SITIOS DORMIDERO Y LETRINAS DE MONOS ARAÑA (*Ateles geoffroyi*) EN BOSQUE CONTINUO Y FRAGMENTADO: IMPLICACIONES PARA LA DISPERSIÓN DE SEMILLAS

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DEDICATORIA

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ÍNDICE

ÍNDICE DE FIGURAS

RESUMEN

Los monos araña (*Ateles geoffroyi*) defecan grandes cantidades de semillas en letrinas localizadas debajo de árboles dormidero. Puesto que este comportamiento puede tener implicaciones importantes para la regeneración del bosque, es fundamental conocer la distribución espacial y densidad de letrinas en bosque continuo y fragmentado. También es importante conocer la fidelidad (i.e., frecuencia de uso de árboles dormidero) y su efecto sobre la lluvia de semillas en estos lugares. En la selva Lacandona, Chiapas, evaluamos la densidad y distribución espacial de letrinas de monos araña, la fidelidad y la diversidad de semillas depositadas en letrinas de ocho comunidades de monos diferentes (cuatro en bosque continuo y cuatro fragmentos). Las letrinas se encontraron ubicadas bajo la copa de pocas especies arbóreas, siendo *Dialium guianense* y *Brosium alicastrum* las más frecuentes. La densidad de letrinas no difirió entre bosque continuo y fragmentado. Su distribución espacial fue agregada, pero variable en cada sitio, particularmente en los fragmentos. Registramos 45,919 semillas de 32 familias, 49 géneros y 68 especies de plantas en 60 letrinas durante 13 meses. El número total de especies (diversidad gamma) fue similar en ambos tipos de bosque, pero el recambio de especies (diversidad beta) y el número promedio de especies por letrina (diversidad alfa) fueron mayores en bosque continuo que en fragmentos. La fidelidad fue variable entre árboles dormidero, pero fue similar entre sitios y entre condición de bosque (i.e., fragmentos y bosque continuo). La fidelidad se asoció positivamente con la abundancia de semillas, diversidad de especies y diversidad beta en la mayoría de los sitios. Sin embargo, la fidelidad tiende a estar negativamente relacionada con la equitatividad. Nuestros resultados demostraron que a través de la fidelidad, los monos araña dan forma a los patrones espaciales de la lluvia de semillas a nivel de la comunidad y crean un patrón de deposición de semillas complejo en tiempo y espacio que puede tener importantes implicaciones ecológicas y de conservación. Sin embargo, el uso de pocas especies de árboles para dormir y la alta diversidad de semillas en letrinas podría fomentar el establecimiento de asociaciones vegetales típicas de las selvas del sureste mexicano, como *Terminalia-Dialium* y *Brosimum-Dialium.*

Palabras clave: árboles dormidero, dispersión de semillas espacialmente agregada, diversidad de especies, regeneración, selva Lacandona.

1. CAPÍTULO I: INTRODUCCIÓN

1.1. La dispersión de semillas

La dispersión de semillas es el movimiento de semillas fuera del árbol parental y es un proceso ecológico fundamental para la regeneración natural de la vegetación (Wang & Smith 2002). Tiene un impacto directo sobre los patrones de deposición de semillas, determinando así la distribución espacial y el éxito de establecimiento de las plantas (Howe & Smallwood 1982; Wenny 2001) (Fig.1). De hecho, la dispersión de semillas contribuye al mantenimiento de la diversidad y estructura de las comunidades vegetales (Nathan & Muller-Landau 2000; Webb & Peart 2000; Condit *et al.* 2000). Además, este proceso está asociado con el flujo de genes dentro y entre poblaciones de plantas (Wilson & Traveset 2000), y determina la probabilidad de ocurrencia de efectos reguladores de mortalidad (i.e., hongos, patógenos y competencia entre plántulas conespecíficas: Janzen 1970; Connell 1971) que emergen como consecuencia de las variaciones en la densidad de semillas (Howe & Smallwood 1982) (Fig. 1).

La dispersión de semillas puede ser llevada a cabo de diferentes formas. Por ejemplo, existen semillas que son dispersadas por animales (zoocoría), viento (anemocoría), agua (hidrocoría) o por sí mismas (autocoría). Dentro de este último grupo se encuentran plantas cuyos frutos cuentan con mecanismos para 'disparar' sus semillas, o los casos en que las semillas simplemente caen al suelo por gravedad (van der Pijl 1982; Levin *et al*. 2003). En los ecosistemas tropicales el síndrome de dispersión más común es la zoocoría, el cual, de acuerdo a sus principales categorías funcionales, puede clasificarse como synzoocoria (cuando las semillas son transportadas fuera del animal, e.g., adheridas al cuerpo), o endozoocoria (cuando el animal ingiere las semillas, son transportadas en el intestino y después defecadas) (Stiles 2000).

