and the Marqués de Comillas region (MCR), Chiapas, Mexico

Study site	Size (ha)	Location	DNF (m)	DCF (m)	YSF	Group size
Continuous forest	331000	Montes Azules Biosphera Reserve				
C1	–	16°06'58.2"N, 90°56'18.4"W	–	–	–	40
C2	–	16°09'32.0"N, 90°54'06.6"W	–	–	–	36
C3	–	16°09'40.0"N, 90°54'04.5"W	–	–	–	44
Forest fragments						
F1	31	16°19'24.5"N, 90°50'43.7"W	150	1200	24	39
F2	14.4	16°19'52.0"N, 90°51'06.1"W	450	200	29	35
F3	1125	(16°15'12.2"N, 90°49'59.5"W)	100	1100	26	41

DNF, distance to the nearest forest fragment; DCF, distance to the continuous forest; YSF, years since fragmentation

Table S3 Principal component scores for the three main axes by study site

Study site	PC 1	PC 2	PC 3
C1	1.2	0.14	-0.61
C2	1.12	-0.23	0.02
C3	1.17	0.8	0.82
F1	1.35	0.07	-0.23
F2	0.94	-1.1	0.44
F3	0.77	0.13	-0.47
Percent of total variance explained	59.40%	15.30%	12.1%

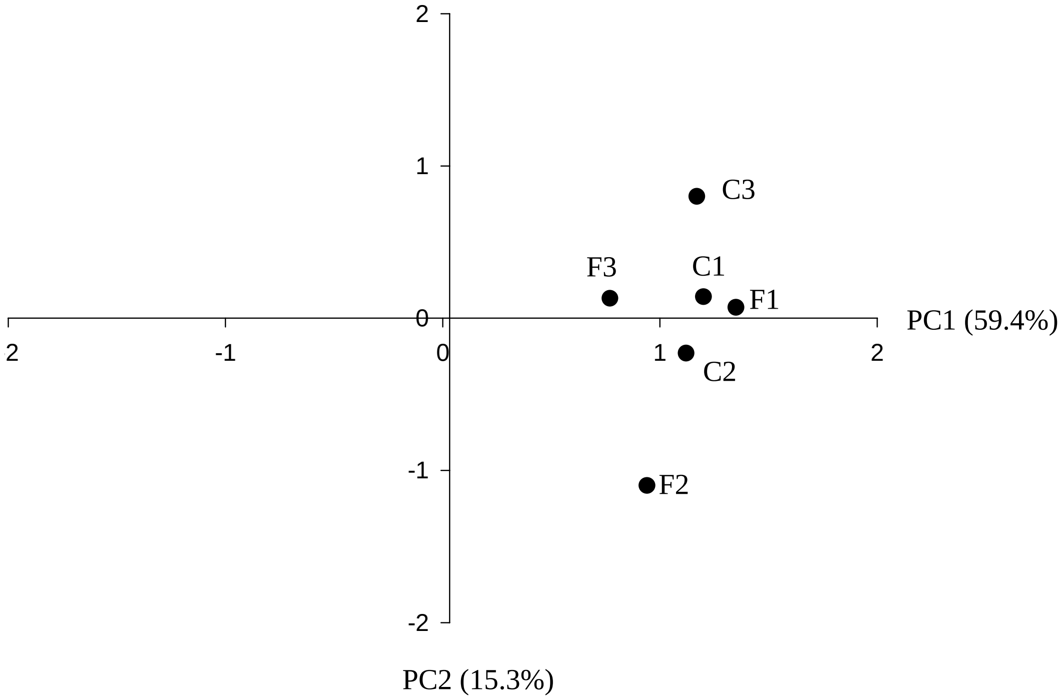

Figure S1. Principal component analysis of tree composition by study site. The percent of total variance explained by each axis is indicated in parenthesis.

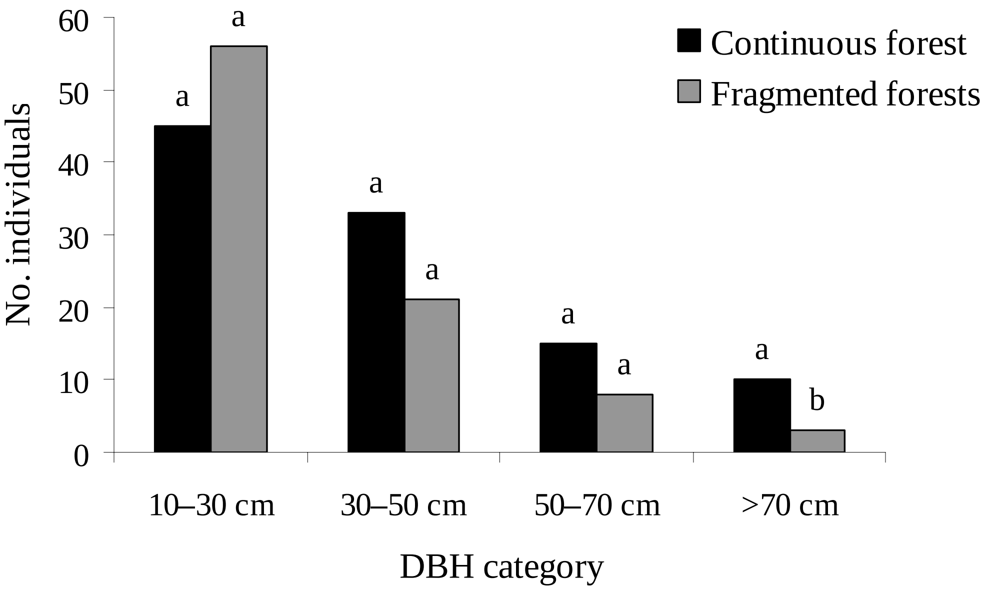

Figure S2. Total abundance of fruit trees in the diet of spider monkeys by forest condition and DBH category. Different letters on the bars indicate significant differences (*p* < 0.05).

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CAPÍTULO III

Short title: Activity Patterns of Spider Monkeys in Mexico

Seasonal Differences and Shifts in Activity Patterns of Spider Monkeys Living in Forest Fragments in Southern Mexico

(accepted with major changes 15 March 2010, International Journal of Primalogy, IF=1.78)

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Abstract. Understanding how primates adjust their behavior to resource limitations imposed by habitat fragmentation is a fundamental challenge for primatologists and conservation biologists. During a 15-month period, we studied the activity patterns of six communities of *Ateles geoffroyi* living in continuous forest and fragments in the Lacandona rainforest, Mexico. We tested, for the first time, the effects of forest type (continuous and fragmented), season (dry and rainy) and the interaction between these variables on activity patterns of this primate. Overall, monkeys spent more time feeding in fragments than in continuous forest, while traveling showed the opposite pattern. These results can be explained by both a more folivorous diet and the spatial limitations in fragments. Regarding seasonality, time spent feeding was higher in the rainy than in the dry season, whereas time spent resting followed the opposite pattern. We suggest these results are likely related to the lower fruit availability during the dry season (and concomitant increase in percent leaves consumed) and higher temperature, both contributing to 'force' monkeys to spend more time resting. Forest type and seasonality did not interact with activity patterns, indicating that the effect of seasonality on activities was similar across all sites. Although our findings confirm that spider monkeys are able to make behavioral shifts in forest fragments and during the dry season, further studies are necessary to assess if these shifts are adequate to assure their health, fitness, and most importantly, their long-term persistence in fragmented habitats.

Keywords *Ateles geoffroyi*; behavioral flexibility; environmental stresses; habitat fragmentation; Lacandona

Introduction

Habitat fragmentation imposes critical resource limitations for survival and reproduction of tropical vertebrates (e.g., fish, mammals: Brook 2003; birds: Sehgal 2010; primates: Chapman *et al.* 2007). This is particularly important for arboreal primates, as they rely on the presence and abundance of large canopy food trees (Arroyo-Rodríguez *et al.* 2007; Arroyo-Rodríguez and Dias 2009; Stevenson 2001), and changes in vegetation derived from fragmentation can result in reduced food availability (e.g., reduced tree basal area: Arroyo-Rodríguez and Mandujano 2006; Laurance *et al*. 1997; reduced plant species richness: López *et al*. 2005). This process may be particularly critical during periods of food scarcity in seasonal forests (e.g., Hemingway and Bynum 2005; Stoner and Timm 2004). Food availability is often lower during the dry season than during the rainy season (Hemingway and Bynum 2005; Zimmerman *et al.* 2007), and hence, this could have negative effects on food availability for primates. Although some primates can make behavioral adjustments to cope with resource limitations in fragmented and/or seasonal habitats (Hemingway and Bynum 2005; Jones 2005), our current knowledge about this topic is scarce, even when considering the most studied primates (e.g., howler monkeys: Arroyo-Rodríguez and Dias 2009).

A few studies have demonstrated that primates can adjust their behavior in response to habitat and seasonal-related differences in resource availability. Overall, these studies indicate that in response to fragmentation and seasonal fruit scarcity and adverse climatic conditions, primates often switch to lower-quality diets (e.g., a more folivorous diet: Hemingway and Bynum 2005; Onderdonk and Chapman 2000), which may increase the time spent feeding and hence can affect time devoted to other core activities such as traveling and/or resting (Dunbar 1992; Korstjens *et al.* 2010). For instance, activity patterns of some primates change in response to resource limitations in fragments (e.g., guenons spend a low time feeding in fragments: Tutin 1999; howler monkeys spend more time feeding after the partial deforestation of their habitats; Clarke *et al*. 2002). In Colombia, populations of *Alouatta seniculus* inhabiting in a continuous forest spend 59% of their total activity budget resting (Stevenson *et al.* 2000), while in forest fragments this percentage increases to 78% (Gaulin and Gaulin 1982).

Seasonal variation in food availability also can 'force' primates to shift activity patterns. For example, African primates respond to seasonal food scarcity by spending less time resting and in social activities (e.g., baboons: Dunbar 1992) or spending more time feeding on leaves and reducing day range and party size during the dry season than during rainy season (e.g., chimpanzees: Doran 1997). Similarly, during periods of high-frugivory (i.e., during the rainy season) gorillas spend less time feeding and more time traveling than during the dry season (Masi *et al.* 2009).

This evidence shows that activity patterns of some species of primates are influenced by forest type and seasonality (Dunbar *et al.* 2009), nevertheless, few studies have evaluated the effects of forest type (i.e., continuous and fragmented) and seasonality simultaneously. In the Neotropics, Ateline primates may be particularly amenable subjects for this type of research since they typically live in seasonal environments where food abundance and distribution can vary greatly over the course of a year (Di Fiore and Campbell 2007). However, studies evaluating the potential effects of fragmentation and/or seasonality on activity patterns of this taxon are scarce, and mainly focused on more folivorous species such as howler monkeys (e.g., Bicca-Marques 2003; Cristóbal-Azkarate and Arroyo-Rodríguez 2007; Stoner 1996). Although a number of studies have briefly described the activity patterns of frugivorous Ateline primates such as *Lagothrix* spp. (e.g., Defler 1995; Stevenson *et al.* 1994) and spider monkeys (*Ateles* spp.) in continuous forests (reviewed by Di Fiore and Campbell 2007; Wallace 2001; Table 1), no studies to date have attempted to determine how resource limitation imposed by fragmentation and seasonality modify their activity patterns.

Here we assess variations in activity patterns of spider monkeys (*Ateles geoffroyi vellerosus*) in two contrasting forest types (continuous and fragmented) and during two seasons (dry and rainy) in the Lacandona rainforest, southern Mexico. We discuss our results in relation to documented variations in primate diet and food availability across the study sites in the same monkey communities (Chaves *et al.* in press). We hypothesize that spider monkeys can adjust their activity patterns in order to deal with food scarcity in forest fragments and during the dry season. We expect that feeding time will be greater in fragments than in continuous forest in order to compensate for the lower abundance and quality of foods for primates frequently found in fragments (e.g., Onderdonk and Chapman 2000). Furthermore, since both fragmentation and fruit scarcity in the dry season often force primates to increase their consumption of low-energy content items such as leaves, we expect that in fragments and during the dry season time spent resting will be higher because resting is an energy-saving strategy particularly important during digestion of fibrous material (Korstjens *et al.* 2010; Milton 1981a). Finally, since during the dry season animals are exposed to more stressful conditions than during the rainy season (e.g., temporal food scarcity, drought, high ambient temperature: Murphy and Lugo 1995; Stoner and Timm 2004), we also expect that spider monkeys will spend less time in high energy-cost activities, such as feeding and traveling (Asensio *et al.* 2009) in the former than in the latter season.

This is a timely study for the conservation of this critically endangered primate, as the Lacandona rainforest has been highly fragmented during the last 40 years, but several small communities of spider monkeys still remain isolated in some forest fragments (Chaves *et al.* in press). Understanding how primates cope with environmental stresses (e.g., food scarcity) in fragmented and seasonal forests, such as the one we studied, is therefore critical for the design and establishment of appropriate management strategies for the conservation of this and many other animal species.

Methods

Study Area

Fieldwork was conducted in the Lacandona rainforest, southern Chiapas, Mexico (16°05'58" N, 90º52'36" W; elevation 10–50 m a.s.l.). This region encompasses the largest portion of tropical rainforest in Mesoamerica, covering parts of Mexico, Guatemala, and Belize (*ca.* 800,000 ha, De la Maza and De la Maza 1991). The original vegetation in the area is lowland tropical rainforest and semideciduous rainforest. The region is highly seasonal presenting two clearly defined seasons: a rainy season (June-December) and a dry season (January-May). Average annual rainfall is 2881 mm, and the greatest rainfall concentration is found in June-September (ranging from 423 to 511 mm/month), while the lowest is found in February-April (ranging from 46 to 60.6 mm/month). Average annual temperature is 24 °C, being greater in the dry season (average per month: 26.3 °C; range 22–28 °C) than in the rainy season (average per month: 23.5 °C; range: 20–25 °C). Average maximum daily temperature occurs in the dry season from March to May (*ca.* 38 °C in each month; Comisión Federal de Electricidad, Mexico, *unpublished data*). Average monthly temperature in fragments is *ca.* 2 °C greater than in continuous forest (González-Di Pierro *et al.* in press). Although there are no long-term published records of phenological data for the region, an 8-year study of tree community dynamics indicates that fleshy fruit (the main food item for *A. geoffroyi*; González-Zamora *et al.* 2009) production at Lacandona is concentrated within the rainy season, while fruit is scarce during the dry season (M. Martínez-Ramos, *unpublished data*). This pattern is consistent with that observed in other Neotropical rainforests (see Zimmerman *et al.* 2007).

The study was conducted in 2 adjacent areas separated by the Lacantún River: the Marqués de Comillas region (MCR, eastern side of the river) encompassing *ca.* 176,200 ha of disturbed forests and human settlements (Marquez-Rosano 2006) and the Montes Azules Biosphere Reserve (MABR, western side) comprising *ca.* 331,000 ha of old-growth undisturbed forest (Gómez-Pompa and Dirzo 1995). Human colonization and deforestation of MCR began in the decade of the sixties and cattle ranching resulted in the rapid disappearance and fragmentation of the forest (Marquez-Rosano 2006). Approximately 50% of the land surface of MCR is nowadays used for agricultural purpose, but several forest fragments (0.5–1500 ha) still remain in the area.

Study Sites and Spider Monkey Communities

We studied activity patterns of 6 independent spider monkey communities: 3 communities located in 3 different areas within the MABR continuous forest separated by at least 4 km, and 3 communities located in 3 different forest fragments within the MCR (Table 2). We chose these sites because they were occupied by well-habituated monkey communities (i.e., the monkeys were habituated to tourists, researchers, and local people that visit these sites).

In addition, all the study fragments were easily accessible, and have been protected by the land owners since 1985 (avoiding potential confounding effects of hunting and selective logging). These communities ranged from 35 to 44 individuals, and their home ranges varied from 14 to 90 ha (Table 2). All fragments in MCR were isolated ≥ 24 years ago, and their sizes were 14, 31, and 1125 ha (Table 2). Despite the variation in size, we consider all three sites as fragments because all: (1) are surrounded by an anthropogenic matrix (i.e., crops, pastures, and human settlements) and are isolated from the continuous forest by 200–1200 m, and (2) the vegetation has noticeable signs of disturbance (e.g., plantations such as *Teobroma cacao* and *Aechmea magdalenae*, and lower density of emergent trees in the canopy, see below). Fragments F1 and F2 each contained 1 monkey community. Although fragment F3 contained 3 monkey communities, they could be distinguished by their home ranges, group composition and individuals with unique marks (see below), and we only studied 1 of the 3 communities. In addition to the forest fragment, the monkey community inhabiting fragment F1 also exploited adjacent areas in the matrix consisting of cocoa plantations (2.5 ha), a 9-year old secondary forest (5 ha), and live fences and pastures (*ca.* 10 ha) with isolated adult trees of several top food species for *A. geoffroyi* including *Ficus insipida*, *Brosimum alicastrum*, *Inga* spp., and *Spondias* spp (see González-Zamora *et al.* 2009). Similarly, the monkey community inhabiting fragment F2 exploited an additional area comprised of cocoa plantations (2 ha) and a 12-year old secondary forest (3.7 ha). During our study, monkey communities did not present inter-site movements between fragments, or between fragments and the continuous forest.

A detailed description of the diet and food availability within the home range of each monkey community has been reported elsewhere (Chaves *et al*. in press); only a brief overview is given here to facilitate the interpretation of our results about activity patterns.