En los ecosistemas tropicales se estima que entre el 70 y 90% de las especies de plantas leñosas son dispersadas por animales (Howe & Smallwood 1982; Gentry 1988), y los animales dispersores de semillas representan la mayoría de la biomasa de vertebrados en estos ecosistemas (Terborgh *et al.* 2008). Dado que muchas de las especies arbóreas en estos ecosistemas producen semillas pequeñas y medianas (< 1.5 cm), éstas pueden ser fácilmente ingeridas por un gran número de especies de vertebrados (e.g., aves y mamíferos), defecándolas (en su mayoría intactas) en diferentes partes del bosque (van der Pijl 1982; Howe & Smallwood 1982; Gentry 1988). Sin embargo, las semillas de mayor tamaño (> 1.5 cm) son ingeridas y dispersadas por un número más reducido de especies de animales, principalmente grandes aves y mamíferos (Janson 1983), como los primates (e.g., van Rossmalen 1988; Stevenson *et al.* 2005; Nunes 1998; Kaplin & Lambert 2002). En conjunto, a través de este proceso de endozoocoria, los animales frugívoros determinan la composición, diversidad y abundancia de semillas en la denominada "lluvia de semillas" (i.e., suma de las sombras de semillas de todos los individuos de una población más las semillas dispersadas de otras poblaciones), así como la configuración espacial de la "sombra de semillas" (i.e., distribución espacial de las semillas dispersas de una planta: Janzen 1970; Nathan & Muller-Landau 2000; Schupp *et al.* 2002) (Fig. 1).

En general, el patrón espacial de deposición de semillas puede ser de dos tipos, disperso o agregado (Howe & Smallwood 1982; Wenny 2001; Schupp *et al.* 2010). Ambos dependen del comportamiento de los animales, o sea del uso del hábitat, el patrón de forrajeo, la selección de micrositios, y la tasa y direccionalidad de los movimientos desde el árbol parental (Howe 1989; Schupp *et al.* 2010). Además, la fisiología de cada especie (i.e., tiempos de retención intestinal: Milton 1980) condicionan las tasas de defecación y la forma en que serán depositadas. Por ejemplo, las semillas pueden ser defecadas de forma individual o en grupos (Schupp 1993; Wenny 2001; Jordano & Godoy 2002).

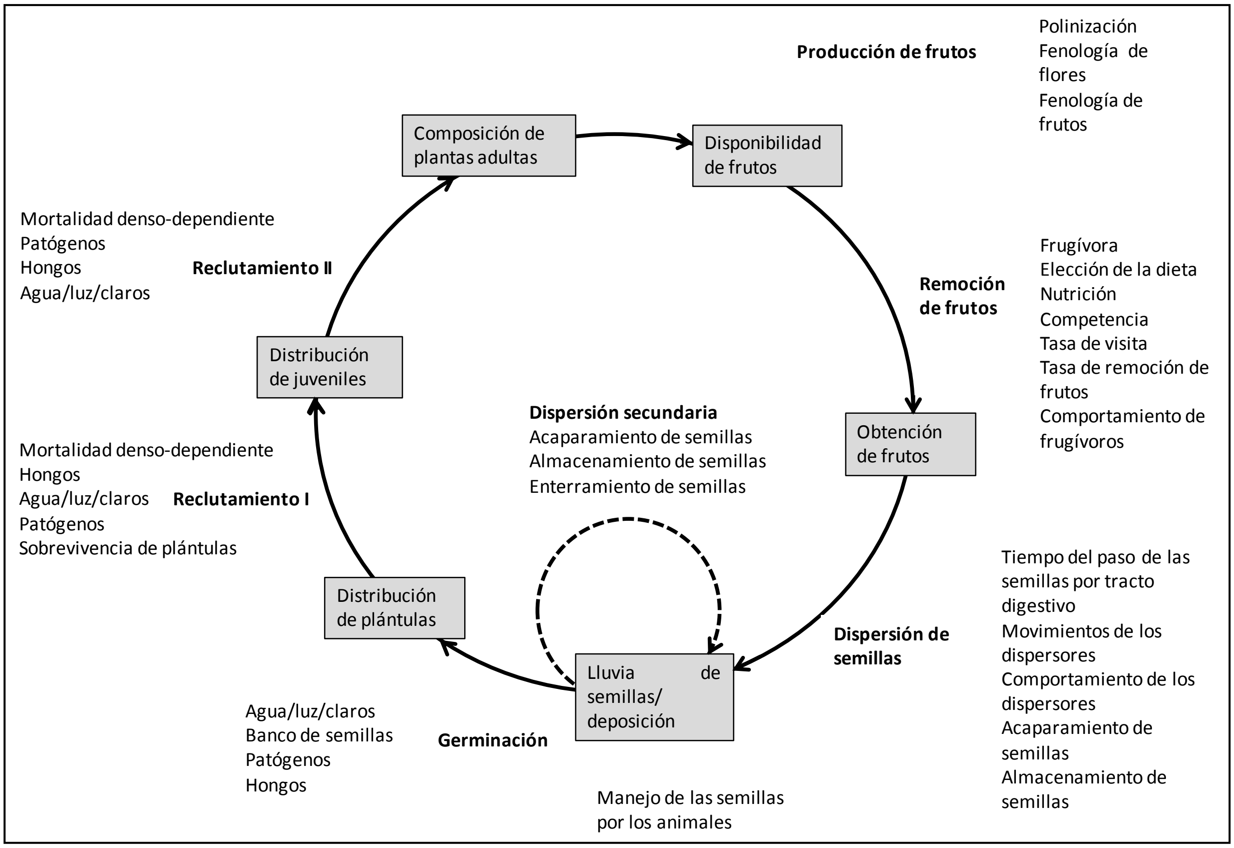

Fig.1. Marco conceptual sobre el proceso de dispersión de semillas. Las diferentes partes del proceso (en negritas) y los patrones (cajas) indican la direccionalidad de las fuerzas, así como las diferentes variables que se interrelacionan en cada fase del proceso. Modificado de Wang & Smith (2002).