The diet of the *A. geoffroyi* communities within the study sites is comprised of 121 plant species belonging to 39 families. Overall, fruits are the most eaten item (56% of total feeding time, 21 species), followed by leaves (18.5%, 66 species), and other plant items. The consumption of both mature and immature leaves is higher in fragments than in continuous forest. In our 6 study sites food availability is lower in forest fragments than continuous forest (Chaves *et al*. in press). Although the average number of food plant species is similar in continuous forest and fragments (71 versus 66 species), the average density of large trees (DBH > 60 cm) of fleshly-fruit species is higher in continuous than fragmented habitats (4 versus 1.3 stems/1000 m^2). Additionally, the sum of the Importance Value Index (IVI) of top food species is also greater in continuous forest (IVI = 249) than in fragments (IVI = 166). Furthermore, some top food species for spider monkeys such as *Ampelocera hottlei*, *Brosimum alicastrum*, *Pouteria campechiana*, and *Virola guatemalensis* are much less abundant (if not absent) in fragments than in continuous forest (Chaves *et al*. in press). Since we did not report seasonal variation in the diet composition of spider monkeys in our previous study on diet, we used the same data base and methodology described by Chaves *et al.* (in press) to calculate this and report it here.

Activity Pattern Data Collection

Activity patterns of spider monkey communities were studied during a 15-mo period: 6 months in the dry season (February-April 2007 and 2008), and 9 months in rainy season (May-October 2007, and August-October 2008). We used high resolution binoculars to record the activity patterns of each of 6 communities during 3 consecutive days once every 3 weeks, using focal animal sampling (Altmann 1974). We alternated observations among communities every 3 days. Individuals were identified utilizing unique marks found in skin pigmentation, hair, genitals (shape, size, and pigmentation of clitoris and penis), face (distinctive facial shapes), body size, and other distinguishing marks such as scars. Focal animals were randomly changed after each 5-min interval or when animals moved out of sight. Whenever possible, data were collected from >1 subgroup throughout the day. Data were collected from 0700 h to 1730 h, totaling 1010 h of focal observations (496 h in continuous forest and 514 h in fragments). To minimize the potential effect of age class (i.e., adults, subadults, juveniles, and infants) on monkey behavior, all focal individuals included in our analyses were adults or subadults.

During the focal observations we recorded 4 mutually exclusive activities: 1) feeding (masticating or consuming food items), 2) resting (period of inactivity), 3) traveling (movement between tree crowns or within the crown of a tree that was not directly food related), and 4) other activities (e.g., social activities).

Data Analysis

We used an analysis of deviance (ANODE) with a generalized linear model (Crawley 2002) to compare activity patterns among forest types and seasons. Since in each study site we observed an independent monkey community, we considered each of the three sites per forest type as replicas. Proportion time data were first arcsine-transformed, and we used a Normal distribution with an identity link-function with the response variable (Crawley 2002). The whole model was: TIME = ACTIVITY + FOREST + ACTIVITY*FOREST + SEASON + SEASON*ACTIVITY + SEASON*FOREST + ACTIVITY*FOREST*SEASON (asterisks indicate interactions among factors). To identify the levels of each factor that were statistically different between each other we used post-hoc analyses with contrasts (Crawley 2002). A similar statistical procedure was used to compare the proportion of time devoted to each plant item (i.e., fruits, leaves, branch piths, flowers, and others) between seasons. Statistical analyses were performed using JMP software (version 7.0, SAS Institute, Cary, N.C.).

Results

Overall, spider monkeys spent different amounts of time per activity (ACTIVITY; χ^2 = 94.9, df = 3, $p < 0.0001$), with time feeding (average percentage ± SD, 44 ± 9% of total time) and resting (34 ± 7%) higher than time spent traveling (12 ± 4%) and other activities (10 ± 3%) (contrast tests, $p < 0.01$ in all cases; Fig. 1). However, notable variations in percentages of time spent in each activity were observed across sites and seasons (Table 3).

Activity patterns differed between forest types (ACTIVITY*FOREST; χ^2 = 9.9, df = 3, $p = 0.02$, Fig. 1A) with the percentage of time spent feeding significantly higher in forest fragments (average percentage ± SD, 48 ± 9%) than in continuous forest (41 ± 8%), whereas traveling was higher in continuous forest (15 ± 4%) than in fragments (9 ± 2%) (contrast test, $p < 0.03$; Fig. 1A). Time spent resting and in other activities did not differ between forest types (contrast tests, $p > 0.1$ in both cases; Fig. 1A).

Activity patterns also differed between seasons (ACTIVITY*SEASON; χ^2 = 17.2, df = 3, $p = 0.0006$; Fig. 1B). The percentage of time spent feeding was higher in the rainy (51 ± 10%) than in the dry season (37 ± 11%; contrast test, $p < 0.001$; Fig. 1B), whereas resting was higher in the dry (38 ± 8%) than in the rainy season (29 ± 9%; contrast test, $p = 0.02$; Fig. 1B). Both of these patterns were observed across most study sites (with exception of C2; Table 3). Time dedicated to traveling and to other activities did not differ between seasons (contrast test, $p > 0.05$ in all cases; Fig. 1B). Finally, we found that forest type and season did not interact with activity patterns (ACTIVITY*FOREST*SEASON; $\chi^2 = 1.3$, df = 3, $p = 0.7$), indicating that the effect of season on activity patterns was similar across all study sites.

We found significant differences in consumption of leaves (young and mature) between seasons ($\chi^2 = 11.5$, df = 2, $p < 0.01$), being higher in the dry than in the rainy season (contrast tests, $p < 0.02$ in all cases; Fig. 2). However, the time spent on fruits (immature and mature) was similar between seasons ($\chi^2 = 0.60$, df = 2, $p = 0.6$; Fig. 2).

Discussion

In general, our results were consistent with our hypothesis and most of our predictions: spider monkeys in Lacandona adjust their activity patterns in order to deal with forest type and seasonal changes in food availability. As a consequence of lower food availability in fragments, leaf consumption is higher in this forest type than in continuous forest (Chaves *et al*. in press; see Methods). Also, we found here that independent of study site, monkeys spent more time feeding on leaves during the dry season (i.e., the period of fruit scarcity; see Methods) than during the rainy season. Our findings are therefore consistent with the idea that variations in food availability can affect the diet of primates, ultimately affecting the time that primates devote to core activities (e.g., feeding, resting, and traveling: Bronikowski and Altmann 1996; Dunbar 1992; Korstjens *et al*. 2010). However, as we discuss below the implications that variations in food availability and diet have on activity patterns of spider monkeys can be different when analyzing: 1) differences between continuous forest and forest fragments, and 2) differences between seasons.

Habitat-Related Shifts in Activity Patterns

Compared to monkeys inhabiting continuous forest, spider monkeys in fragments spent more time feeding, less time traveling and similar time resting. Fruit scarcity in fragments would promote spider monkeys to compensate energy expenditure by increasing their time feeding on items that are less nutritious, and low in energy (i.e., poorer in nonstructural carbohydrates) such as leaves. As the digestive system of *A. geoffroyi* is designed essentially for a diet mainly composed of easily digestible food items like fleshly fruits (Lambert 1998; Milton 1981 a, b), monkeys must invest more time feeding when eating leaves (i.e., for procuring more leaves) to obtain sufficient amounts of energy and nutrients. This would be particularly true for those nutrients that are poor in leaves but abundant in fleshy fruits, such as lipids and carbohydrates (Milton 2008). This idea is supported by different primate studies in Paleotropical continuous forests (e.g., baboons: Dunbar 1992; lemurs: Overdorff 1996; gorillas: Masi *et al.* 2009), which indicate that time spent feeding is directly related to the proportion of leaves in the diet. Our results for fragments are consistent with this prediction. Iwamoto and Dunbar (1983) also found that time spent feeding by gelada baboon populations in three different habitats was inversely related to variation in food quality among habitats; a pattern similar to that reported by Watts (1988) for mountain gorillas.

The observation that monkeys spent less time traveling in fragments compared to continuous forest may partially be explained by the limited foraging area available in the fragments. In fragments as small as 14 ha, food is scarce and space is limited, and hence there is not much traveling that they can do. Furthermore, since traveling is an energy-cost activity (Chapman and Chapman 2000), the reduction of time traveling in fragments could also be an energy-saving strategy to cope with resource limitations in fragments. Finally, spider monkeys in fragments might spend less time traveling because they spend more time feeding on leaves (Chaves *et al*. in press), which are generally more readily available (in contrast to the patchiness of fruits; Milton 1981b). Overall, in conjunction these factors would explain why monkeys in fragments spent less time traveling than in continuous forest.

The lack of significant differences between continuous and fragmented forests in time spent resting could indicate that this activity is more constrained by changes in temperature between seasons (as suggested by Korstjens *et al*. 2010), than changes in food sources between forest types since in Lacandona differences in average daily temperature are higher between seasons than between forest types (see Methods). Nevertheless, further studies assessing the potential effect of temperature on activity patterns of spider monkeys are needed to evaluate this hypothesis.

Seasonal-Related Differences in Activity Patterns

Overall, independent of the forest type, time spent feeding was higher during the rainy than during the dry season. This pattern may be explained by two nonexclusive explanations. First, in this region fruit availability is higher during the rainy season (see Methods), and monkeys spent less time feeding on leaves during this season (Fig. 2). Although we found that time spent on fruits did not differ between seasons, other studies have demonstrated that when fruits are temporally available, spider monkeys include more fruit in their diet (Chapman 1987; Felton *et al.* 2008). It is reasonable to expect that time spent feeding should be lower when eating on highly energetic, nutritionally balanced and easily digestible plant items such as fruits. Nevertheless, Felton *et al*. (2009) interpret greater feeding in the rainy season as a strategy for spider monkeys to take advantage of peak seasonal foods allowing them to ingest surplus energy and store it as fat in preparation for the impending period of food scarcity. This and other Ateline species (e.g., *Ateles paniscus*: Milton 1998; *A. chamek*: Wallace 2005) accumulate fat during peaks of fruit abundance, which is a logical strategy for animals experiencing fluctuating food supply (Felton *et al.* 2009). Second, evidence suggests that seasonal increase in ambient temperature, such as that occurring during the dry season (*ca.* 3 °C; see Methods), may propitiate that primates reduce heat-generating activities like feeding in order to avoid thermal overload and its associated energetic costs (Dunbar *et al.* 2009; Korstjens *et al.* 2010), which is consistent with several studies on spider monkeys (Chapman 1988; Korstjens *et al.* 2006; Table 1). However, further information on energetic strategies of spider monkeys is needed to determine the relative influence of each of these factors.

Primate socio-ecological models indicate that in spider monkeys and other tropical primates, time spent resting is a function of seasonality, the percentage of leaves in their diet, and the mean annual temperature (e.g., Korstjens *et al.* 2006; 2010). Thus, as the percentage of leaves in the diet and the mean temperature increase, the enforced resting time (i.e., resting needed for digestive and/or thermoregulatory purposes: Korstjens *et al.* 2010) also increases (Dunbar *et al.* 2009; Korstjens *et al.* 2010). In concurrence with this hypothesis, we found that time resting was higher during the dry season (when consumption of leaves was greater; Fig. 2) than during the rainy season. This may facilitate more efficient digestion of foliar material (Milton 1981a) and at the same time minimize thermoregulatory costs during the hottest period of year (Korstjens *et al.* 2006; 2010). Similar findings also have been reported in other studies in Mesoamerica and South America. For instance, in the tropical dry forest of Santa Rosa, Costa Rica, the time that *A. geoffroyi* devote to resting is directly related to the proportion of time devoted to eating leaves (Chapman 1991). Other Atelids also spend more time resting during the dry season when fruit is scarce (e.g., *Ateles paniscus*: van Roosmalen 1980; *Lagothrix lugens*: Stevenson *et al.* 1994). Finally, a recent meta-analysis of the activity patterns of *A. geoffroyi* through Mesoamerica shows that time spent resting is mainly related (positively) to the average annual temperature in seasonal forests (González-Zamora *et al.*, *unpublished data*).

Our study has some limitations (e.g., we did not measure directly spatial and temporal food availability in each site), but it is unique in that we studied multiple spider monkey communities´ activity budgets in the context of both fragmentation and seasonality and the interaction between them. We suggest, however, that further long-term behavioral studies of spider monkeys are needed to improve our understanding of the behavioral responses of primates to environmental stresses imposed by habitat disturbance, fragmentation, and seasonality, as our knowledge about this topic is still very scarce. Although, in general, our findings indicate that spider monkeys in Lacandona can adjust their activity patterns and diet in order to cope with food scarcity in forest fragments and during the dry season, it is not clear if this behavioral flexibility is large enough to assure their health and persistence in the long-term, especially if we consider the high rates of deforestation and forest fragmentation affecting Neotropical forests. Studies analyzing the consequences of these behavioral adjustments on health, fitness and long-term persistence of primates are therefore needed to help in the design of appropriate management strategies for primate populations in the Lacandona region and other disturbed tropical forests.

Acknowledgements This research was supported by grants from the Consejo Nacional de Ciencia y Tecnología (CONACyT Grant CB2005-C01-51043 and CB2006-56799). OMC obtained a scholarship from the Dirección General de Estudios de Posgrado, UNAM, as part of the Programa de Posgrado en Ciencias Biológicas and from Secretaría de Relaciones Exteriores (SRE) of Mexico. A postdoctoral fellowship given to VAR by the Consejo Técnico de la Investigación Científica (UNAM) is gratefully acknowledged. The Instituto para la Conservación y el Desarrollo Sostenible, Costa Rica (INCODESO) provided logistical support. This study would not have been possible without the collaboration of A. M. González Di-Pierro and the local people in Loma Bonita, Chajul, Reforma Agraria and Zamora Pico de Oro ejidos. We thank C. Hauglustaine, C. Balderas, K. Amato, S. Martínez, J. Herrera, and R. Lombera for field assistance. A. Estrada and J. Benítez-Malvido made useful suggestions during the design of this research. J. M. Lobato and G. Sánchez provided technical support. We also thank two anonymous reviewers for valuable criticism and suggestions that improved the manuscript.

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Table 1 Activity budgets for 7 frugivorous atelids in different forest types.

Primate species	Activity pattern				Site[a]	Forest type (vegetation type)[b]	Season (study length)[c]	Ref.[d]
	Feed	Rest	Travel	Other				
Lagothrix lagotricha	36	36	24	4	TNP	C (TWF)	Annual (13, 672)	1
L. lagotricha	26	30	39	6	EBC	C (TWF)	Annual (12, 720)	2
L. lugens	36	36	24	4	TNP	C (TWF)	Annual (12, 624)	3
Ateles chamek	19	45	30	6	NKM	C (TDF)	Annual (11, —)	4
A. chamek	29	45	26	0	MNP	C (TMF)	Annual (21, 1360)	5
A. hybridus	23	27	42	8	SJC	F (TWF)	Annual (8, —)	6
A. paniscus	35	41	23	—	VOL	C (TMF)	Annual (12, —)	7
A. belzebuth	17	58	25	0	YNP	C (TWF)	Annual (12, 1268)	8
A. belzebuth	50	24	18	8	TAW	C (TDF)	Annual (12, —)	9
A. belzebuth	22	63	15	—	TNP	C (TWF)	Annual (12, —)	10
A. belzebuth	18	45	36	—	MES	C (TWF)	Annual (—,—)	11
A. geoffroyi	26	45	29	0	SNP	C (TDF)	Rainy (24, 335)	12
A. geoffroyi	19	55	27	0	SNP	C (TDF)	Dry (24, 335)	12
A. geoffroyi	35	43	22	0	PUL	F (TDF)	Annual (47, —)	13
A. geoffroyi	26	54	16	4	BCI	C (TWF)	Rainy (10, —)	14
A. geoffroyi	51	29	10	10	LAC	C, F (TWF)	Rainy (15, 1010)	15
A. geoffroyi	37	38	14	11	LAC	C, F (TWF)	Dry (15, 1010)	15

[a] Site: TNP, Tinugua National Park, Colombia; EBC, Estación Biológica Caparú, Colombia; NKM, Noel Kempff Mercado National Park, Bolivia; MNP, Manú National Park, Peru; SJC, San Juan del Carare, Colombia; VOL, Voltzberg, Surinam; YNP, Yasuní National Park, Ecuador; TAW, Tawadu, Venezuela; MES, Maraca Ecological Station, Brazil; SNP,

Santa Rosa National Park, Costa Rica; PUL, Punta Laguna, Mexico; BCI, Barro Colorado Island, Panama; LAC, Lacandona rainforest, Mexico

[b] C, continuous forest; F, fragmented forest; TWF, tropical wet forest; TMF, tropical moist forest; TDF, tropical dry forest

[c] Number of months and observation hours

[d] References: 1. Stevenson *et al*. (2000); 2. Defler (1995); 3. Stevenson *et al.* (1994); 4. Wallace (2001); 5. McFarland Symington (1988); 6. Aldana (2009); 7. van Roosmalen (1980); 8. Suarez (2006); 9. Castellanos (1995); 10. Klein and Klein (1977); 11. Nunes (1995); 12. Chapman (1988); 13. Ramos-Fernández and Ayala-Orozco (2003); 14. Milton (1981a); 15. this study

Table 2 Characteristics of the sites and groups of *Ateles geoffroyi* studied in Lacandona, Chiapas, Mexico (Modified from Chaves *et al.*, in press).

Sites	Size (ha)	Location	Elevation (m a.s.l.)[a]	DNF (m)	DCF (m)	YSF	Group size	Home range (ha)[b]
Continuous forest	331000	Montes Azules Biosphere Reserve						
C1	–	16°06'58.2"N, 90°56'18.4"W	125–170	–	–	–	40	29.7
C2	–	16°09'32.0"N, 90°54'06.6"W	130–180	–	–	–	36	47.3
C3	–	16°09'40.0"N, 90°54'04.5"W	130–210	–	–	–	44	89.6
Forest fragments		Marqués de Comillas Municipality						
F1	14.4	Zamora Pico de Oro 16°19'52.0"N, 90°51'06.1"W	125–140	450	200	29	35	14.4
F2	31	Zamora Pico de Oro 16°19'24.5"N, 90°50'43.7"W	130–145	150	1200	24	39	31.0
F3	1125	Reforma Agraria 16°15'12.2"N, 90°49'59.5"W	150–250	100	1100	26	41	63.1

Abbreviations: DNF, distance to nearest forest fragments; DCF, distance to continuous forest; YSF, years since fragmentation

[a] Meters above sea level. Range is indicated

[b] Home range was determined for monkey communities in continuous forest and in the fragment F3. In the other two fragments, monkeys used the entire fragment area (see further details on Chaves *et al.* in press).