Las aves y murciélagos frugívoros de tamaño pequeño (e.g., 10 a 500 g) y mediano (e.g., 500 g a 3 kg) generalmente dispersan semillas de forma individual, en pares o en pequeños grupos, creando un patrón de deposición de semillas disperso. La dispersión de semillas por regurgitación o defecación es la norma en trogones (*Trogon massena*), momotos (*Baryphthengus martii*), tucanes (*Ramphastos sulfuratus* y *R. swainsonii*), y pavas (*Penelope purpurascens*) que se alimentan de semillas ariladas de nuez moscada en Panamá (*Virola sebifera* y *V. surinamensis*; Myristicaceae) (Howe & vande Kerckhove 1981; Howe & Richter 1982). Murciélagos frugívoros como *Artibeus* spp. y *Carollia perspicillata* dispersan semillas durante el vuelo desde y hacia los árboles de alimentación, refugios diurnos y dormideros en Centro y Sudamérica (Morrison 1978; Heithaus 1982; Charles-Dominique 1986; Melo *et al.* 2009), promoviendo un patrón de deposición mixto, con una porción de semillas dispersadas de forma dispersa y otra porción depositada de forma agregada. De forma similar, en muchas especies de mamíferos terrestres, como rinocerontes (*Rhinocerus unicornis*: Dinerstein & Wemmer 1988), Tejon (*Meles meles*: Revilla & Palorames 2002), Tapir (*Tapirus terrestris*: Fragoso *et al.* 2003), Elefantes (*Loxodonta africana* y *Elephas maximus*: Campos Arceis & Black 2010), Zorro (*Vulpes vulpes*: González Varo *et al.* 2012) y Gacelas (*Gazella arabica*: Wronski & Plath 2010) entre otros, es común que una proporción importante de las semillas sean depositadas de manera agregada en letrinas. Este patrón de deposición también es común en primates (*Alouatta seniculus*: Julliot 1996; *A. seniculus* y *Lagothrix lagothricha*: Yumoto *et al.* 1999; *A. caraya*: Bravo 2012; *Ateles paniscus*: Russo & Augspurguer 2004; *A. belzebuth*: Link & Di Fiore 2006).

En aves, estas letrinas pueden surgir de comportamientos particulares como el descanso constante en las mismas perchas o claros dentro del bosque (Hoppes 1988; Levey 1988; Wenny 2001), lugares de apareamiento ("*leks*"; e.g., *Procnias tricarunculata*: Wenny & Levey 1998; *Cephalopterus penduliger*: Karubian & Duraes 2009; *Manacus manacus*: Cestari & Pizo 2013) y sitios de nidificación (Wenny & Levey 1998). En mamíferos, las letrinas suelen estar asociadas a lugares específicos para la defensa del territorio, como por ejemplo en zorros (*V. vulpes*: González Varo *et al.* 2012), tejones (*M. meles*: Revilla & Palomares 2002) y gacelas (*G. arabica*: Wronski & Plath 2010). También pueden estar asociadas a sitios de alimentación y/o descanso, como por ejemplo en murciélagos (*Artibeus watsoni*: Melo *et al.* 2009). En primates, las letrinas también pueden estar localizadas debajo de los árboles que utilizan para descansar (*Saguinus fuscicollis* y *Saguinus mystax*: Muñoz-Lazo *et al.* 2011), o pernoctar (*A. seniculus*: Julliot 1996; *A. seniculus* y *L. lagothricha*: Yumoto *et al.* 1999; *A. paniscus*: Russo & Auguspurger 2004; *A. caraya*: Bravo 2012; *Gorilla gorilla*: Rogers *et al.* 1998), de forma que en estos animales el patrón de deposición también suele ser mixto.

1.2. Importancia de la dispersión de semillas para la regeneración del bosque

Entre las ventajas que ofrece la dispersión de semillas para las plantas, cabe destacar tres (Howe & Smallwood 1982): Primero, la dispersión de semillas permite a las semillas escapar de la alta competencia entre plantas y de los factores de alta mortalidad (e.g., depredadores, patógenos) asociados con la alta densidad de semillas y plántulas cerca de los árboles parentales (Janzen 1970; Connell 1971). Así, además de alejar las semillas de los árboles parentales, la dispersión de semillas reduce la densidad de semillas cerca del árbol que las dio origen (hipótesis de escape; Howe & Smallwood 1982). Segundo, permite la colonización de sitios azarosamente ubicados dentro del bosque que pueden ser particularmente adecuados para el establecimiento de plántulas, como por ejemplo, los claros que son causados por la caída de árboles y ramas (hipótesis de colonización). Finalmente, la dispersión de semillas puede ser dirigida hacia lugares específicos donde la probabilidad de germinación y supervivencia puede ser mayor (hipótesis de dispersión directa). Todas estas ventajas no son mutuamente excluyentes, ya que muchas especies de plantas pueden verse favorecidas por más de una de estas ventajas (Wenny 2001).