Table 3. Percent time spent by spider monkeys in different activities according to study site per season.

Site	Season	Activity patterns			
		Feeding	Resting	Traveling	Others
Continuous forest					
C1	Rainy	59.2	18.2	13.2	9.4
	Dry	42.6	26.7	20.6	10.1
C2	Rainy	38.8	40.3	9.7	11.2
	Dry	33.9	37.2	10.8	18.1
C3	Rainy	43.4	32.8	15.9	7.9
	Dry	20.2	48.4	19.9	11.5
Forest fragments					
F1	Rainy	60.7	21.4	6.9	11.1
	Dry	51.3	31.6	9.4	7.7
F2	Rainy	56.9	26.9	8.1	8.1
	Dry	43.3	43.2	7.7	5.7
F3	Rainy	42.7	36.7	8.5	12.1
	Dry	30.9	42.3	14.5	12.3

Figure legends

Fig. 1 Percent time (average ± SD) spent by spider monkeys in different activities according to forest type (A), and season (B). Different letters indicate significant differences between forest types or seasons ($p < 0.05$).

Fig. 2 Seasonal diet composition of spider monkeys. The percentages of total feeding time (average ± SD) consuming different plant items are indicated: mature fruits (MF), immature fruits (IF), mature leaves (ML), immature leaves (IL), young branch piths (BR), flowers (FW), and other plant items (OT, decayed wood, plant secretions, moss, and epiphyte roots). Different letters above bars indicate significant differences ($p < 0.05$).

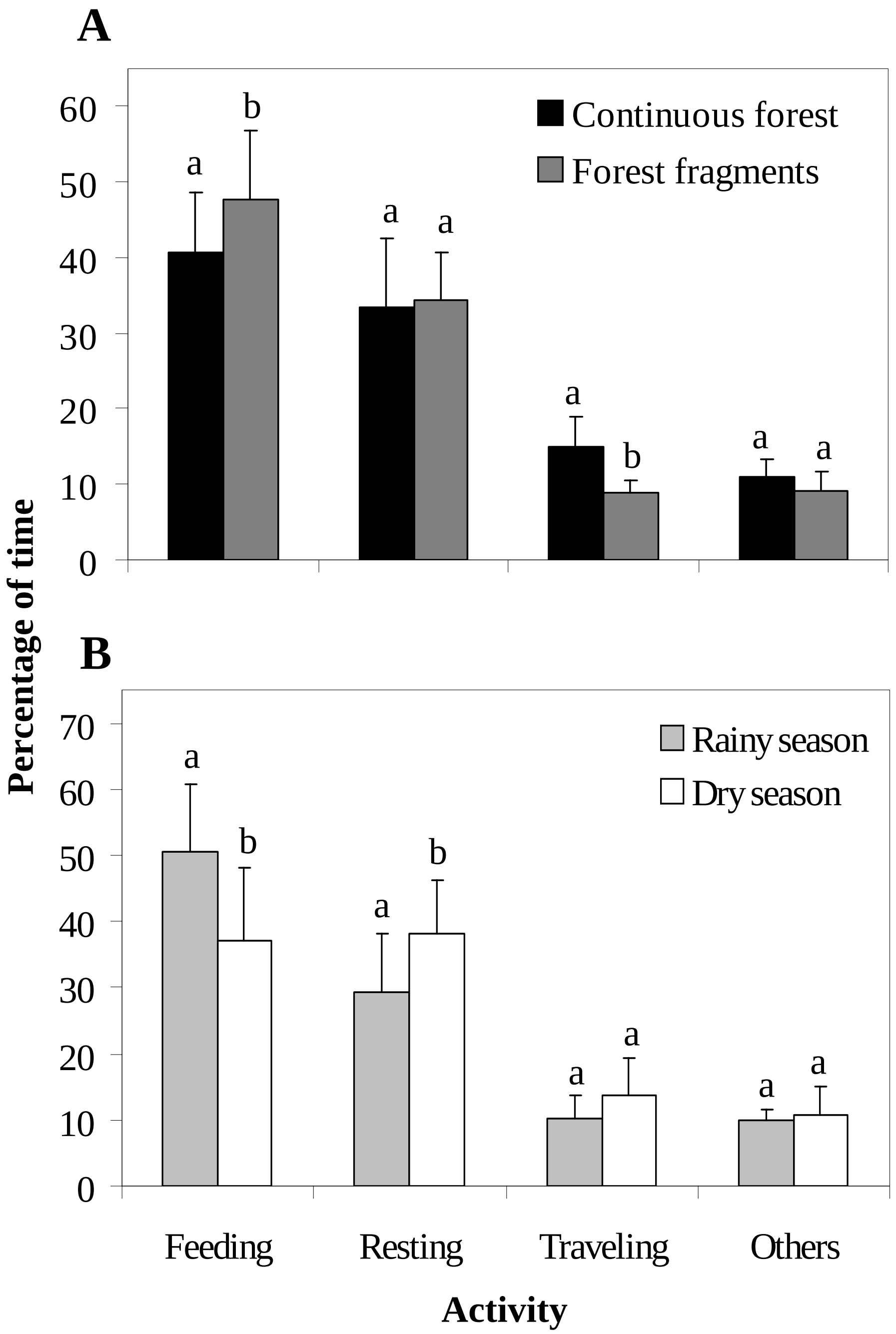
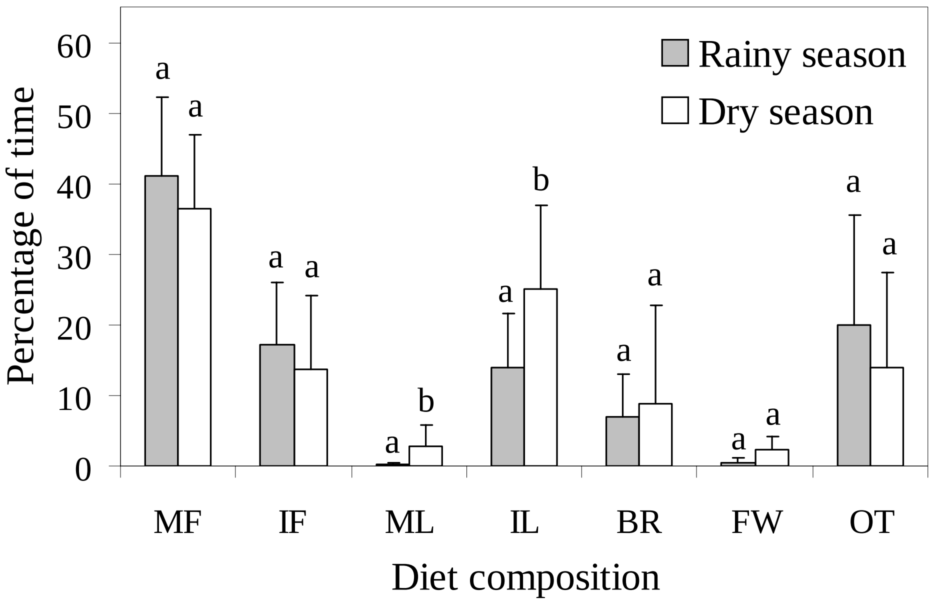

A
Continuous forest
Forest fragments
Percentage of time
0
10
20
30
40
50
60
a
b
a
a
a
b
a
a
B
Rainy season
Dry season
0
10
20
30
40
50
60
70
a
b
a
b
a
a
a
a
Feeding
Resting
Traveling
Others
Activity

Fig. 1



60
50
40
30
20
10
0
Percentage of time
Rainy season
Dry season
a
a
a
a
a
b
a
b
a
a
a
a
a
a
MF
IF
ML
IL
BR
FW
OT
Diet composition

Fig. 2

CAPÍTULO IV

Running title: Absence of spider monkeys affects seedling composition

Absence of spider monkeys in small forest fragments affects the composition of seedlings in Southern Mexico

(manuscript in preparation, Biological Conservation, IF= 3.16)

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ABSTRACT

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Seed dispersal by arboreal vertebrates is a critical process for successful recruitment of many tropical tree species and hence for the maintenance of tropical plant diversity. We evaluated the richness, diversity and abundance of seedling species in forest fragments where spider monkeys (*Ateles geoffroyi*) have disappeared in Lacandona rainforest, Mexico We identified, counted and marked seedlings in three areas of continuous forest and six fragments (three fragments with monkeys and three fragments without monkeys). We classified the seedling species into four categories according to their dispersal mode: (1) primate-dispersed species, (2) small and medium vertebrate-dispersed species, (3) wind-dispersed species, and (4) gravity-dispersed species. Abundance and diversity of primate-dispersed seedling species were higher in continuous forest and fragments with monkeys than in fragments without monkeys. In contrast, overall species richness, richness of small and medium vertebrate-dispersed species, and abundance of abiotic-dispersed species were higher in the latter habitats. Species-rank abundance curves showed that primate-dispersed species and small and medium vertebrate-dispersed species were dominant in continuous forest and fragments with monkeys, whereas in fragments without monkeys the seedling community was dominated by small and medium vertebrate-dispersed species and abiotic-dispersed species. Canonical Correspondence Analysis showed that seedling composition was best correlated (positively) with spider monkey abundance and to a lesser degree large-bodied frugivore richness, and that it was poorly correlated with adult tree community structure, canopy openness, fragment size, fragment age, and isolation level. Our results suggest that the disappearance of spider monkeys could ultimately affect tree composition, favoring small and medium seed-size vertebrate-dispersed species and abiotic-dispersed species in fragments.

Keywords: forest fragmentation, tropical rain forest, seedling recruitment, seed dispersal, spider monkey disappearance

1. Introduction

Fragmentation and other human disturbances have negative effects on the reproduction and survival of many species of plants and animals worldwide (Brook et al., 2003; Vellend et al., 2006). However, tropical forests are likely the most affected ecosystems due to their rapid continued degradation (FAO, 2007; Malhi et al., 2008). For instance, tropical rainforest clearing, fragmentation, hunting, and other disturbances have resulted in the great reduction and/or extirpation of many frugivorous vertebrates (Moran et al., 2009; Terborgh et al., 2008). This is a serious conservation problem because the lower abundance or local extinction of many frugivorous dispersers may affect the population dynamics of plant species (Stoner et al., 2007).

Since vertebrates are the main seed dispersers of 70–95 percent of woody plants in tropical forests (Fleming et al., 1987; Jordano, 2000), regeneration of these plant communities largely depends on these animals (Terborgh et al., 2008; Wright et al., 2007). However, dispersal services, and hence their effect on seedling recruitment, depends on both vertebrate and fruit species´ characteristics. There is an inverse relationship between the number of dispersers and fruit and seed size, due to the mechanical and physical constrains derived from fruit and seed handling (Donatti et al., 2007; Jordano, 1995). Thus, plant species with small fruits and seeds (e.g. *Ficus* spp. and *Miconia* spp.) can be handled and potentially swallowed and dispersed by a wide assemblage of vertebrate dispersers, but large-seeded plant species (e.g. *Spondias* spp., *Virola* spp., and *Pouteria* spp.) depend on large-bodied specialized dispersers (Donatti et al., 2007; Wright et al., 2007). In spite of the overlap in fruit species exploited by primates and other arboreal frugivores (e.g. birds, bats, kinkajou, coati-mundis) there are several examples of plants that primarily depend on primates for seed dispersal (see Nunez-Iturri & Howe 2007). Peres and Van Roosmalen (2002) propose that large-bodied Atelinae primates in the Amazon Basin are practically exclusive dispersers of large-seeded plants (> 1 cm width). Similarly, in French Guiana Julliot (1997) found that howler monkeys (*Alouatta seniculus*) are the main disperser of some large-seeded plants (e.g. *Chrysophyllum lucentifolium*, *Pouteria torta*). Large-bodied primates are a highly vulnerable group due to their dependence on well-preserved tropical forest (Mittermeier and Cheney, 1987), hunting pressures (de Thoisy et al., 2009), and drastic population declines reported in different primate species living in fragments (reviewed by Isabirye-Basuta and Lwanga, 2008).

Loss or severe population decline of key frugivores (e.g. primates and birds) can lead to a reduction in seed dispersal and seedling recruitment, particularly in the case of large-seeded plants (Melo et al., 2010; Sethi and Howe, 2009; Terborgh et al., 2008). The disappearance of primates may alter considerably plant population dynamics because it is unlikely that dispersal services provided by them can be compensated for by other frugivorous vertebrates. Nevertheless, our ability to understand this phenomenon in forest fragments is seriously limited by the fact that most primate studies have been conducted in large protected areas (e.g. Southeastern Peru: Nuñez-Iturri & Howe 2007). Furthermore, results may be confounded with changes in other ecological variables in fragments (e.g. large bodied-frugivore richness, vegetation structure, canopy openness, isolation level, and fragment size and age: Saunders et al. 1991; Laurance 2005) and therefore, not a direct result of changes in disperser abundance. For this reason, it is necessary to take into consideration these variables in order to determine the relative impact of disappearance of a specific seed disperser on seedling recruitment. .

In Mesoamerica the assessment of potential effects of local disappearance of large-bodied frugivores in forest fragments on seedling recruitment and composition remain practically unexplored (but see Melo et al. 2010, Gonzalez-Di Pierro et al. unpublished data). Based on the available evidence, we hypothesize that in forest fragments the lack of spider monkeys (*Ateles geoffroyi vellerosus*) deprive large-seeded plants of efficient dispersers and hence limit community-wide recruitment of primate-dispersed species in comparison with forests containing monkeys. To address this hypothesis we: (1) compare the abundance, dominance, richness and diversity of seedlings according to their dispersal mode in continuous forest, and in fragments with and without spider monkeys, (2) determine the relative dominance of seedling species with different dispersal modes in each habitat; and (3) determine the relative contribution of spider monkeys abundance, large-bodied frugivore richness, adult tree composition, canopy openness, and fragment size, age and isolation level to the observed patterns. Finally, we discuss the conservation implications of local disappearance of large-bodied primates on regeneration of tropical rainforest fragments and suggest directions for future research.

2. Methods

2.1. Study area

We conducted this study during a 17-mo period in 2007 (January-June, August-November) and 2008 (February-May, July-September) in the Lacandona rainforest, southern Chiapas, Mexico (16°05'58" N, 90º52'36" W). Covering parts of Mexico, Guatemala, and Belize, this region encompasses the largest portion of tropical rainforest in the Neotropics (Dirzo, 1994). The average annual temperature in the region is 23.9°C and the average annual rainfall is 2881. Greatest rainfall concentration is found in June–September (range: 423–511 mm/month), and lowest in February-April (46–60.6 mm/month) (Comisión Federal de Electricidad, Mexico, unpublished data).

The study sites were located in two adjacent areas separated by the Lacantún river: the fragmented region of Marqués de Comillas (MCR, eastern side of the river), and the undisturbed Montes Azules Biosphere Reserve (MABR, western side). In contrast to MABR, MCR was colonized and deforested in the sixties, and today, most of the original forest cover has been modified (Marquez-Rosano, 2006). Approximately 50% of the land surface of MCR is nowadays used for agricultural purposes, but small (0.5–30 ha) and large (> 1000 ha) forest fragments still remain in the area. The protected area of MABR was created in 1978 and consists of approximately 300,000 ha of undisturbed forest, and contains approximately 4314 species of vascular plants (Martínez et al., 1994).

2.2. Study sites

We carried out this study in 9 sites: 3 areas within the MABR (hereafter continuous forest, CF) separated by at least 4 km from each other, 3 forest fragments with monkeys (hereafter occupied fragments, OF), and 3 forest fragments without monkeys (hereafter unoccupied fragments, UF). In CF and OF spider monkey groups ranged from 35 to 44 individuals in size (Supplementary Table 1). All OF and UF fragments were isolated ≥ 17 years ago, and their sizes ranged from 6.4 to 1125 ha (Supplementary Table 1). Despite the large size of the latter fragment, we considered it as a fragment due to the distance from the continuous forest (1100 m), the surrounding anthropogenic matrix (cattle ranches, pastures, and human settlements), the vegetation structure, and the high perturbation level (O.M. Chaves et al., unpublished data). Contrasting to CF and OF, in UF sites howler monkeys (*Alouatta pigra*) and most large-bodied frugivores are absent (Supplementary Table 2). Furthermore, a Principal Component Analysis grouped the adult tree (> 10 cm DBH) structure of fragments without monkeys (UF) and forests with monkeys (OF and CF) in two separate groups ($KW = 5.7$, df = 2, $p < 0.05$).

2.3. Primates in the study area

Two sympatric primate species are present in the study area: the black-handed spider monkey (*Ateles geoffroyi*) and the black howler monkey (*Alouatta pigra*). The former species is distributed from the state of Veracruz, Mexico, throughout most of Central America and the Choco Region of the Pacific coast of South America to northern Ecuador. The latter species is endemic to southern Mexico, Belize, and Guatemala (Rylands et al., 2006). In Mexico there are two subspecies of spider monkeys: *A. geoffroyi vellerosus* (present in most of southern Mexico, including our study area) and *A. g. yucatanensis* (restricted to the Yucatán peninsula) (Watts & Rico-Gray 1987). In MABR the population density of *A. geoffroyi* is estimated as 2.9 ind/km^2, while that for *A. pigra* is 14.4 ind/km^2 (Estrada et al., 2004). *Alouatta pigra* is considered primarily folivorous, but may devote as much as 50% of their feeding time to consuming fruits (Pavelka and Knopff, 2004). Conversely, *A. geoffroyi* is well-recognized as a fruit specialist and ripe fruits can account for more than 70% of its feeding time (González-Zamora et al., 2009; van Roosmalen and Klein, 1988). Further details about spider monkey ecology are provided by Di Fiore & Campbell (2007).