Aunque la cantidad de semillas y plántulas que ocurren bajo los árboles parentales puede variar ampliamente entre especies (Augspurger 1984; Howe *et al.* 1985; Howe 1989; Chapman & Chapman 1996), las probabilidades de sobrevivencia de semillas y plántulas aumentan al incrementarse la distancia con la planta madre, e incluso la distancia con árboles conespecíficos (e.g., Howe & Smallwood 1982; Augspurger 1984; Clark & Clark 1984; Harms *et al.* 2000; Balcomb & Chapman 2003; Jansen *et al.* 2008). Sin embargo, a pesar de la baja sobrevivencia, la elevada densidad de semillas cerca del árbol parental permite el reclutamiento de plántulas en estos sitios (Hubbell 1980). Por ejemplo, la alta densidad de semillas puede favorecer la saturación de los depredadores y contribuir a aumentar el número de semillas que logran establecerse (Augspurger & Kitajima 1992; Burkey 1994, Crawley 2000; Boudreau & Lawes 2008). Esta saturación de los depredadores de semillas y herbívoros puede ayudar a explicar que el patrón de distribución agregado de semillas de *Virola calophylla* (Myristicaceae) en letrinas de monos araña (*A. paniscus*) permanezca en las plántulas y en árboles adultos de esta especie (Russo & Augspurger 2004). De hecho, la constante deposición de excretas en letrinas incrementa la cantidad de nutrientes en el suelo (e.g., N, P, y diversos minerales) comparado con áreas alrededor de estas (Feeley 2005; Pouvelle *et al.* 2008; Neves *et al.* 2010), lo que puede favorecer el reclutamiento y la sobrevivencia de plántulas en letrinas (Russo & Augspurger 2004; Bravo 2012). En particular, la sobrevivencia per cápita de juveniles mayores a 1 m es relativamente más alta en letrinas de monos aulladores (*A. caraya*) que fuera de ellas (Bravo 2012). Así, de acuerdo con la hipótesis de dispersión directa, las letrinas podrían representar sitios adecuados para la germinación de semillas y el reclutamiento y crecimiento de plántulas (Wenny 2001; Chapman & Russo 2006). Por tanto, evaluar la lluvia de semillas en estos lugares es fundamental para tener un mejor entendimiento del papel que juegan las letrinas en la dispersión de semillas; un tema para el que existe muy pocas evidencias empíricas.

1.3. Eficacia en la dispersión de semillas: el caso de los primates

Desde el punto de vista de las plantas, la cantidad de dispersores es importante, pero lo es aún más la eficacia con la que éstos animales dispersan sus semillas (Schupp 1993; Schupp *et al.* 2010). La eficacia depende de la cantidad y calidad de la dispersión. La cantidad de dispersión se refiere al número de semillas dispersadas, el cual depende del número y duración de las visitas del dispersor a la planta, y del número de semillas dispersadas por visita (Schupp 1993). La calidad de dispersión depende del comportamiento de procesamiento interno y de la manipulación externa de las semillas, así como de la probabilidad de que las semillas dispersadas logren convertirse en plantas adultas (Schupp 1993).

Los primates se encuentran entre los dispersores primarios de semillas más importantes en los bosques tropicales (Stevenson 2000; Peres & van Roosmalen 2002; Chapman & Russo 2006, Stevenson & Aldana 2008), comprendiendo entre el 25 y 40% de la biomasa de vertebrados frugívoros en estos ecosistemas (Chapman 1995). La mayoría consume grandes cantidades de frutos, y defecan o escupen un gran número de semillas viables (Lambert 1999), por lo que, en general, han sido destacados como dispersores eficaces de semillas. Muchos primates son de gran tamaño (> 5 kg) e ingieren y dispersan un gran número de semillas de diferentes tamaños (Chapman 1995; Lambert & Garber 1998; Vidal *et al.* 2013). De hecho, en términos de la cantidad de la dispersión (sensu Schupp 1993), se ha comprobado que dispersan incluso el doble de la cantidad de semillas que dispersan las aves (Clark *et al.* 2005). Sin embargo, al igual que otros frugívoros, la eficacia de los primates como dispersores de semillas puede ser muy variable debido a diferencias en su morfología, fisiología, alimentación y comportamiento (Rowell & Mitchell 1991; Zhang & Wang 1995; Kaplin & Moermond 1998), por lo que su contribución relativa a la dispersión de semillas y la regeneración del bosque puede variar considerablemente.

La dispersión de semillas por primates ha sido ampliamente documentada en México (Estrada & Coates-Estrada 1984, 1986; Chaves *et al.* 2011) y Centroamérica Chapman 1989a), Sudamérica (Garber 1986; Julliot 1996; Stevenson 2000; Dew 2001), África (Gautier-Hion 1984; Gautier-Hion *et al.* 1985; Wrangham *et al.* 1994; Chapman & Chapman 1996; Kaplin & Moermond 1998; Lambert 1999; Voysey *et al.* 1999a,b), y Asia (Corlett & Lucas 1990; Davies 1991; Leighton 1993; Lucas & Corlett 1998; McConkey 2000). Todos estos estudios demuestran que los primates dispersan miles de semillas, muchas de ellas de gran tamaño (entre 4 x 3 mm) y con cubierta (testa) dura (Gautier-Hion 1984; Gautier-Hion *et al.* 1985). De hecho, la ingestión de las semillas por los primates permite el adelgazamiento de la testa (escarificación) por medio de la acción corrosiva de los ácidos gástricos, favoreciendo así el intercambio de gases y agua entre el interior y exterior de la semilla al ser expulsada (Traveset *et al.* 2007). La eliminación de la pulpa también permite la remoción de los inhibidores de la germinación (desinhibición), lo que incrementa la tasa de germinación (Robertson *et al.* 2006). Además, al ser defecadas con materia fecal, los primates fertilizan las semillas favoreciendo el crecimiento y supervivencia de las plántulas. Por tanto, además de ser eficaces en términos de cantidad de semillas dispersadas, pueden ser fundamentales en términos de calidad de dispersión, ya que no dañan las semillas y favorecen su germinación. De hecho, se ha propuesto para algunas especies de primates (*L. lagotricha* y *A. belzebuth:* Stevenson & Aldana 2008; Link & Di Fiore 2006; *Pan paniscus*: Beaune *et al.* 2013) que su remoción del ecosistema podría acarrear importantes consecuencias negativas para un gran número de especies de plantas, en particular para las de semillas más grandes, que son principalmente dispersadas por primates (Link & Stevenson 2004; Chaves *et al.* 2011; González-Di Pierro *et al.* 2011).

Una gran diversidad de árboles tropicales producen semillas de gran tamaño (> 1.5 cm) (Gautier-Hion 1984; Gautier-Hion *et al.* 1985; Garber 1986; White 1983; Chapman 1989a, 1995). Entre los primates frugívoros neotropicales, los miembros de la familia Atelidae (i.e., *Lagrotrix*, *Alouatta* y *Ateles*) son los dispersores más eficaces de semillas grandes (Russo & Chapman 2006), ya que los primates de esta familia tienen tamaños corporales relativamente grandes (> 6 kg: Russo & Chapman 2006). Además, de dispersar semillas grandes y pequeñas (Chapman & Chapman 1995), ocupan áreas de actividad relativamente grandes, de más de 100 ha en el caso de *L. lagotricha* y *A. belzebuth* (Stevenson & Aldana 2008), lo que permite que dispersen las semillas a grandes distancias (Stevenson 2000; Link & Di Fiore 2006; revisado por Chaves *et al.* 2011).

1.4 Los monos arañas como dispersores de semillas

En los bosques tropicales de América no existe un animal que disperse un mayor número de semillas que los monos araña (género *Ateles*) (van Roosmalen 1985; Link & Di Fiore 2006; Dew 2008; Chaves *et al.* 2011). Los miembros de este género juegan un papel clave en la dispersión de semillas, ya que su servicio de dispersión es crítico para un gran número de especies (i.e., más de 100 especies de plantas reportadas en la literatura: Link & Di Fiore 2006; Di Fiore *et al.* 2008; González-Zamora *et al.* 2009; Chaves *et al.* 2011). Su importancia como dispersor se ha demostrado en términos de la cantidad de especies dispersadas (van Roosmalen 1985), número de semillas removidas (Russo 2003), tamaño de las semillas ingeridas (Dew 2001, 2005, Russo *et al.* 2005), distancias de dispersión (Dew 2001; Link & Di Fiore 2006), sobrevivencia de semillas dispersadas (Dew 2001) y, eficacia de dispersión (Chaves *et al.* 2011). De hecho, se ha sugerido que los monos araña son los agentes dispersores más importantes de algunas especies de plantas con semillas grandes (Dew 2008).

Los monos araña son frugívoros obligados. Su dieta está compuesta principalmente por frutos maduros (Chapman 1987, 1989b; Di Fiore *et al.* 2008; González-Zamora *et al.* 2009). Se encuentran entre los primates Neotropicales de mayor tamaño (8 kg) y pueden desplazarse diariamente en un rango de 1,000 a 1,500 m (Di Fiore *et al.* 2008). Así, pueden dispersar sus semillas a distancias promedio mayores a 100 m (Suarez 2006; Di Fiore & Campbell 2007). En el Parque Nacional Tiputini, en Ecuador, *A. belzebuth* dispersa semillas en distancias promedios de entre 245 y 425 m (Link & Di Fiore 2006), pero se han llegado a reportar distancias mayores a 1,000 m (Dew 2001; Link & Di Fiore 2006). En cuanto a la dispersión espacialmente agrupada, aunque ha sido muy poco estudiada, algunos estudios sugieren que la distancia entre sitios dormidero puede ser un buen indicador de las distancias a las que los monos arañas dispersan las semillas (Dew 2008; Fig. 2). Por estas y otras razones, los miembros de este género de primate han sido descritos como uno de los más importates dispersores de semillas (Peres 1994; Stevenson 2000; Stevenson *et al.* 2005; Link & Di Fiore 2006).