2.4. The seedling community

Before establishing the sampling plots within each study site, we conducted systematic troop follows for 6 spider monkey groups (3 groups in CF and 3 groups in OF), as part of a larger ecological study focused on collecting foraging data. We used this information to place the seedling sampling areas along foraging route of spider monkeys at the OF and CF, whilst in UF sites these areas were selected randomly.

To evaluate seedling recruitment we implemented an experimental design similar to that in Benítez-Malvido (1998). In each CF, OF and UF site, we located three 50 x 50 m blocks separated by at least 30 m from each other. Within each block, we located three 50 m-linear transects and fifteen 1-m^2 plots, for a total of 45 1-m^2 plots in each one of the nine study sites, totaling 405 1-m^2 plots in all sites. In each 1-m^2 plot we marked (with individually numbered aluminum tags), identified and counted all woody seedlings and palms 5–100 cm tall. The only climbers considered were a few large-seeded (seeds > 1.5 cm in length) fleshy-fruited vines that were highly consumed by spider monkeys (e.g. *Abuta panamensis*, and *Paullinia costata*: González-Zamora et al., 2009). The sampling plots were surveyed every 3-mo during a 16-mo period to record new recruitments.

Seedling identification was achieved with the collaboration of an experienced local para-taxonomist. Plant nomenclature was used according to the Missouri Botanical Garden nomenclatural update database (http://mobot.org/W3T/ search/ vast.html). Individuals not identified in the field were assigned to morphospecies, and collected for later identification using the Lacandona reference collection located at the Centro de Investigaciones en Ecosistemas (UNAM, Morelia, Mexico).

2.5. Dispersal mode

Following Nuñez-Iturri and Howe (2007) we classified seedlings according to their seed dispersal mode into four categories which include abiotic and biotic vectors: (1) primate-dispersed species (PD)–fleshy fruit species with seeds 1.5–5 cm in length, which are mainly consumed by large primates such as *A. geoffroyi*; (2) small and medium vertebrate-dispersed species (SMD)–fleshy fruit species with seeds <0.1– < 1.5 cm in length, which are dispersed by bats, small mammals, and birds, among others; (3) wind-dispersed species (WD)–all species having winged seeds/fruits, and (4) gravity-dispersed species (GD)—those lacking any obvious dispersal mechanism or disperser reward. Dispersal mode of each species was assigned to one of these four categories based on fruit and seed traits (e.g. morphology, size, type of pulp/aril), complemented with recent reviews on spider monkey diet (Di Fiore et al., 2008; González-Zamora et al., 2009).

2.6. Ecological variables

In order to determine if any differences in seedling community structure among CF, OF and UF may be attributed to the presence/absence of spider monkeys, we evaluated a variety of ecological variables that have been recognized as important factors influencing seedling community structure and composition. These variables include: (1) spider monkey abundance, (2) large-bodied frugivore richness (3) vegetation structure, (4) canopy openness, (5) fragment age, (6) fragment size. Furthermore, as an indicator of isolation we measured (7) distance to the nearest fragment, and (8) distance to the continuous forest.

Further methodological details on these variables are provided in the Supporting Information.

2.7. Data analysis

For each study site we pooled data from all seedlings sampled, and then we estimated seedling species richness using four nonparametric estimators provided by EstimateS 7.5 (Colwell, 2005). After 1000 randomizations of sample order we estimated the: incidence-based coverage estimator (ICE), abundance-based coverage estimator (ACE), Chao2, and bootstrap. To test for differences in species richness and diversity among habitat types (CF, OF and UF), we standardized the number of individuals sampled to control for differences in individual density using the rarefaction approach and calculated the Shannon index (EcoSim; Gotelli and Entsminger, 2001). To test for differences in abundance, species richness, diversity and evenness among habitat types we used Kruskal-Wallis tests considering each of the three sites as replicas within each habitat. To identify which habitats were statistically different among each other we used Nemenyi post-hoc comparisons. To evaluate whether seedling composition was affected by dispersal mode, we constructed species rank-abundance curves for each study site within each habitat. We plotted the relative abundance of seedling species against the rank of the species, from the most abundant to the rarest species (Magurran, 2004). These analyses were carried out using SYSTAT software (version 11.0, SPSS Institute Inc, Chicago).

To evaluate the relationship between seedling composition of PD-species and the different ecological variables for each site, we used Canonical Correspondence Analysis (CCA) processed by the program PC-ORD 4.0 (McCune and Mefford, 1997). The CCA is a direct gradient analysis technique that relates species composition to measured environmental or ecological variables (ter Braak, 1987). The main CCA matrix consisted of seedling abundances of PD-species, whereas the secondary CCA matrix consisted of the 8 ecological variables measured in each one of the 9 study sites. Finally, a Monte Carlo permutation test was performed to assess the significance of the correlations found.

3. Results

3.1. Seedling community structure

Overall, after 16 months we registered 6879 seedlings (2087 seedlings in CF, 1472 in OF, and 3320 in UF) comprised of 90 species (and an additional 43 morphospecies), 59 genera and 37 families in the 405 1-m^2 plots. Of these species, 78.9% were trees, 15.6% were shrubs, 4.4% were vines and 1.1% were palms. When assigned to dispersal mode, 68.9% were SMD-species, 12.2% were WD-species, 11.1% were PD-species, and 7.8% were GD-species. Of the top ten seedling species in CF, four were PD-species, compared to three species in OF and one species in UF (Supplementary Table 3). The three most abundant seedling species in CF were *Ampelocera hottlei* (33%) followed by *Castilla elastica* (15%) and *Brosimum aliscastrum* (12%), in OF they were *Inga punctata* (22%), *B. alicastrum* (18%) and *C. elastica* (11%), and in UF they were *Licania hypoleuca* (21%), *B. alicastrum* (17%) and *Vochysia guatemalensis* (16%) (Supplementary Table 3). In general, sampling completeness ranged from 60 to 80% in most cases, indicating that the inventories were reasonably complete (Supplementary Table 4).

3.2. Species richness and diversity

We found that abundance of individuals of PD-species differed among habitat types (Kruskal-Wallis: $H = 9.3$, df = 2, $p = 0.04$), being higher in CF and OF than in UF ($p < 0.05$ in both cases), but it was similar between CF and OF ($p > 0.1$). Similarly, rarefied diversity of PD-species was higher in CF and OF than in UF (mean, 1.5, 1.4 and 1, respectively; Kruskal-Wallis: $H = 7.1$, df = 2, $p < 0.05$; Table 1). By contrast, overall species richness was greater in UF than in OF or CF (49, 40 and 37 species, respectively; Kruskal-Wallis: $H = 6.8$, df = 2, $p < 0.05$; Table 1). Similarly, SMD-species richness also was greater in UF than in OF or CF (31, 20 and 23 species, respectively; Kruskal-Wallis: $H = 7.6$, df = 2, $p < 0.05$; Table 1). Finally, the abundance of individuals of both WD-species and GD-species differed significantly among habitat types (Table 1), being greater in UF than in OF or CF ($p < 0.05$ in both cases) and similar between OF and CF ($p > 0.1$ in both cases). However, we did not detect other significant differences among habitat types for species richness, diversity and evenness (Table 1).

3.3. Species-rank curves

Assemblage structure differed among habitat types, depending on the seed dispersal mode (Fig. 1). In the continuous forest areas, SMD-species and PD-species were clearly dominant species (Fig. 1a). Similarly, in occupied fragments, dominancy of SMD-species and PD-species were also observed, but the number of PD-species in the top ten ranked species tended to decrease (Fig. 1b). By contrast, in unoccupied fragments the seedling community was dominated by SMD-, WD- and GD-species, and the number of PD-species in the top ten ranked species was negligible (Fig. 1c).

3.4. Seedling composition and ecological variables

According to the CCA analysis axis 1, 2 and 3 together explained 95.6% of the variance in species data (69.8%, 18.6% and 7.2%, respectively). Pearson correlations for species-environment for each axis (1.0, 0.9 and 0.9, respectively) were significant for the three canonical axes (Monte Carlo test, $p < 0.02$ in all cases). Eigenvalues were relatively high for species (> 0.3) indicating considerable species turnover along the gradients summarized in axis 1 and 2 (Fig. 2a). Axis 1 and 2 separated seedling species assemblages of forests with monkeys (CF and OF) and unoccupied fragments (Fig. 2b). Spider monkey abundance was the most important ecological variable in axis 1, followed by large-bodied frugivore richness (Table 2). Spider monkey abundance was positively correlated with large-bodied frugivore richness ($r = 0.77$), adult tree community structure ($r = 0.52$) and fragment age ($r = 0.61$). Similarly, large-bodied frugivore richness was positively related to adult tree community structure and fragment age, but negatively correlated to canopy openness and distance to nearest fragments (Table 2). Finally, adult tree community structure was negatively correlated to canopy openness and positively correlated to fragment age (Table 2).

4. Discussion

As we hypothesized, higher abundance, diversity and dominance of PD-species was found in CF and OF compared to UF. Overall species richness, SMD-species richness, and abundance and dominance of individuals of abiotic-dispersed species were higher in UF than in CF and OF, suggesting that the disappearance of spider monkeys (as well as the disappearance of other large-bodied vertebrates, Supplementary Table 2) altered the community seedling structure in these habitats.

4.1. Shifts in seedling composition in fragments without monkeys

Our findings support results of different studies in fragmented forests of the Neotropics and Paleotropics. For instance, detrimental effects on PD-species recruitment and an increase in abiotic-dispersed species recently have been reported in sites with intensive hunting pressures on large-bodied primates in southeastern Peru (Nunez-Iturri et al., 2008). In fragments with howler monkeys (*Alouatta pigra*) in Community Baboon Sanctuary, Belize (Marsh and Loiselle 2003) and in Lacandona (González-Di Pierro et al. unpublished data), howler monkey-dispersed seed species had lower abundances in fragments without howlers, which presumably reflects increased recruitment of howler fruit trees in fragments that contain howlers. In fragments of La Macarena, Colombia, the absence of *Ateles belzebuth* and *Lagothrix lagotricha* results in the low representation of seedlings and saplings of large-seeded species compared with the undisturbed continuous forest of Tinigua, Colombia, but the proportion of small and medium-seeded species was similar between continuous and fragmented forests (Stevenson and Aldana 2008). Finally, in

Yucatán Peninsula, Mexico, the absence of *A. geoffroyi* in logged sites results in a greater accumulation of *Manilkara zapota* saplings under tree canopies than in the unlogged sites (all of which present communities of spider monkeys), whilst sapling species richness is greater in the unlogged than in the logged sites (Gutiérrez-Granados and Dirzo, 2010).

Similar results have also been reported for the Paleotroics. In Kibale National Park, Uganda, Chapman and Onderdonk (1998) found that in contrast with intact forest, which presented healthy populations of large-bodied primates, twenty studied fragments had lower density and richness of seedling species, particularly for large-seeded species. In fragments of the tropical dry forest of western Madagascar, the presence of the brown lemur (*Eulemur fulvus*) results in a higher regeneration of lemur-dispersed species (seeds > 1 cm width) than in fragments without lemurs, suggesting that the regeneration of a complete set of primary forest tree species depend upon the presence of lemurs (Ganzhorn et al., 1999). Despite the methodological differences among the studies mentioned above and our study, all studies consistently demonstrate that the disappearance of large-bodied monkeys has a remarkable negative effect on the regeneration of large-seeded species.

4.2. Large-seeded species assemblage and ecological variables

We found that spider monkey abundance was the most important ecological variable explaining the large-seeded seedling assemblages in the different habitat types (r = 0.65), followed by large-bodied frugivore richness (r = 0.55), whereas none of the other ecological variables showed high correlations with seedling assemblages (Table 2). These findings reinforce our hypothesis that spider monkeys function as non-redundant specialized dispersers and hence their absence in fragments alters seedling assemblages.

Similar conclusions also have been highlighted by other studies with large-bodied primates in southeastern Peru (Nunez-Iturri et al., 2008), Colombia (Stevenson and Aldana, 2008), in our same study area (Gonzalez-Di Pierro et al., unpublished data), and in fragments with a poor large-bodied frugivore richness in Yucatan Peninsula, southern Mexico (Melo et al., 2010).

Conversely, some authors suggest that secondary seed dispersal, low post-dispersal survivorship of seeds and seedlings, and the overlap in fruit resources used by primates and non-primate dispersers, dilute the influence that any primate species can have on recruiting the next generation of adult trees (Lambert and Chapman, 2005; Lambert and Garber, 1998). Some studies on Neotropical primates have shown that an important percentage of seeds defecated by monkeys are predated or removed and relocated by the action dung beetles (e.g. *A. seniculus*, *Ateles paniscus*: Andresen, 1999) and scatter-hoarding rodents (e.g. *Ateles paniscus*: Forget and Cuiljpers, 2008). Nevertheless, in our study we assume that primary dispersal by spider monkey is highly associated with recruitment of defecated seeds due to several reasons. First, most secondary dispersal by animals results in moving seeds relatively short distances (e.g. < 1m in dung-beetles: Andresen 2002; ca. 5 m in scatterhoarding rodents: Forget & Cuijpers 2008). Second, recent studies have shown that secondary seed dispersal is not a critical process for recruitment, but rather a process that contributes to higher survival of cached seeds in comparison with uncached seeds (Forget and Cuijpers, 2008). Third, spider monkeys are capable of memorizing and following specific foraging routes over time (Valero and Byrne, 2007), directly affecting recruitment and plant structure and composition across many generations (Di Fiore and Suarez, 2007), with or without the intervention of secondary dispersers or predators. Finally, some alternate primary and secondary dispersers, other than spider monkeys, of large-seeded species in Lacandona (e.g. howler monkeys, tapirs, deer, Supplementary Table 2) are also capable of moving seeds several hundred meters. Nevertheless, it is reasonable to expect that their relative contribution to seedling recruitment is low compared to spider monkeys, because most seeds are commonly deposited in large clumps at feeding roosts, latrines and sleeping trees (e.g. howler monkeys: Howe 1989; Pouvelle et al. 2009; tapir: Fragoso 1997) and hence seeds are more vulnerable to density/distance-dependent mortality predicted by the Janzen-Connell model (Howe, 1989).

4.3. Conservation implications

Our findings highlight the importance of spider monkeys on plant population dynamics. Local extinction of this large-bodied primate in fragments, results in important structural changes in seedling assemblages, including a reduction in recruitment and diversity of PD-species and the prevalence of SMD-species and abiotic dispersed species (WD and GD-species). Our results also indicate that these changes are mainly related to abundance of spider monkeys and to a lesser degree large-bodied frugivore richness. Similar results also have been found in Lacandona for the composition of seedlings and seedbank in small fragments without howler monkeys (*Alouatta pigra*) and fragments and continuous forest with this primate (González-Di Pierro et al., unpublished data). These findings suggest that in the Lacandona region (and probably other Mesoamerican forest fragments), forest management strategies and conservation efforts should take into consideration the key role of large-bodied primates in forest regeneration and ecosystem function. Evidence suggests that relationships among angiosperms and their animal dispersers are generally best described as diffuse networks rather than close coevolutionary relationships (see Herrera

1985). Under this scenario, local extinctions of large-bodied frugivores is rarely followed by extinction of the large-seeded species they disperse (Donatti et al., 2007). Certainly ecological redundant seed dispersers (e.g. most small frugivorous birds, rodents, and opportunistic frugivoruous-carnivorous animals) may play an important role in the recruitment of small and medium-seeded species in both continuous and fragmented forests, but apparently they are unable to compensate for the specialized services provide by large-bodied frugivores (Babweteera and Brown, 2009; Cramer et al., 2007; Melo et al., 2010). However, more studies evaluating the effect of large-bodied Neotropical primates (and other similar frugivores) on regeneration in fragmented tropical forests are needed to develop a better understanding of this phenomenon.

Acknowledgments

This research was supported by grants from the Consejo Nacional de Ciencia y Tecnología, Mexico (CONACyT Grant CB2005-C01-51043 and CB2006-56799). O.M.C. obtained a scholarship from the Dirección General de Estudios de Posgrado (UNAM), as part of the Programa de Posgrado en Ciencias Biológicas, UNAM, Mexico. The Instituto para la Conservación y el Desarrollo Sostenible, Costa Rica (INCODESO) provided logistical support. This study would not have been possible without the collaboration of the local people in Loma Bonita, Chajul, Reforma Agraria and Zamora Pico de Oro ejidos. We are grateful to C. Hauglustaine, C. Balderas, S. Martínez, J. Herrera, and R. Lombera for field assistance during monkey follows and seedling samplings. M. Quesada provided useful comments and suggestions in early drafts of this paper. J. Rodriguez collaborated with the identification of seedlings. We are grateful for technical support provided by J. M. Lobato Garcia and G. Sánchez Montoya.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version, at doi:

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Table 1

Observed and rarefied species richness and diversity for the unoccupied fragments (UF), occupied fragments (OF), and continuous forest (CF) by dispersal mode. Mean and standard error are indicated. Abundance represents the total number seedling recruitment during the 16-mo study period in the 45 1-m^2 plots in each site. For comparisons, *p* is the probability for the two-tailed Kruskal-Wallis statistic. Significant differences are indicated in bold.