1.5 Dispersión de semillas por *Ateles geoffroyi*

El mono araña de manos negras (*A. geoffroyi*) tiene una dieta diversa. Cerca de 365 especies de plantas de 76 familias han sido reportadas en su dieta a lo largo de su distribución geográfica (González-Zamora *et al.* 2009), que va desde el sureste de México hasta el norte de Colombia (Rylands *et al.* 2006). Entre las partes vegetales que consume, se estima que en promedio dedican 67.0 ± 16.3% del tiempo total de alimentación al consumo de frutos (González-Zamora *et al.* 2009). Así, un número creciente de estudios ha documentado el papel de estos primates en la dispersión de semillas (Chapman 1989a; Cant 1990; Chaves *et al.* 2011).

Estos primates tienen una estructura social compleja, denominada ‘fisión-fusión’ porque las comunidades de monos de entre 20 y 42 individuos (Shimooka *et al.* 2008) se dividen durante el día en pequeños subgrupos (2.3 a 14.4 individuos: Chapman *et al.* 1995) para alimentarse de diferentes recursos localizados en su área de actividad (Aureli *et al.* 2008). Los subgrupos (uno o varios) se reúnen por las noches para pernoctar en sitios dormidero formados por uno o más árboles (“árboles dormidero” de aquí en adelante; Chapman 1989). Así, se les ha denominado forrajeradores de múltiples sitios centrales (sensu Orians & Pearson 1979) porque utilizan varios puntos focales (sitios dormidero) para pernoctar, y como centro de partida para realizar sus excursiones de forrajeo durante el día (Chapman 1989). La disponibilidad temporal y espacial de los recursos condiciona el uso del espacio (Asensio *et al.* 2011; Ramos- Fernández *et al.* 2013). Por tanto, el número de sitios dormideros varían en tiempo y espacio dependiendo de la disponibilidad de alimento. Su área de actividad varía de 95 a 962 ha (Wallace 2008). Dentro de estas áreas, hay zonas con mayor concentración de recursos que son utilizadas más frecuentemente (denominadas "*core areas*" en inglés; Asensio *et al.* 2011; 2012; Ramos-Fernández *et al.* 2013). Dado que los monos pueden utilizar estos sitios dormideros por varios días consecutivos, debajo de estos árboles se acumulan grandes cantidades de excretas y semillas en letrinas (Chapman 1989; Russo & Augspurguer 2004; Link & Di Fiore 2006).

El comportamiento social y dietético descrito arriba tiene como consecuencia que el patrón de deposición de semillas producido por este primate sea mixto, esto es, una fracción de las semillas ingeridas son depositadas de forma dispersa en diferentes zonas de su territorio donde los animales se mueven en busca de alimento ("zonas de tránsito", de aquí en adelante), y otra fracción es dispersada de forma agrupada en letrinas ubicadas debajo de los árboles dormidero (Russo & Augspurger 2004, Bueno *et al.* 2013; Fig. 2). La sombra de semillas dispersadas en zonas de transito es mayor, de modo que las semillas dispersadas de esta forma reclutan en plántulas aisladaa y tienen más probabilidades de sobrevivir que aquellas que son defecadas en letrinas (Fig. 2). Sin embargo, ambos patrones de deposición de semillas son complementarios y contribuyen a aumentar la magnitud y forma de la sombra de semillas dentro de los ámbitos hogareños, lo cual puede ser determinante para el establecimiento de plántulas en diferentes áreas de su territorio (Chapman & Russo 2006; Fig. 2).

Los estudios sobre dispersión de semillas con monos araña se han enfocado en analizar la dispersión de semillas espacialmente dispersa (Link & Di Fiore 2006; Dew 2008; Chaves *et al*. 2011). La dispersión de semillas espacialmente agregada en letrinas ha sido pobremente estudiada. De hecho, ningún estudio a la fecha ha cuantificado la diversidad de especies que puede dispersar este primate en letrinas. Es probable que la dificultad para localizar los sitios dormideros y letrinas haya sido un factor limitante para la generación de información sobre este importante componente de la dispersión de semillas. Puesto que estos lugares pueden representar áreas de gran reclutamiento de plantas dentro del bosque (ver arriba), es fundamental conocer la identidad de los árboles dormidero, sus características morfológicas, su densidad y distribución espacial, así como la abundancia y diversidad de semillas que son depositadas en las letrinas, y el papel de la fidelidad de uso de los árboles dormidero sobre las características de la lluvia de semillas. Aunado a esto, es importante notar que estos primates están siendo cada vez más forzados a habitar en paisajes fragmentados (Garber *et al.* 2006). Puesto que la eficacia en la dispersión puede ser menor en fragmentos de bosque que en áreas de bosque continuo (Chaves *et al.* 2011), es fundamental evaluar si las características de los árboles dormidero y la lluvia de semillas pueden verse alterados en fragmentos. Esta información tiene implicaciones ecológicas y de conservación muy importantes.

1.6 Dispersión de semillas por monos araña en paisajes fragmentados

La creciente demanda mundial por productos agrícolas representa la mayor fuerza de transformación de bosques tropicales a tierras de cultivo y pastizales para el ganado (Gibbs *et al.* 2010). De hecho, los bosques tropicales representan el ecosistema más deforestado a nivel mundial (FAO 2011), particularmente en América Latina (Aide *et al.* 2013). Los bosques tropicales son los principales reservorios de biodiversidad, por lo que esta situación amenaza el mantenimiento de la biodiversidad y los procesos ecológicos en los que está involucrada (Gibson *et al.* 2011; Melo *et al*. 2013). Por tanto, la desaparición de especies y procesos ecológicos puede generar alteraciones muy importantes en el funcionamiento del ecosistema (Estes *et al.* 2011).

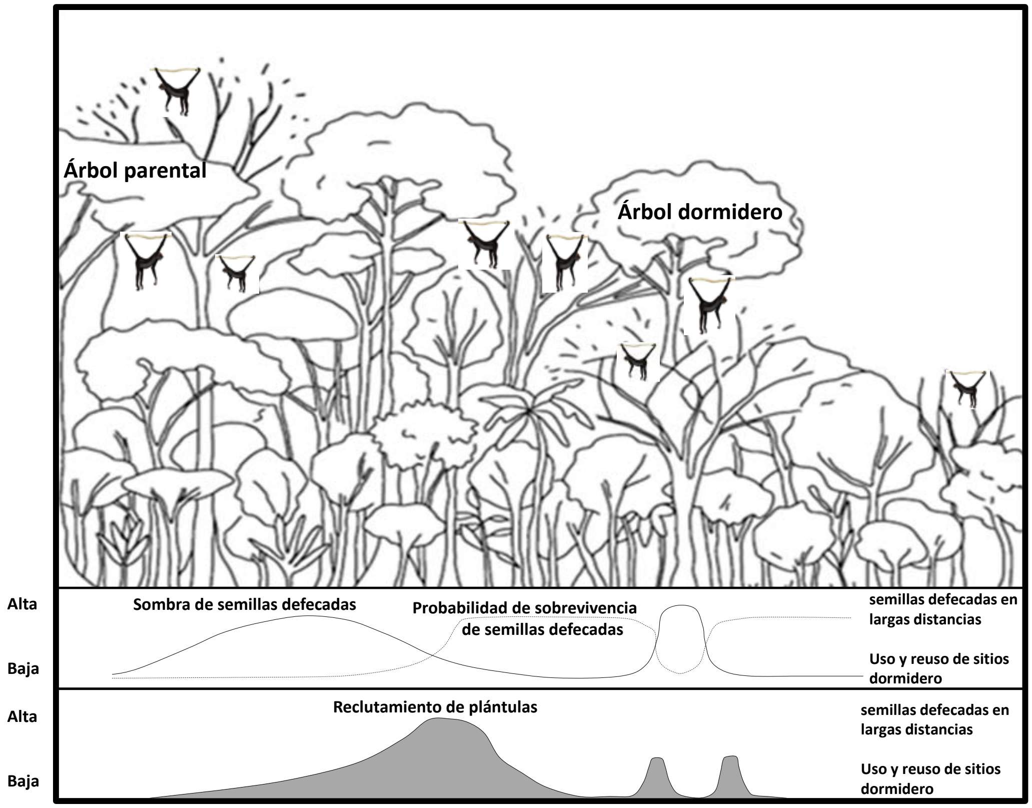

Fig. 2. Esquema representativo que indica el patrón mixto de dispersión de semillas (i.e., disperso y agrupado) por monos araña (modificado de Chapman & Russo 2006).

Como se ha mostrado arriba, la dispersión de semillas es una de las interacciones planta-animal más importantes para el mantenimiento de la diversidad en bosques tropicales, y un número creciente de estudios han demostrado que este proceso ecológico puede verse alterado en paisajes fragmentados (Cordeiro & Howe 2003; Stoner *et al.* 2007; Morris 2010; Galetti & Dirzo 2013). Por ejemplo, la deforestación a menudo resulta en la fragmentación de bosques tropicales, lo que obliga a muchas especies de animales a vivir aisladas en fragmentos rodeados de tierras agrícolas (Fahrig 2003). A medida que el grado de fragmentación aumenta, el número de parches se incrementa, disminuye su tamaño medio y aumenta su aislamiento (Fahrig 2003). Estos cambios en la configuración del paisaje pueden resultar en la extinción local de especies, siendo las especies de mayor tamaño las primeras en desaparecer de los fragmentos (Peres 2000; Peres & Palacios 2007), no sólo porque tienen requerimientos de hábitat mayores, sino porque suelen ser los animales preferidos por los cazadores (Stoner *et al.* 2007). Entre estas especies, destacan los frugívoros de mayor tamaño, incluyendo muchas especies de primates (Peres 2001; Peres & Palacios 2007; Arroyo-Rodríguez & Dias 2010). De hecho, el aumento de la tala selectiva en fragmentos también puede reducir la disponibilidad de árboles grandes y, en consecuencia, de frutos, amenazando así la supervivencia de primates en fragmentos (Kirika *et al.* 2008; Lambert 2011; Arroyo-Rodríguez *et al.* 2007; Fig. 3).