Seed dispersal mode[a]	Unoccupied fragments					Occupied fragments					Continuous forest					
	UF1	UF2	UF3	Average	SE	OF1	OF2	OF3	Average	SE	CF1	CF2	CF3	Average	SE	*p*
All dispersal modes																
abundance	1070	1230	1020	1107	63.5	277	724	471	490.7	129.3	445	665	977	695.7	154.1	0.061
species richness	51	47	49	49	1.2	41	37	40	39.3	1.8	39	36	37	37.3	1.2	**0.043**
species richness rarefied	36.4	24.7	25.6	28.9	3.8	42	25.8	32.3	33.4	4.7	32.0	30.8	26.7	29.8	1.6	0.5
H’	3.3	1.9	2.4	2.5	0.4	3.1	2.3	2.7	2.7	0.2	2.8	2.6	2.2	2.5	0.2	0.87
H" rarefied	3.2	1.8	2.3	2.4	0.4	3.1	2.3	2.6	2.7	0.2	2.7	2.6	2.1	2.5	0.2	0.83
evenness	0.9	0.6	0.7	0.7	0.1	0.8	0.7	0.7	0.8	0.04	0.8	0.8	0.6	0.7	0.04	0.9
PD-species																
abundance	73	30	46	49.7	12.5	63	93	74	76.7	8.8	118	123	484	241.7	121.2	**0.039**
species richness	9	4	5	6.0	1.5	8	9	6	7.7	0.9	8	8	7	7.7	0.3	0.64
species richness rarefied	6.8	3.9	5	5.23	0.85	7	6.5	5.2	6.2	0.5	6.5	6.6	4.3	5.8	0.7	0.62
H’	1.5	0.6	1.6	1.2	0.3	1.4	1.6	1.4	1.5	0.07	1.6	1.5	1.6	1.6	0.03	0.47
H" rarefied	1.1	0.9	1.1	1.0	0.01	1.4	1.5	1.3	1.4	0.06	1.5	1.4	1.5	1.5	0.03	**0.046**
evenness	0.7	0.4	0.7	0.6	0.1	0.7	0.8	0.8	0.8	0.03	0.8	0.7	1.0	0.9	0.1	0.44
SMD-species																

abundance	569	201	759	509.67	163.79	105	393	248	248.67	83.14	211	180	374	255.00	60.17	0.43
species richness	31	32	30	31.0	0.6	19	18	24	20.3	1.9	24	19	25	22.7	2.6	**0.048**
species richness rarefied	15.4	25.4	14.9	18.6	3.4	18.3	11.2	18.6	16.03	2.42	18.9	14.1	16.6	16.5	1.39	0.96
H’	2.2	2.8	1.9	2.3	0.3	2.4	1.6	2.1	2.0	0.2	2.1	1.6	2.1	1.9	0.2	0.56
H" rarefied	2	2.7	1.8	2.2	0.3	2.4	1.5	2	2.0	0.3	2.0	1.5	2	1.8	0.2	0.86
evenness	0.7	0.8	0.7	0.7	0.05	0.8	0.6	0.7	0.7	0.06	0.7	0.6	0.7	0.6	0.04	0.57
WD-species																
abundance	108	98	298	168.0	65.1	1	12	11	8.0	3.5	16	12	12	13.3	1.3	**0.035**
species richness	2	3	5	3.3	0.9	1	5	4	3.3	1.2	2	4	2	2.7	0.7	0.8
species richness rarefied	1.9	1.2	1.2	1.4	0.2	–	4.7	3.9	4.3	0.3	2	3.9	2	2.6	0.6	0.3
H’	0.7	0.1	0.1	0.3	0.2	–	1.3	1.3	1.3	0.01	0.7	1.3	0.4	0.8	0.3	0.57
H" rarefied	0.6	0.08	0.06	0.2	0.2	–	1.3	1.2	1.3	0.02	0.7	1.3	0.4	0.8	0.2	0.41
evenness	0.9	0.4	0.3	0.6	0.2	–	0.8	0.9	0.9	0.03	0.9	0.9	0.6	0.8	0.10	0.3
GD-species																
abundance	58	491	90	213	139.3	10	18	9	12.3	4.0	20	31	10	20.3	6.1	**0.044**
species richness	5	4	6	5	0.6	5	3	3	3.7	0.7	2	4	4	3.3	0.7	0.22
species richness rarefied	2.9	1.2	1.9	2	0.5	3.9	2.3	2.9	3.0	0.5	1.3	2.2	3.4	2.3	0.6	0.31
H’	1.2	0.1	0.6	0.7	0.3	1.5	0.9	0.4	0.9	0.3	0.2	0.7	1.3	0.7	0.3	0.67
H" rarefied	1.0	0.08	0.4	0.50	0.3	1.3	0.7	0.4	0.8	0.2	0.1	0.5	1.1	0.6	0.3	0.67
evenness	0.9	0.4	0.7	0.7	0.1	0.9	0.8	0.4	0.7	0.2	0.5	0.7	0.9	0.7	0.1	0.99

Table 2

CCA intra-set and inter-set correlations for the first and second ordination axes for seedlings of PD-species and weighted correlation matrix for ecological variables. Correlations with absolute values > 0.5 are enhanced in bold. Abbreviations: SA, spider monkey abundance; LF, large-bodied frugivore richness; AT, adult tree community structure; CO: canopy openness; DC, distance to continuous forest; FA, fragment age; FS, fragment size; DF, distance to nearest fragment.

	Intra-set correlations		Inter-set correlations		Ecological variables							
Ecological variable	Axis 1	Axis 2	Axis 1	Axis 2	SA	LF	AT	CO	DC	FA	FS	DF
SA	**0.65**	0.25	**0.65**	0.25	—	**0.77**	**0.52**	-0.41	-0.32	**0.61**	0.33	-0.32
LF	**0.55**	-0.02	**0.55**	-0.02		—	**0.56**	**-0.64**	-0.42	**0.80**	0.19	**-0.61**
AT	-0.41	0.21	-0.41	0.21			—	-0.50	-0.28	0.49	0.11	-0.18
CO	0.40	0.27	0.40	0.27				—	**0.67**	**-0.79**	0.04	**0.66**
DC	0.35	-0.23	0.35	-0.23					—	**-0.75**	0.40	**0.62**
FA	-0.27	-0.04	-0.27	-0.04						—	0.03	**-0.83**
FS	-0.26	-0.27	-0.26	-0.27							—	-0.27
DF	0.06	0.11	0.06	0.11								—

Figure legends

Figure 1.

Species/ rank abundance plots for the top 25 seedling species according to seed dispersal mode in each area of continuous forest (a), occupied (b), and unoccupied (c) fragments. Species rank is ordered from the most to the least abundant species.

Figure 2.

Canonical correspondence analyses ordination of (a) seedling species assemblages and (b) study sites. Species: Ah, *Ampelocera hottlei*; Dg, *Dialium guianense*; Gg, *Guarea glabra*; Ip, *Inga pavoniana*; Pc, *Pouteria campechiana*; Pl, *Posoqueria latifolia*; Sm, *Spondias mombin*; and Sr, *S. radlkoferi*.

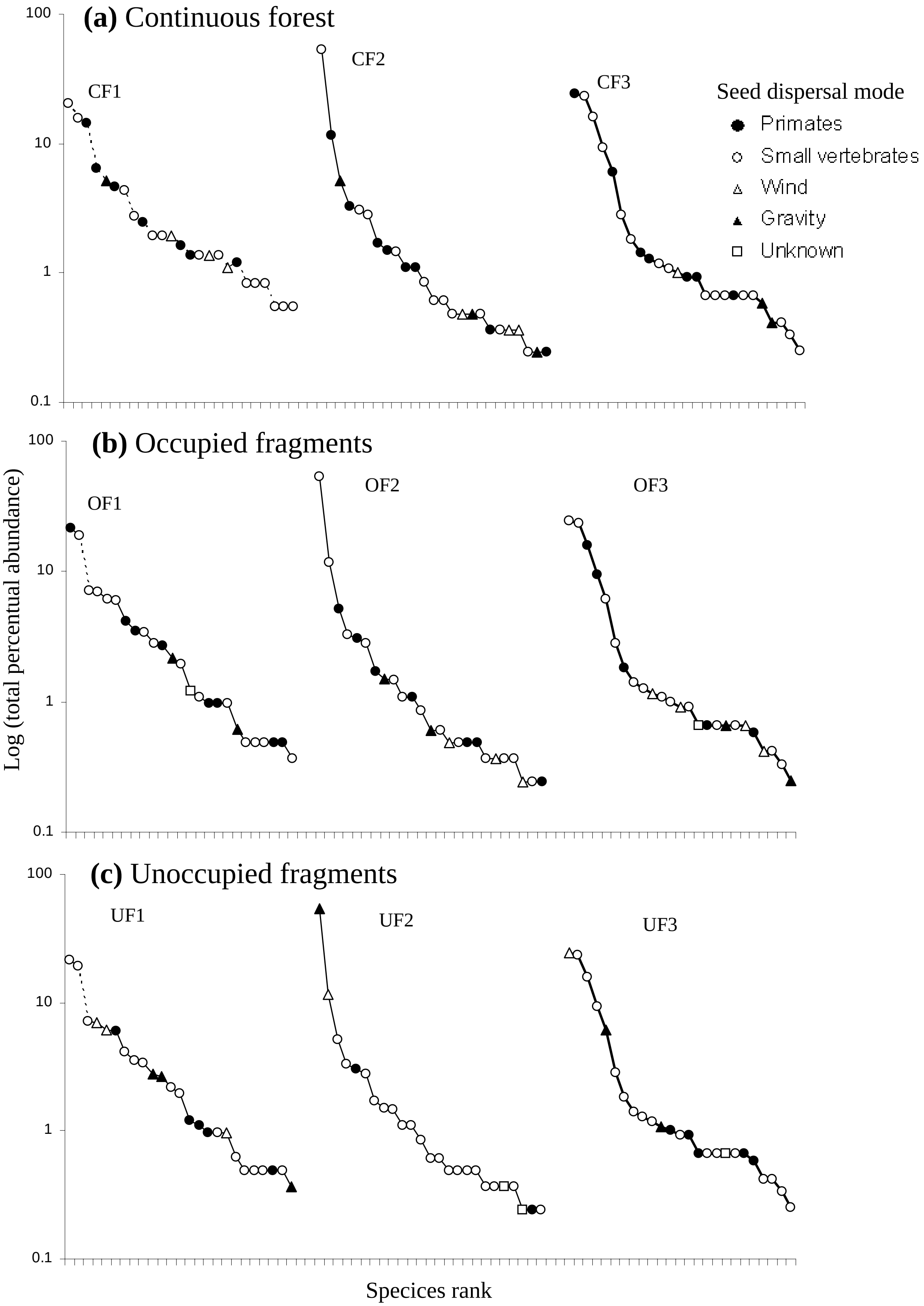
(a) Continuous forest
CF1
CF2
CF3
(b) Occupied fragments
OF1
OF2
OF3
(c) Unoccupied fragments
UF1
UF2
UF3
Seed dispersal mode
● Primates
○ Small vertebrates
△ Wind
▲ Gravity
□ Unknown
100
10
1
0.1
Log (total percentual abundance)
Species rank

Figure 1.

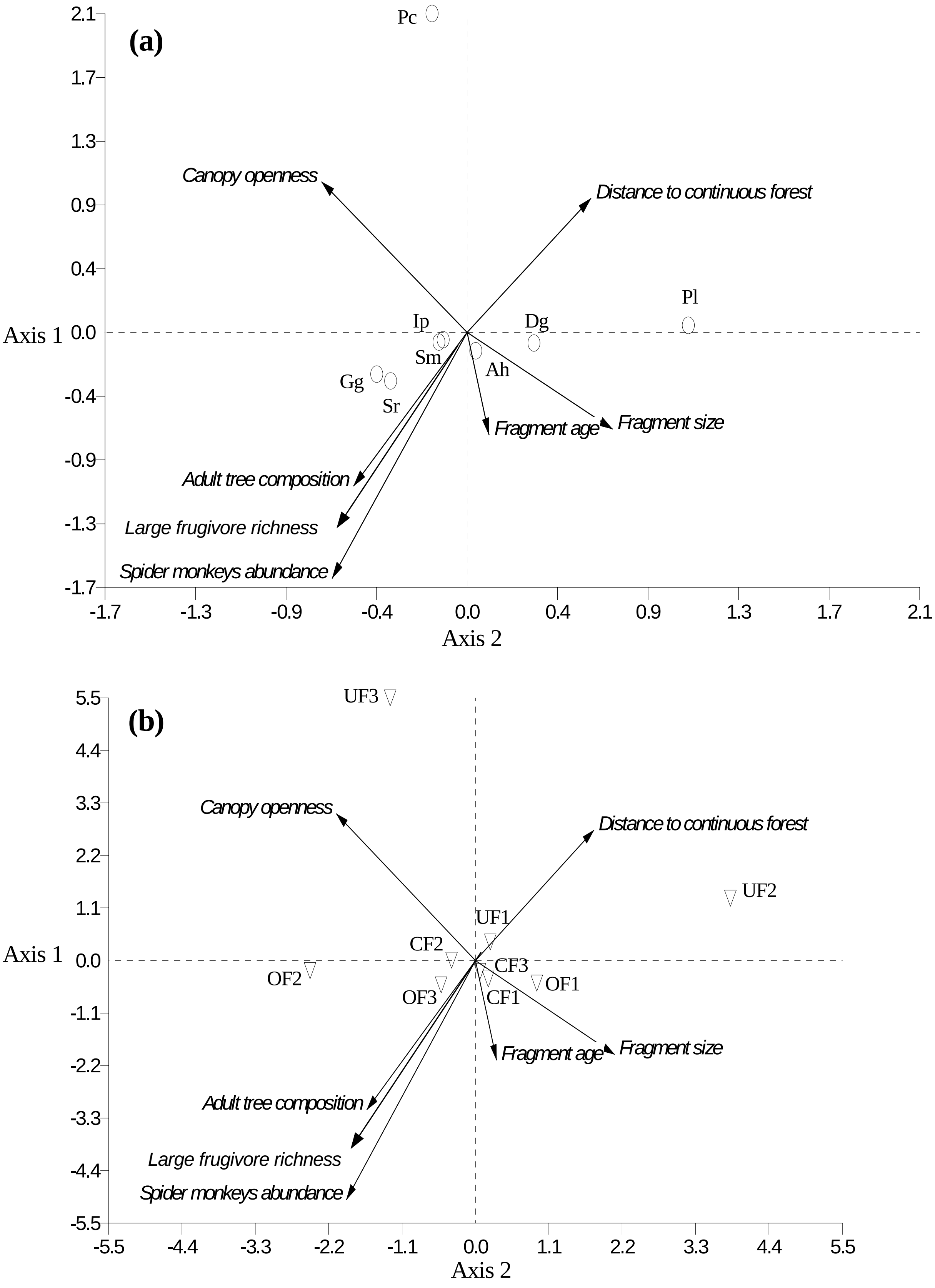
(a)
Pc
Pl
Dg
Ip
Sm
Ah
Gg
Sr
Canopy openness
Distance to continuous forest
Fragment age
Fragment size
Adult tree composition
Large frugivore richness
Spider monkeys abundance
Axis 1
Axis 2
2.1
1.7
1.3
0.9
0.4
0.0
-0.4
-0.9
-1.3
-1.7
-1.7
-1.3
-0.9
-0.4
0.0
0.4
0.9
1.3
1.7
2.1
(b)
UF3
UF2
UF1
CF2
CF3
CF1
OF1
OF2
OF3
Canopy openness
Distance to continuous forest
Fragment age
Fragment size
Adult tree composition
Large frugivore richness
Spider monkeys abundance
Axis 1
Axis 2
5.5
4.4
3.3
2.2
1.1
0.0
-1.1
-2.2
-3.3
-4.4
-5.5
-5.5
-4.4
-3.3
-2.2
-1.1
0.0
1.1
2.2
3.3
4.4
5.5

Figure 2.

Methodological Details on Ecological Variables

Abundance of spider monkeys in each CF and OF was estimated by visual counts during the preliminary follows complemented with our data from a15-mo period of systematic spider monkey follows (see Chaves et al., 2010). Richness of large-bodied frugivores was focused on: (1) terrestrial mammals weighing >1.5 kg and (2) large-bodied birds common in Lacandona (e.g., toucans, guans, and trogons). For the first group we estimated richness by two methods: direct observation along trails and water holes during day and night and looking for and identifying tracks and signs (Reid, 1997), whilst richness of birds was determined via direct observations using high resolution binoculars (Swarovski SLC 10 x 42). These samplings were carried out weekly during a 10-mo period (March-July 2007 and June-October 2008). Furthermore, we complemented our censuses by conducting interviews with local people working in tourism and/or those who regularly hunted in the region.

To determine the vegetation structure in each CF, OF and UF sites we fixed ten 50 × 2 m linear transects randomly (Gentry, 1982), for a total of 90 transects. We recorded all trees and shrubs with diameter at breast height (DBH) ≥10 cm. With this information, we conducted a Principal Component Analysis (PCA) for PD-species and used component scores of the most important axes as ecological variables in subsequent analysis. We quantified the percentage of canopy openness with a spherical concave densiometer (Model C, Forest Densiometers, Oklahoma). We carried out brief interviews with land-owners to determine fragment age. Finally, to determine fragment size, distance to the nearest fragment/continuous forest we used recent LANDSAT satellite images (Instituto Nacional de Estadística y Geografía, México, http://mapserver.inegi.org.mx/rni/index.cfm?s=geo&c=1311) of the study area complemented with direct field-measures using a GPS (Garmin 76 CSX).

Supplementary Table 1. Description of study sites in Lacandona, Chiapas, Mexico.

Sites	Size (ha)	Location	Distance to nearest fragment(m)	Distance to continuous forest (m)	Years since fragmentation	Spider monkey abundance	Years since disappearance of monkeys
Continuous Forest	331,000	Montes Azules Biosphere Reserve					
CF1	–	16°06'58.2"N, 90°56'18.4"W	–	–	–	40	–
CF2	–	16°09'32.0"N, 90°54'06.6"W	–	–	–	36	–
CF3	–	16°09'40.0"N, 90°54'04.5"W	–	–	–	44	–
Occupied fragments		Marqués de Comillas region					
OF1	14.4	Zamora Pico de Oro ejido (16°19'52.0"N, 90°51'06.1"W)	450	200	29	35	–
OF2	31	Zamora Pico de Oro ejido (16°19'24.5"N, 90°50'43.7"W)	150	1200	24	39	–
OF3	1125	Reforma Agraria ejido (16°15'12.2"N, 90°49'59.5"W)	100	1100	26	41	–
Unoccupied fragments		Marqués de Comillas region					
UF1	6.4	Chajul ejido (16°06'39.5"N, 90°56'04.6"W)	200	150	19	0	15

Supplementary Table 2. Large-bodied frugivore composition of continuous and fragmented forests.

Animal taxon	Common name	Continuous forest			Occupied fragments			Unoccupied fragments		
		CF1	CF2	CF3	OF1	OF2	OF3	UF1	UF2	UF3
Mammalia										
Rodentia										
Agoutidae										
Agouti paca	Paca		+	+						
Primates										
Atelinidae										
Alouatta pigra	Black howler monkey	+	+	+	+	+	+			
Ateles geoffroyi vellerosus	Black-handled spider monkey	+	+	+	+	+	+			
Artiodactyla										
Tayassuidae										
Dicotyles pecari	White-lipped peccary	+	+	+						
Tayassu tajacu	Collared peccary	+	+	+						+
Cervidae										
Manzama americana	Red brocket	+	+	+						
Odocoileus virginianus	White-tailed deer	+	+	+	+	+	+			+
Perissodactyla										
Tapiridae										
Tapirus bairdii	Baird’s tapir	+	+	+		+	+			
Carnivora										
Procyonidae										
Potos flavus	Kinkajou		+	+		+				+
Aves										

Cracidae										
Crax rubra	Great curassow	+	+	+	+		+			
Ortalis vetula	Plain chachalaca	+	+	+		+	+	+	+	+
Penelope purpurascens	Crested guan	+	+	+		+	+			+
Ramphastidae										
Pteroglossus torquatus	Collared aracari		+	+		+	+			
Ramphastos sulfuratus	Keel-billed tucan	+	+	+	+	+	+	+		+
Trogonidae										
Trogon elegans	Elegant trogon	+	+	+	+	+	+	+		+
Trogon massena	Slaty-tailed trogon	+	+	+		+	+	+	+	+
Total number of species		13	16	16	6	11	11	4	2	8

Presence is indicated with plus (+) signs.

Supplementary Table 3. Top ten seedling species found in continuous forest and fragments in Lacandona.

Habitat type	Seedling species	Family	Growth form	Dispersal Mode[a]	%Total seedling abundance
Continuous forest	*Ampelocera hottlei*	Ulmaceae	Tree	PD	32.8
	Castilla elastica	Moraceae	Tree	SMD	15.1
	Brosimum alicastrum	Moraceae	Tree	SMD	12.3
	Virola guatemalensis	Myristicaceae	Tree	SMD	6.7
	Guarea glabra	Meliaceae	Tree	SMD	5.6
	Acacia usumacintensis	Fabaceae	Tree	GD	3.0
	Dialium guianense	Fabaceae	Tree	PD	2.3
	Celtis iguanaea	Vitaceae	Vine	SMD	2.2
	Abuta panamensis	Menispermaceae	Vine	PD	1.8
	Inga pavoniana	Fabaceae	Tree	PD	1.4
Occupied fragments	*Inga punctata*	Fabaceae	Tree	SMD	22.1
	Brosimum alicastrum	Moraceae	Tree	SMD	17.7
	Castilla elastica	Moraceae	Tree	SMD	11.1
	Guarea glabra	Meliaceae	Tree	SMD	10.4

	Dialium guianense	Fabaceae	Tree	PD	6.3
	Brosimum lactescens	Moraceae	Tree	SMD	3.4
	Nectandra reticulata	Lauraceae	Tree	SMD	2.4
	Paullinia costata	Sapindaceae	Vine	SMD	2.2
	Spondias radlkoferi	Anacardiaceae	Tree	PD	1.9
	Posoqueria latifolia	Rubiaceae	Tree	PD	1.8
Unoccupied fragments	*Licania hypoleuca*	Chrysobalanaceae	Tree	GD	20.8
	Brosimum alicastrum	Moraceae	Tree	SMD	17.1
	Vochysia guatemalensis	Vochisiaceae	Tree	WD	16.2
	Brosimum lactescens	Moraceae	Tree	SMD	12.6
	Xylopia frutescens	Annonaceae	Shrub	SMD	4.6
	Inga vera	Fabaceae	Tree	SMD	3.7
	Ampelocera hottlei	Ulmaceae	Tree	PD	2.1
	Hirtella americana	Chrysobalanaceae	Tree	SMD	1.9
	Pseudolmedia oxyphyllaria	Moraceae	Tree	SMD	1.9
	Vatairea lundellii	Ulmaceae	Tree	WD	1.8

[a] *Dispersal mode: PD, primate-dispersed; SMD, small and medium vertebrates-dipserded; GD, gravity-dispersed; WD, wind-dispersed.*

Supplementary Table 4. Observed and expected species richness in seedling communities in continuous and fragmented forests in Lacandona, Chiapas, Mexico.

Seed dispersal mode by Habitat type[a]	Number of observed species	ACE[b]	ICE[c]	Chao 2	Bootstrap	Completeness[d]
All dispersal modes						
UF1	51	77	71	84	86	71-86
UF2	47	78	76	87	86	76-87
UF3	49	66	60	49	86	49-86
OF1	42	69	72	79	84	69-84
OF2	36	74	60	74	85	60-85
OF3	40	80	73	78	86	73-86
CF1	37	81	75	71	87	71-87
CF2	35	91	84	93	89	84-93
CF3	45	72	70	67	86	67-86
Primate Dispersed Species						
UF1	9	94	95	100	92	92-100
UF2	4	84	84	100	87	84-100
UF3	5	100	100	100	100	100
OF1	8	100	100	100	93	93-100
OF2	9	92	85	97	90	85-97
OF3	6	90	90	100	92	90-100
CF1	8	95	96	100	95	95-100
CF2	8	100	100	100	98	98-100
CF3	7	100	100	100	100	100
Small and Medium Vertebrate Dispersed Species						
UF1	31	79	73	89	86	73-89
UF2	32	84	84	93	88	84-93
UF3	30	75	69	89	87	69-89
OF1	19	80	86	93	88	80-93
OF2	17	76	62	77	85	62-85

OF3	26	70	65	66	85	66-85
CF1	25	75	65	70	84	65-84
CF2	17	79	78	92	87	78-92
CF3	27	68	62	55	85	55-85
Wind Dispersed Species						
UF1	2	100	100	100	100	100
UF2	3	75	76	76	81	75-81
UF3	5	45	46	46	77	45-77
OF1	1	—	—	—	—	—
OF2	5	51	41	48	78	41-78
OF3	4	100	100	100	94	94-100
CF1	2	100	100	100	100	100
CF2	4	100	87	100	87	87-100
CF3	2	100	100	100	95	95-100
Gravity Dispersed Species						
UF1	5	85	59	84	87	59-87
UF2	4	80	55	80	85	55-85
UF3	6	50	36	50	81	36-81
OF1	5	77	78	100	85	77-100
OF2	3	85	86	100	88	85-100
OF3	3	100	97	100	100	97-100
CF1	2	100	65	100	85	65-100
CF2	4	85	85	100	87	85-100
CF3	4	90	89	100	89	89-100

[a] *Abbreviations: UF, unoccupied fragments; OF, occupied fragments; CF, continuous forest areas of the MABR (for further details see methods).*

[b] *Abundance-based coverage nonparametric richness estimator.*

[c] *Incidence-based coverage nonparametric richness estimator.*

[d] *Percentage of expected richness covered by sampling effort (range).*

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DISCUSIÓN GENERAL

Influencia de la disponibilidad de alimento en la dieta

Diferentes estudios en primates tropicales han demostrado que su dieta es más diversa en fragmentos de bosque que en bosque continuo (e.g., *Alouatta pigra*: Rivera & Calmé 2006, *A. palliata*: Cristóbal-Azkarate & Arroyo-Rodríguez 2007), lo cual se ha relacionado con una menor disponibilidad de alimento en fragmentos (Arroyo-Rodríguez & Mandujano 2006, Dunn *et al*. 2009). Por ejemplo, en África, Asia y América se ha reportado que en fragmentos y/o periodos de escasez de frutos, los primates se alimentan de partes vegetales alternativas (e.g., frutos inmaduros, hojas, corteza: Chapman 1987, Fairgrieve & Muhumuza 2003, Cristóbal-Azkarate & Arroyo-Rodríguez 2007) y de formas de crecimiento no arbóreas (e.g., trepadoras, hierbas, palmas: Onderdonk & Chapman 2000, Silver & Marsh 2003). De forma similar, los resultados de esta tesis sugieren que debido a la reducción de alimento en fragmentos (e.g., menor densidad de árboles grandes de las principales especies en la dieta), el mono araña se ve forzado a realizar importantes ajustes en su dieta. Así, en fragmentos los monos araña: (1) consumieron módulos de una mayor cantidad de especies de plantas; (2) incrementaron el consumo de hojas; y (3) incrementaron el consumo de formas de hemiepífitas y palmas. En general, la evidencia disponible indica que cuando los primates frugívoros se ven forzados a reducir el consumo de frutos e incrementar el consumo de otros módulos vegetales de menor contenido energético (como ocurrió en este estudio), tienden a diversificar su dieta. Este comportamiento les permite diluir el posible efecto que pueden tener los metabolitos secundarios en la salud (Freeland & Janzen 1974, Glander 1982) y a la vez incrementa la probabilidad de que los animales puedan satisfacer sus necesidades nutricionales, ya que ningún módulo vegetal en particular contiene todos los nutrientes que requiere un primate (Lambert 2007). Esto es especialmente cierto en sitios con una baja disponibilidad de alimentos con alto contenido energético (e.g., frutos), como es el caso de los fragmentos boscosos de la Selva Lacandona.

El mayor consumo de material foliar en fragmentos podría afectar negativamente tanto la salud del mono araña como la dinámica de la comunidad de plantas. Por ejemplo, los monos araña podrían estar limitados en cuanto a la cantidad de material foliar que pueden consumir debido a que su sistema digestivo está especializado para una dieta compuesta principalmente de frutos maduros (Milton 1981, 1993, Lambert 1998). Como consecuencia de una dieta más folívora, en algunas especies de atelinidos se ha reportado una reducción abrupta del peso corporal (e.g., *Alouatta palliata*: Glander 2006; *Ateles chamek*: Karesh *et al.* 1998), lo cual a largo plazo puede afectar la fertilidad y sobrevivencia de los animales. Además, en estos mismos grupos de monos, nuestros datos sugieren que la eficiencia de *A. geoffroyi* como dispersor de semillas podría ser menor en fragmentos que en bosque continuo ya que en fragmentos se reduce tanto el porcentaje de excretas con semillas como el porcentaje de semillas ingeridas (ver capítulo II).

Pese a la diversidad de la dieta en cuanto a especies de plantas y formas de vida (ver Anexo), en ambos hábitats el mono concentró su tiempo de alimentación (≥ 80% del tiempo total de alimentación) en un grupo relativamente pequeño de especies (*Ficus* spp., *Spondias* spp., *Brosimum* spp., *Dialium guianense,* y *Licania platypus*), las cuales también han sido reportadas como 'top' especies en la dieta de *A. geoffroyi* a lo largo de Mesoamérica (González-Zamora *et al.* 2009). Este comportamiento puede estar relacionado con una mayor abundancia de especies, el gran tamaño de los árboles y la consecuente mayor producción de alimento. Además, en el caso particular de *Ficus* spp., los ciclos fenológicos asincrónicos de estas especies (Ibarra-Manríquez & Oyama 1992), permiten que el mono araña consuma sus síconos a lo largo de todo el año (Weghorst 2007, Felton *et al*. 2008). Por tanto, la abundancia de estas especies debe considerarse un factor fundamental a la hora de evaluar la calidad del hábitat para los monos araña ya que puede influir directamente en su dinámica poblacional y sobrevivencia a largo plazo.

Eficiencia en la dispersión de semillas

Como se predijo, los monos araña fueron dispersores eficientes en términos cuantitativos y cualitativos tanto en bosque continuo como en fragmentos, lo cual es consistente con otros estudios en monos araña que han demostrado que éstos son eficientes en términos de la diversidad de frutos en la dieta, la manipulación de las semillas, la riqueza de semillas defecadas y el patrón de defecación (e.g., *Ateles* spp.: Russo *et al*. 2005, *A. belzebuth*: Link & Di Fiore 2006, Dew 2008). No obstante, los servicios de dispersión brindados por el mono araña en Lacandona probablemente sean más importantes para especies con semilla grande (>1 cm de diámetro) como *Ampelocera hottlei* (Ulmaceae), *Spondias* spp. (Anacardiaceae) y *Attalea butyracea* (Arecaceae) debido a que existe una relación inversa entre el tamaño de la semilla y el número potencial de dispersores (Jordano 1995).

Las relaciones entre las angiospermas y sus dispersores generalmente son descritas como un tipo de coevolución "difusa" y no como una coevolución estrecha entre pares (Herrera 1985, Ericksson 2008), lo cual implica que la desaparición de cualquiera de los interactuantes muy rara vez conduciría a la desaparición del otro. Pese a esta realidad, los servicios de los dispersores legítimos (como es el caso del mono araña) indudablemente pueden favorecer el flujo génico y el reclutamiento de las especies de frutos más importantes en sus dietas (Stevenson & Aldana 2008, Gutiérrez-Granados & Dirzo 2010).

Los resultados también sugieren que la eficiencia del mono araña como dispersor podría ser menor en fragmentos debido a que en comparación con el bosque continuo: 1) se redujo la proporción de semillas tragadas y se incrementó la proporción de semillas escupidas bajo el árbol parental, y 2) se redujo considerablemente el porcentaje de excretas que contenían semillas, lo cual es reflejo de la mayor folivoría de los monos araña en los fragmentos. Este resultado puede tener importantes implicaciones ecológicas, ya que la regeneración de la comunidad de plantas podría ser más lenta (particularmente en el caso de especies con semilla grande) en los fragmentos en comparación con el bosque continuo, tal y como se ha encontrado en estudios recientes con monos araña y otras especies emparentadas (e.g., *Ateles belzebuth* y *Lagothrix lagotricha*: Stevenson & Aldana 2008, *A. geoffroyi*).

Influencia de la disponibilidad de recursos sobre los patrones de actividad

Los resultados también indicaron que como probable respuesta a la menor disponibilidad de recursos alimenticios para los monos en fragmentos y durante la estación seca (ver capítulo III de esta tesis), éstos fueron capaces de realizar importantes ajustes en el tiempo dedicado a actividades vitales como la alimentación, la locomoción y el descanso. Los datos sugieren que para compensar la menor disponibilidad y calidad de alimento en fragmentos, los monos dedicaron más tiempo a la alimentación, lo cual también ha sido reportado en diferentes poblaciones de *A. geoffroyi* en fragmentos de Punta Laguna, México (Ramos-Fernández & Ayala-Orozco 2003). Debido a que el sistema digestivo de los monos araña está diseñado para una dieta basada en módulos vegetales con un bajo contenido de fibra (Milton 1981, Lambert 1998), cuando aumenta el consumo de hojas (como ocurrió en Lacandona, ver capítulo I), los monos deben invertir más tiempo en alimentación para poder obtener suficiente cantidad de energía y nutrientes. Resultados similares también se han reportado para babuinos (Iwamoto & Dunbar 1983) y gorilas de montaña (Watts 1988). Sin embargo, en contraste con lo esperado, el tiempo dedicado a la alimentación fue mayor en la época lluviosa y no en la seca. Este resultado podría explicarse por el hecho de que durante la estación lluviosa la disponibilidad de frutos es mayor y el mono araña tiende a alimentarse más durante este periodo con el fin de ingerir energía y almacenarla en forma de grasa que utilizará para sobrevivir durante los periodos de escasez (Felton *et al*. 2009). Adicionalmente, estudios recientes sugieren que el incremento en la temperatura durante la estación seca, obliga a muchas especies de primates (incluyendo a los monos araña) a reducir el tiempo dedicado a actividades como la alimentación para minimizar los costos energéticos relacionados con la termoregulación (Campos & Fedigan 2009, Dunbar *et al.* 2009, Korstjens *et al.* 2010).

Como resultado de la escasez de frutos, el mayor consumo de hojas y un menor tiempo de alimentación durante la estación seca en Lacandona, los monos se vieron obligados a descansar más tiempo, lo cual puede representar una estrategia no solamente para minimizar los costos del sobrecalentamiento como ya se mencionó, sino también porque el descanso es una demanda fisiológica de una dieta más folívora (Milton 1981, Korstjens *et al.* 2010). En general, en la mayoría de primates el tiempo de descanso es una función directa de la estacionalidad, la temperatura promedio, y el porcentaje de hojas en la dieta (Korstjens *et al.* 2010). Además, el hecho de que el tiempo dedicado al descaso fuera similar en bosque continuo y en fragmentos, sugiere que esta actividad está más afectada por los cambios en temperatura (como sugieren Korstjens *et al.* 2010) y/o disponibilidad de alimento entre estaciones que por cambios en la disponibilidad de alimento entre estos dos hábitats. Sin embargo, debido a que no existen datos climatológicos para todos los sitios de estudio, no es posible confirmar esta hipótesis.

De acuerdo con la teoría de forrajeo óptimo, el tiempo que invierten los animales en sus movimientos de forrajeo es una función de la cantidad y la calidad de parches de alimentación disponibles en su hábitat (MacArthur & Pianka 1966). Por tanto en aquellos animales que se alimentan de recursos con un alto grado de agregación espacial y temporal (e.g., frutos maduros: Zimmerman *et al.*2007), es de esperarse que el tiempo invertido en desplazamiento entre parches de alimentación esté directamente relacionado con la disponibilidad de los mismos (Charnov & Orians 1973). Esta hipótesis puede ser particularmente cierta en el caso de *Ateles* spp., ya que estos primates prefieren alimentarse en parches de alimentación (i.e., conglomerados de plantas que producen frutos importantes en la dieta de los monos araña) de frutos carnosos que están muy espaciados entre sí, lo cual los obliga a moverse constantemente de un lugar a otro (Chapman & Chapman 2000). Los datos de la tesis apoyan esta idea ya que en bosque continuo los monos araña invirtieron más tiempo en locomoción que en fragmentos, probablemente porque estos primeros hábitats presentaron una mayor disponibilidad de recursos alimenticios importantes para los monos araña (ver capítulo I de esta tesis).

No obstante, en contraste con la predicción, durante la estación seca los monos tendieron a invertir más tiempo moviéndose, lo cual también se ha reportado en primates de Madagascar (*Eulemur* spp.: Overdorff 1993) e Indonesia (*Tarsius spectrum*: Gursky 2000). Esto sugiere que para compensar la menor disponibilidad y el mayor espaciamiento de los parches de frutos durante la estación seca (Zimmerman *et al.* 2007), los monos requieren invertir más tiempo moviéndose para incrementar la probabilidad de encontrar suficiente alimento para satisfacer sus necesidades nutricionales. Pese a que los resultados muestran que el mono araña tiene la capacidad de realizar ajustes conductuales en respuesta a la limitación de recursos en fragmentos y durante la estación seca, no se sabe si esta flexibilidad es suficiente como para garantizar la sobrevivencia de los monos a largo plazo.

Reducción en la abundancia de especies de semilla grande en fragmentos sin monos

Finalmente, los resultados indicaron que la ausencia de primates alteró la composición de plántulas, reduciendo la abundancia y riqueza de especies de semilla grande y favoreciendo tanto la riqueza de especies dispersadas por vertebrados pequeños como la abundancia de especies dispersadas por medios abióticos (ver capítulo IV, Anexo). Estos resultados concuerdan con lo que se ha encontrado en sitios sometidos a una alta presión de cacería de primates grandes en el sureste de Perú (Nuñez-Iturri & Howe 2007, Nuñez-Iturri *et al*. 2008). Estos estudios demuestran que la reducción de las poblaciones de primates ha tenido afectos negativos sobre el reclutamiento de especies de semilla grande y ha favorecido el reclutamiento de especies dispersadas por medios abióticos. Resultados similares también se han encontrado en poblaciones de primates en fragmentos de la Selva Lacandona (González-Di Pierro *et al*. datos no publicados), en Uganda (Chapman & Onderdonk 1998), en Madagascar (Ganzhorn *et al.* 1999), en Belize (Marsh & Loiselle 2003), y en Colombia (Stevenson & Aldana 2008). Por ejemplo, en este último país la desaparición de *Ateles belzebuth* y *Lagothrix lagotricha* en fragmentos de La Macarena se ha traducido en una baja representación de especies de semilla grande en comparación con el bosque continuo de Tinigua, el cual presenta poblaciones protegidas de ambas especies de primates (Stevenson & Aldana 2008). De igual forma, en sitios sometidos a tala selectiva, en la Península de Yucatán, México, la desaparición de *A. geoffroyi* propició un incremento en la densidad y la dominancia de plántulas de *Manilkara zapota* (una especie con semilla >1.5 cm de largo) bajo los parentales y una reducción de la diversidad de plántulas de sotobosque en comparación con los sitios no talados que contenían monos araña (Gutiérrez-Granados & Dirzo 2010). A pesar de las diferencias metodológicas entre todos estos estudios y el mío, todos consistentemente muestran que la desaparición de los primates frugívoros tiene profundas repercusiones sobre la composición de la comunidad de plántulas, limitando el reclutamiento de las especies que producen frutos carnosos con semillas grandes (las cuales son principalmente dispersadas por este tipo de primates).

Además, como se menciona en el capítulo IV de esta tesis, de ocho diferentes variables ecológicas analizadas, la abundancia de monos araña junto con la riqueza de animales frugívoros grandes son las que están más correlacionadas con la composición de plántulas en cada tipo de bosque. Resultados similares también han sido observados recientemente para diferentes primates en Sudamérica (*Ateles belzebuth*: Stevenson & Aldana 2008) y en la Selva Lacandona (*Alouatta pigra*: Gonzalez-Di Pierro *et al., datos no publicados*).

Todo lo anterior sugiere que las estrategias de manejo y los esfuerzos de conservación del bosque en la Selva Lacandona (y probablemente en otras regiones de Mesoamérica) deben tomar en consideración el papel clave que juegan los monos araña como dispersores no redundantes de especies con semilla grande. Debido a que los datos de esta tesis sugieren que la eficiencia del mono araña como dispersor podría ser menor en fragmentos (ver capítulo II), es importante que las futuras estrategias de conservación consideren el establecimiento de corredores biológicos que conecten los fragmentos más pequeños con los fragmentos grandes y/o bosques continuos. Esto contribuiría tanto a una dispersión más eficiente de las semillas (especialmente de las semillas más grandes), como a mejorar el estado de salud de las poblaciones de monos presentes en los diferentes fragmentos. Es de esperarse que al conectar los fragmentos más pequeños en los cuales habitan los monos con los fragmentos grandes, también aumentará la disponibilidad de recursos para los monos (e.g., frutos, dormideros, acceso a parejas), lo cual podría minimizar la aparición de los problemas de salud relacionados con el estrés (e.g., pérdida de peso, baja fertilidad, mayor vulnerabilidad al parasitismo) que se presenta en los monos araña que habitan en fragmentos (Rangel-Negrín *et al.* 2009).

CONCLUSIONES GENERALES

1) En comparación con el bosque continuo, los fragmentos presentaron una menor disponibilidad de recursos alimenticios para *A. geofroyi*, lo cual se tradujo en cambios considerables en su dieta, en su papel como dispersores de semillas, y en el tiempo que invierten en alimentación, locomoción y descanso en ambos tipos de hábitat.

2) En Lacandona, *Ficus* spp., *Spondias* spp., *Brosimum* spp., *Dialium guianense*, y *Licania platypus* representan las especies más importantes en la dieta del mono araña en bosque continuo y en fragmentos. Por tanto, la densidad de árboles grandes de estas especies se podría usar como un importante indicador de calidad de hábitat para el mono en fragmentos. Así, el tamaño de las poblaciones de monos que un determinado fragmento boscoso puede tolerar podría estar en función no sólo del tamaño del fragmento, sino de la densidad de árboles adultos de estas especies, tal y como se ha encontrado para los monos aulladores en Los Tuxtlas (Arroyo-Rodríguez & Mandujano 2006) y en la Lacandona (González-Di Pierro *et al.* datos no publicados). Esto se debe tener en consideración a la hora de realizar cualquier programa de conservación y/o reintroducción de esta especie.

3) Debido a la menor disponibilidad de recursos alimenticios para los monos araña en los fragmentos en comparación con el bosque continuo, éstos se ven forzados a realizar cambios conductuales que le permiten tolerar el estrés alimenticio. Entre estos cambios destacaron el incremento en el consumo de hojas y formas de vida no arbóreas (e.g., hemiepífitas y palmas), el incremento del tiempo total de alimentación, y la reducción del tiempo invertido en actividades energéticamente costosas (e.g., locomoción). De igual

forma, el estrés alimenticio durante la estación seca se tradujo en un mayor tiempo de descanso en comparación con la estación seca. Probablemente estos cambios conductuales representan una estrategia adaptativa para lidiar con una dieta de menor calidad (i.e., con mayor contenido de fibra) y minimizar los costos energéticos relacionados con la locomoción y la termoregulación tal y como sugieren los modelos socio-ecológicos de primates (e.g., Korstjens *et al.* 2006, 2010, Dunbar 2009). Sin embargo, son indispensables más estudios en fragmentos y bosques continuos para determinar si la plasticidad conductual del mono araña (en la dieta y en los patrones de actividad) es suficiente como para garantizar su sobrevivencia a largo plazo, particularmente en los fragmentos de bosque más pequeños.

4) Debido a que la eficiencia del mono araña como dispersor tiende a ser menor en fragmentos como resultado de cambios en la manipulación de las semillas y a un menor porcentaje de excretas con semillas, es necesario que los esfuerzos de conservación en Lacandona se enfoquen en incrementar la conectividad entre fragmentos, especialmente entre los fragmentos pequeños y los fragmentos más grandes. Esto se traducirá en una mayor disponibilidad de recursos alimenticios (particularmente frutos) para los monos araña y por tanto, es razonable esperar que aumente su eficiencia como dispersores. A largo plazo, y bajo el supuesto de que las alteraciones antropogénicas sean mínimas, la dispersión de semillas por los monos podría contribuir considerablemente a la regeneración de la selva.

5) La desaparición de los monos araña puede tener profundas repercusiones en la composición de la comunidad plántulas y por ende en la futura comunidad de árboles.

Como se ha reportado en otros trabajos similares (ver discusión), la desaparición de los primates tropicales propicia una reducción en el reclutamiento de especies de semilla grande (e.g., *Spondias* spp., *Ampelocera hottlei* y *Virola* spp.) y un incremento del reclutamiento de especies dispersadas por vertebrados pequeños y por medios abióticos.

6) Todo lo anterior sugiere que las estrategias de manejo y los esfuerzos de conservación en la Selva Lacandona deben tomar en consideración el papel clave que juegan los monos araña como dispersores eficientes de muchas especies de árboles con semilla grande y su capacidad relativa para realizar ajustes conductuales que le permitan lidiar con el aumento de la deforestación, la pérdida de hábitat y el calentamiento global. En este sentido, la pérdida de hábitat quizás sea la mayor amenaza para las poblaciones silvestres de *A. geoffroyi* (Ramos-Fernández & Wallace 2008). No obstante, los modelos socio-ecológicos (e.g., Korstjens *et al.* 2006) también indican que incrementos relativamente pequeños en la temperatura ambiental (e.g., 2-5 °C) podrían comprometer seriamente la sobrevivencia de los monos araña e incluso propiciar su extinción. Esto difícilmente conduciría a la desaparición de sus especies de frutos preferidos (incluso en el caso de las plantas que tienen semillas grandes como *Spondias* spp. y *Attalea butyracea*.) debido a que la relación entre dispersores y plantas es generalmente una coevolución “difusa” (Herrera 1985). No obstante, los resultados del capítulo IV sugieren que en ausencia de los monos la composición y estructura de las comunidades de árboles de la Selva Lacandona podrían cambiar considerablemente a largo plazo, dando origen a bosques dominados por especies dispersadas por medios abióticos y/o vertebrados pequeños.

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Anexo

Listados de las especies de plantas en la dieta del mono araña y de las especies de plántulas encontradas en los diferentes hábitats estudiados en la Selva Lacandona

Cuadro 1. Lista de 152 especies de plantas consumidas por las comunidades de monos araña estudiadas en bosque continuo y en fragmentos de la Selva Lacandona, Chiapas. **1**= frutos maduros, **2**= frutos inmaduros, **3**= hojas maduras, **4**= hojas nuevas, **5**= flores, **6**= madera podrida, **7**= ramas, **8**= zarcillos, **9**= secreciones vegetales, **10**= estípula terminal, **11**= raíces, **12**= semillas, **% TTA**= porcentaje del tiempo total de alimentación (*n* = 205 h en bosque continuo y *n* = 243 h en fragmentos, ver más detalles en capítulo I).

Especie/Morfoespecie	**Familia**	**Forma de vida**	**Parte consumida**	**% TTA**	
				Bosque	Fragmentos
Licania platypus	Chrysobalanaceae	Árbol	1,4,6,7	31.2	4.9
Spondias radlkoferi	Anacardiaceae	Árbol	1,2,7	22.5	10.7
Spondias mombin	Anacardiaceae	Árbol	1,2,5	6.2	1.9
Ficus tecolutensis	Moraceae	Hemiepífita	1	4.6	12.2
Brosimum alicastrum	Moraceae	Árbol	1,2,4	4.4	9.7
Dialium guianense	Fabaceae	Árbol	1,2,4	3.8	18.3
Ampelocera hottlei	Ulmaceae	Árbol	1	3.6	0
Ficus obtusifolia	Moraceae	Hemiepífita	1,2	2.5	0.8
Strychnos tabascana	Loganiaceae	Bejuco	1,7	1.86	0.54
Ficus sp1	Moraceae	Hemiepífita	1,2	1.6	8.2
Celtis iguanaea	Ulmaceae	Bejuco	1	1.6	0.5
Calatola laevigata	Icacinaceae	Árbol	1	1.5	2.2
Philodendron scandens	Araceae	Hemiepífita	4	1.25	0.64
Guarea glabra	Meliaceae	Árbol	1,2,7	1.1	1.31
Swietenia humilis	Meliaceae	Árbol	7	0.8	0
Ficus sp2	Moraceae	Hemiepífita	1	0.8	2.2
Mortoniodendron guatemalense	Malvaceae	Árbol	1	0.68	0
Paullinia clavigera	Sapindaceae	Bejuco	4	0.71	0.023
Attalea butyracea	Arecaceae	Palma	1	0.63	0.22
Cecropia obtusifolia	Cecropiaceae	Árbol	1,4,10	0.53	0.14
Cissus verticillata	Vitaceae	Bejuco	1	0.45	0.041
Brosimum lactescens	Moraceae	Árbol	1	0.41	0.25
Abuta panamensis	Menispermaceae	Árbol	1,2	0.38	0.05
Pseudolmedia oxyphyllaria	Moraceae	Árbol	1	0.3	0.02

Cuadro 1. *Continuación.*

Especie/Morfoespecie	**Familia**	**Forma de vida**	**Parte consumida**	**% TTA**	
				Bosque	Fragmentos
Bejuco Msp8 (periquillo)	Sapindaceae	Bejuco	1,2	0.3	0.03
Syngonium chiapense	Araceae	Epífita	1	0.26	0.24
Alchornea latifolia	Euphorbiaceae	Árbol	1,2	0.26	0
Cecropia peltata	Cecropiaceae	Árbol	1,4	0.25	0.11
Manilkara sapota	Sapotaceae	Árbol	1,2	0.25	0.01
*Machaerium*sp.	Fabaceae	Bejuco	4	0.23	0.11
Monstera acuminata	Araceae	Epífita	4	0.22	0.25
Ceiba pentandra	Bombacaceae	Árbol	4,5	0.21	0.24
Monstera sp1	Bromeliaceae	Epífita	4	0.21	0.23
Nectandra ambingea	Lauraceae	Árbol	1,2	0.2	0.45
Ocotea dendrodaphne	Lauraceae	Árbol	1,2	0.2	1.1
Virola guatemalensis	Myristicaceae	Árbol	1	0.2	0.08
Pouteria campechiana	Sapotacea	Árbol	1,2,7	0.2	0.016
Ocotea sp.	Lauraceae	Árbol	1,5	0.19	0
Guarea grandifolia	Meliaceae	Árbol	1,2,7	0.18	0.45
Guarea sp.	Meliaceae	Árbol	1,2	0.14	0.17
Trophis racemosa	Moraceae	Árbol	1	0.14	0.45
Passiflora ambigua	Pasifloraceae	Bejuco	1	0.14	0
Philodendron radiatum	Araceae	Hemiepífita	4	0.13	0.32
Philodendron sp1	Araceae	Hemiepífita	4	0.13	0.23
Cojoba arborea	Fabaceae	Árbol	1,4	0.13	0.51
Inga pavoniana	Fabaceae	Árbol	1,2	0.13	0.15
Paragonia pyramidata	Bignoniaceae	Bejuco	3,4	0.12	0.005
Combretum fructicosum	Combretacea	Bejuco	5	0.11	0.33
Orquidea Msp1	Orchidaceae	Epífita	11	0.11	0.008
Hirtela sp.	Chrysobalanaceae	Árbol	1	0.1	0.007
Cupania dentata	Meliaceae	Arbusto	7	0.09	0
Castilla elastica	Moraceae	Árbol	1,7	0.09	0.14
Talauma mexicana	Magnoliaceae	Árbol	1	0.08	0
Brosimum costaricanum	Moraceae	Árbol	1,4,7	0.08	0
Bejuco Msp4	Bignoniaceae	Bejuco	3,4	0.08	0
Combretum laxum Jacq.	Combretacea	Bejuco	5	0.07	0.39
Inga vera	Fabaceae	Árbol	1	0.07	0.02
Bravaisia integerrima	Acanthaceae	Árbol	3	0.06	0.85
Dioscorea mexicana	Dioscoreaceae	Bejuco	8	0.06	0

Cuadro 1. *Continuación.*

Especie/Morfoespecie	**Familia**	**Forma de vida**	**Parte consumida**	**% TTA**	
				Bosque	Fragmentos
Trichilia sp.	Meliaceae	Árbol	1	0.06	0
Árbol Msp3	—	Árbol	4	0.06	0
Zanthoxylum kellermanii	Rutaceae	Árbol	4	0.05	0.72
Árbol Msp2	—	Árbol	4	0.05	0.31
Orquidea Msp4	Orchidaceae	Epífita	11	0.05	0
Thevetia ahouai	Apocinaceae	Arbusto	1	0.04	0.005
Protium copal	Burseraceae	Árbol	1,2	0.04	0
Inga punctata	Fabaceae	Árbol	1,2	0.04	1.08
Pterocarpus sp.	Fabaceae	Árbol	4	0.04	0
Brosimum sp.	Moraceae	Árbol	4	0.04	0.01
Bejuco Msp7	—	Bejuco	4,7	0.04	0
Hirtella americana	Chrysobalanaceae	Árbol	1,7	0.03	0
Acacia sp1	Fabaceae	Árbol	1,2	0.03	0.23
Ficus popenoei	Moraceae	Hemiepífita	1	0.03	0.2
Posoqueria latifolia	Rubiaceae	Árbol	1,7	0.03	0.08
Ramdia sp.	Rubiaceae	Arbusto	1	0.03	0.034
Astronium graveolens	Anacardiaceae	Árbol	4	0.02	0
Cymbopetalum mayanum	Anonaceae	Árbol	1	0.02	0.01
Mostera sp2	Bromeliaceae	Epífita	4	0.02	0.015
Tetracera sp.	Dilleniaceae	Bejuco	1	0.02	0
Albizia leucocalyx	Fabaceae	Árbol	4	0.02	0.06
Inga sp1	Fabaceae	Árbol	1,2	0.02	0.034
Acacia cornigera	Fabaceae	Arbusto	1	0.02	0.015
Lonchocarpus sp1	Fabaceae	Bejuco	4,7	0.02	0.011
Lonchocarpus sp2	Fabaceae	Bejuco	4	0.02	0
Calophyllum brasiliense	Guttiferaceae	Árbol	1,2	0.02	0
Licaria capitata	Lauraceae	Árbol	1	0.02	0
Luehea semanni	Malvaceae	Árbol	7	0.02	0.51
Quararibea funebris	Malvaceae	Árbol	1,2	0.02	0
Psidium sp.	Myrtaceae	Árbol	1,2	0.02	0
Passiflora sp.	Pasifloraceae	Bejuco	8	0.02	0.01
Bejuco Msp5	—	Bejuco	4	0.02	0
Bejuco Msp9	Fabaceae	Bejuco	4	0.02	0
Iresine sp.	Amaranthaceae	Bejuco	1	0.01	0
Stemmadenia donnel-smithii	Apocinaceae	Árbol	2	0.01	0

Cuadro 1. *Continuación.*

Especie/Morfoespecie	**Familia**	**Forma de vida**	**Parte consumida**	**% TTA**	
				Bosque	Fragmentos
Monstera sp.	Araceae	Epífita	4	0.01	0
Philodendron tripartitum	Araceae	Hemiepífita	4	0.01	0
Syngonium podophyllum	Araceae	Epífita	1,4	0.01	0
Capparis quiriguensis	Caparidaceae	Árbol	1,2	0.01	0.1
Schizolobium parahybum	Fabaceae	Árbol	2,5	0.01	0.71
Souroubea guianensis	Marcgraviaceae	Bejuco	1	0.01	0.1
Parathesis sp	Myrsinaceae	Arbusto	2	0.01	0
Epidendrum sp.	Orchidaceae	Epífita	11	0.01	0
Passiflora cookii	Pasifloraceae	Bejuco	1	0.01	0
Peperomia sp.	Piperaceae	Epífita	4	0.01	0
Paullinia fibrigera	Sapindaceae	Bejuco	4	0.01	0.03
Orquidea Msp5	Orchidaceae	Epífita	4	0.01	0
Bejuco Msp2	Bignoniaceae	Bejuco	4	0.01	0
Anthurium sp.	Araceae	Epífita	1	0.004	0
Nectandra reticulata	Lauraceae	Árbol	1,7	0.003	0.18
Reinhardtia gracilis	Arecaceae	Palma	1,2	0.001	0
Epiphyllum phyllanthus	Cactaceae	Epífita	1	0.001	0
Clusia sp.	Clusiacae	Árbol	4	0.001	0
Hibiscus sp.	Malvaceae	Árbol	5	0.001	0
Dendropanax arboreum	Araliaceae	Árbol	1,2	0	0.022
Bactris mexicana	Arecaceae	Palma	1	0	0.16
Bactris baduca	Arecaceae	Palma	1	0	0.15
Sabal mexicana	Arecaceae	Palma	1,9	0	2.2
Pithecoctenium crucigerum	Bignoniaceae	Árbol	5	0	0.016
Bromelia sp.	Bromeliaceae	Epífita	4	0	0.001
Tetracera volubilis	Dilleniaceae	Bejuco	1	0	0.1
Inga sp2	Fabaceae	Árbol	1	0	0.031
Acacia farnesiana	Fabaceae	Árbol	1,2	0	0.17
Acacia sp2	Fabaceae	Arbusto	1,2	0	0.28
Mucuna pruriens	Fabaceae	Bejuco	2	0	0.038
Semialarium sp.	Hippocrateaceae	Bejuco	12	0	0.19
Ochroma pyramidale	Malvaceae	Árbol	1	0	0.009
Pachira aquatica	Malvaceae	Árbol	5	0	0.013
Theobroma cacao	Malvaceae	Árbol	1,2	0	0.35
Mouriri mirtilloides	Melastomataceae	Arbusto	1,7	0	0.038

Cuadro 1. *Continuación.*

Especie/Morfoespecie	**Familia**	**Forma de vida**	**Parte consumida**	**% TTA**	
				Bosque	Fragmentos
Coussapoa oligocephala	Moraceae	Árbol	4	0	0.34
Maclura tinctoria	Moraceae	Árbol	1,2	0	1.66
Poulsenia armata	Moraceae	Árbol	1	0	1.61
Ficus insipida	Moraceae	Hemiepífita	1,6	0	3.2
Ficus yoponensis	Moraceae	Hemiepífita	4	0	0.31
Ficus sp3	Moraceae	Hemiepífita	1,6	0	0.1
Ficus sp4	Moraceae	Hemiepífita	1	0	1.4
Ficus sp5	Moraceae	Hemiepífita	1	0	0.03
Blepharidium mexicanum	Rubiaceae	Árbol	7	0	0.18
Faramea occidentalis	Rubiaceae	Arbusto	1	0	0.08
Psychotria papantlensis	Rubiaceae	Arbusto	1,7	0	0.043
Zanthoxylum procerum	Rutaceae	Árbol	4	0	0.03
Paullinia costata	Sapindaceae	Bejuco	1,2	0	0.001
Serjania goniocarpa	Sapindaceae	Bejuco	4	0	0.027
Serjania mexicana	Sapindaceae	Bejuco	4	0	0.01
Árbol Msp1 (c.f. de *Ocotea)*	Lauraceae	Árbol	5	0	0.01
Árbol Msp4	Anonaceae	Árbol	1	0	0.041
Árbol Msp5	Myrtaceae	Árbol	4	0	0.2
Árbol Msp 6 (Palo blanco)	—	Árbol	3	0	0.39
Orquidea Msp2	Orchidaceae	Epífita	11	0	0.034
Bejuco Msp1 (c.f. de *Bahuinia*)	Fabaceae	Bejuco	4	0	0.18
Bejuco Msp3	Bignoniaceae	Bejuco	4	0	0.13
Bejuco Msp6	—	Bejuco	7	0	0.03

Cuadro 2. Lista de 88 especies de plántulas encontradas en bosque continuo (BC), fragmentos ocupados por monos (FO), y fragmentos desocupados (FD). Para cada especie se indica el porcentaje de abundancia relativa en cada uno de los tres hábitats.

Especie/Morfoespecie	**Familia**	**Forma de crecimiento**	**Dispersor**	**% de abundancia**		
				BC	FO	FD
*Abuta panamensis (*Standl.) Krukoff & Barneby	Menispermaceae	Bejuco	primates	1.8	0.87	0.29
Acacia cornigera (L.)Willd.	Fabaceae	Arbusto	otros vertebrados	0.13	0.58	0
Acacia sp1	Fabaceae	Arbusto	otros vertebrados	0.22	0.87	0
Acacia sp2	Fabaceae	Arbusto	otros vertebrados	0.15	0	0
Acacia sp3	Fabaceae	Arbusto	otros vertebrados	0	0.27	0
Acacia usumacintensis Lundell	Fabaceae	Árbol	otros vertebrados	2.97	0.97	0.81
Albizia leucocalyx Standley	Fabaceae	Árbol	gravedad	0.26	1.26	0.11
Ampelocera hottlei (Standl.) Standl.	Ulmaceae	Árbol	primates	32.8	0.87	2.1
Andira inermis(W. Wright) DC.	Fabaceae	Árbol	otros vertebrados	0	0	0.1
Astronium graveolens Jacq.	Anacardiaceae	Árbol	viento	0	0.29	0.07
Bravaisia integerrima Standl.	Acanthaceae	Árbol	otros vertebrados	0.12	0.19	0
Brosimum alicastrum Sw.	Moraceae	Árbol	otros vertebrados	12.28	17.67	17.06
Brosimum costaricanum Liebm.	Moraceae	Árbol	otros vertebrados	0.12	0.25	0
Brosimum lactescens (S. Moore) C.C. Berg	Moraceae	Árbol	otros vertebrados	0.42	3.39	1.81
Bursera simaruba (L.) Sarg.	Burseraceae	Árbol	otros vertebrados	0	0	0.58

Cuadro 2. *Continuación.*

Especie/Morfoespecie	Familia	FC	Dispersor	% de abundancia		
				BC	FO	FN
Calatola laevigata Standley	Icacinaceae	Árbol	otros vertebrados	0.19	0.19	0.47
Calatola sp.	Icacinaceae	Árbol	otros vertebrados	0.01	0	0
Calophyllum brasiliense Cambess.	Guttiferaceae	Árbol	otros vertebrados	0	0	0.38
Calophyllum sp.	Guttiferaceae	Árbol	otros vertebrados	0	0	0.14
Casearia sp,	Flacourtiaceae	Arbusto	otros vertebrados	0	0	0.11
Castilla elastica Sessé	Moraceae	Árbol	otros vertebrados	15.13	11.07	1.19
Cecropia obtusifolia Bertol.	Cecropiaceae	Árbol	otros vertebrados	0	0	0.1
Ceiba pentandra (L.) Gaertn.	Bombacaceae	Árbol	viento	0.17	0.01	0
Celtis iguanaea (Jacq.) Sarg.	Vitaceae	Bejuco	otros vertebrados	2.19	0.29	0.25
Cojoba arborea (L.)Britton & Rose	Fabaceae	Árbol	otros vertebrados	0.29	1.07	0
Cordia alliodora(Ruiz. & Pav.) Oken	Boraginaceae	Árbol	viento	0	0.29	0.57
Cordia sp.	Boraginaceae	Árbol	viento	0	0.19	0.34
Croton schiedeanus Schlecht.	Euphorbiaceae	Árbol	otros vertebrados	0	0.49	1.29
Croton sp.	Euphorbiaceae	Árbol	otros vertebrados	0	0.58	0.15
Cupania dentata	Sapindaceae	Arbusto	otros vertebrados	0.13	0.11	0.57
Cupania sp1	Sapindaceae	Arbusto	otros vertebrados	0	0.11	0.23

Cuadro 2. *Continuación.*

Especie/Morfoespecie	Familia	FC	Dispersor	% de abundancia		
				BC	FO	FN
Cupania sp2	Sapindaceae	Arbusto	otros vertebrados	0	0	0.09
Paullinia costata	Sapindaceae	Bejuco	otros vertebrados	0.42	2.24	0.15
Cymbopetalum mayanum Lundell	Annonaceae	Árbol	otros vertebrados	0.46	0.79	0.19
Cymbopetalum sp.	Annonaceae	Árbol	otros vertebrados	0	0	0.18
Dendropanax arboreum Decne. & Planch.	Araliaceae	Árbol	otros vertebrados	0	0	0.08
Dialium guianense (Aubl.)Sandwith	Fabaceae	Árbol	primates	2.26	6.31	0.75
Eugenia sp1	Myrtaceae	Árbol	otros vertebrados	0	0.97	0.15
Eugenia sp2	Myrtaceae	Árbol	otros vertebrados	0	0.19	0.18
Garcinia intermedia (Pittier) Hammel	Clusiaceae	Árbol	otros vertebrados	0.46	0.68	0
Guarea glabra Vahl	Meliaceae	Árbol	primates	5.62	10.39	0.15
Guarea grandifolia DC.	Meliaceae	Árbol	primates	0.09	0.19	0
Guarea sp.	Meliaceae	Árbol	otros vertebrados	0	0.04	0
Hirtella americana L.	Chrysobalanaceae	Árbol	otros vertebrados	0.39	0	1.92
Hirtella sp.	Chrysobalanaceae	Árbol	otros vertebrados	0.23	0	0.36
Hirtella tiandra Swartz	Chrysobalanaceae	Árbol	otros vertebrados	0.11	0	0
Inga pavoniana G. Don	Fabaceae	Árbol	primates	1.42	0.39	0.37

Cuadro 2. *Continuación.*

Especie/Morfoespecie	**Familia**	**FC**	**Dispersor**	**% de abundancia**		
				BC	FO	FN
Inga punctata Willd.	Fabaceae	Árbol	otros vertebrados	1.19	22.14	1.67
Inga sp1	Fabaceae	Árbol	otros vertebrados	0.19	0.19	0
Inga sp2	Fabaceae	Árbol	otros vertebrados	0.11	0	0
Inga sp3	Fabaceae	Árbol	otros vertebrados	0.21	0	0.07
Inga vera Willd.	Fabaceae	Árbol	otros vertebrados	0.63	0	3.67
*Licania hypoleuca*Benth.	Chrysobalanaceae	Árbol	gravedad	0	0.39	20.79
Licania platypus (Hemsl.) Fritsch	Chrysobalanaceae	Árbol	gravedad	0.23	0.11	0
Lonchocarpus guatemalensis Benth.	Fabaceae	Árbol	viento	0	0	0.29
Lonchocarpus sp.	Fabaceae	Árbol	viento	0	0	0.13
Maclura tinctoria (L.) D. Don ex Steud.	Moraceae	Árbol	otros vertebrados	0.12	0.29	0
Miconia sp1	Melastomataceae	Árbol	otros vertebrados	0	0	0.42
Miconia sp2	Melastomataceae	Árbol	otros vertebrados	0	0	0.17
Mouriri myrtilloides (Swartz)	Melastomataceae	Árbol	otros vertebrados	0.22	0.17	0.41
Nectandra ambingea	Lauraceae	Árbol	otros vertebrados	1.42	2.43	1.38
Nectandra reticulata (Ruiz & Pavón) Mez	Lauraceae	Árbol	otros vertebrados	0.9	0.33	0
Ouratea lucens	Ochnaceae	Arbusto	otros vertebrados	0.19	0	1.21

Cuadro 2. *Continuación.*

Especie/Morfoespecie	Familia	FC	Dispersor	% de abundancia		
				BC	FO	FN
Platymiscium yucatanum Standley	Fabaceae	Árbol	viento	0	0.79	0.14
Porouma bicolor	Cecropiaceae	Árbol	otros vertebrados	0	0	1.52
Posoqueria latifolia(Rudge) Roem. & Schult.	Rubiaceae	Árbol	primates	0.93	1.85	0.39
Pouteria campechiana (Kunth) Baehni	Sapotaceae	Árbol	primates	1.36	0.38	1.52
Protium copal (Schltdl. & Cham.) Engl.	Burseraceae	Árbol	otros vertebrados	0.47	0.38	0
Pseudolmedia oxyphyllaria J. D. Smith	Moraceae	Árbol	otros vertebrados	0.31	0	1.85
Pterocarpus sp	Fabaceae	Árbol	viento	0.19	0.38	0.47
Quararibea funebris (Llave) Vischer	Bombacaceae	Árbol	otros vertebrados	0.81	0.29	0
Quararibea guatemalteca (J.D. Smith) Standley & Steyerm	Bombacaceae	Árbol	otros vertebrados	0.32	0	0
Roupala montana Aubl.	Proteaceae	Arbusto	otros vertebrados	0	0	0.97
Sabal mexicana Mart.	Arecaceae	Palma	otros vertebrados	0	0.01	0
Spondias mombin L.	Anacardiaceae	Árbol	primates	0	0.61	0.21
Spondias radlkoferi Donn.Sm.	Anacardiaceae	Árbol	primates	0.26	1.94	0
Stemmadenia donnel-smithii (Rose ex Donn. Sm.) Woodson	Apocinaceae	Árbol	otros vertebrados	0.33	0.03	0
Tabebuia guayacan (Seem.) Hemsley	Bignoniaceae	Árbol	viento	0	0	0.12
Teobroma cacao L.	Sterculiaceae	Arbusto	gravedad	0.17	0.34	0

Cuadro 2. *Continuación.*

Especie/Morfoespecie	Familia	FC	Dispersor	% de abundancia		
				BC	FO	FN
Tetracera volubilis L.	Dilleniaceae	Bejuco	otros vertebrados	0	0	0.12
Thevetia ahouai (L.) A. DC.	Apocinaceae	Árbol	otros vertebrados	0	0.01	0
Trichilia martiana C. DC.	Meliaceae	Árbol	otros vertebrados	0	0	0.02
Trophis racemosa (L.) Urban	Moraceae	Árbol	otros vertebrados	1.05	1.46	0.42
*Vatairea lundellii (*Standley) Killip ex Record	Ulmaceae	Árbol	viento	0.62	1.16	1.91
Virola guatemalensis Warb	Myristicaceae	Árbol	otros vertebrados	6.72	0	0.75
Vochysia guatemalensis Donn. Sm.	Vochisiaceae	Árbol	viento	0.12	0	16.22
Xylopia frutescens Aublet	Annonaceae	Arbusto	otros vertebrados	0	0	4.61
Zanthoxylum procerum Donn. Sm.	Rutaceae	Árbol	otros vertebrados	0	0.01	1.1