La desaparición de dispersores primarios de semillas, y el incremento en la distancia entre fragmentos puede limitar de forma significativa la cantidad y diversidad de semillas dispersadas, así como las distancias de dispersión (Chapman & Onderdonk 1998; Willson & Traveset 2000). El aumento en la mortalidad de árboles grandes (diámetro a la altura del pecho, DAP > 60 cm) en fragmentos (Laurance *et al.* 2000), no sólo reduce la disponibilidad de alimento para los animales frugívoros (Arroyo-Rodríguez & Mandujano 2006; Fig. 3), sino que limita la disponibilidad de fuentes de semillas. Además, para el caso de los monos araña que seleccionan árboles grandes para dormir, la falta de árboles grandes en fragmentos podría alterar la lluvia de semillas en las letrinas ubicadas debajo de estos árboles. En particular, cabría esperar que la escasez de árboles grandes en fragmentos obligue a los primates a utilizar los árboles disponibles con mayor frecuencia, incrementando la cantidad de semillas en las letrinas, pero limitando significativamente las distancias de dispersión. Esta hipótesis requiere ser probada, pues no existen estudios sobre la disponibilidad de árboles dormidero en fragmentos de bosque, ni evaluaciones de las diferencias en la frecuencia de uso de diferentes árboles dormidero.

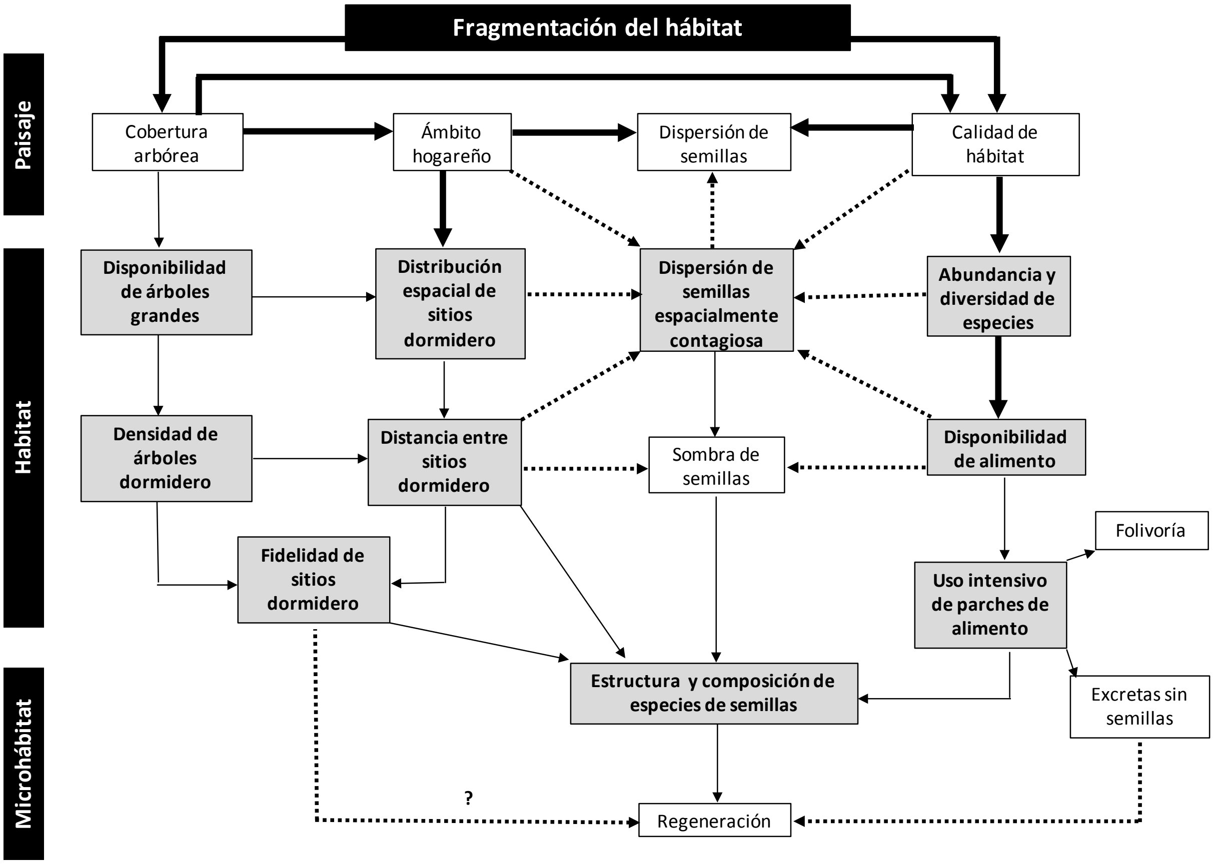

Fig. 3. Marco conceptual que indica los factores que determinan el proceso de regeneración natural del bosque en paisajes fragmentados a diferentes escalas espaciales. Las cajas grises con letras en negritas indican los temas tratados en la presente tesis. Las flechas indican la relación entre cajas. Las flechas gruesas denotan relaciones teóricas documentadas, mientras que las delgadas han sido poco documentadas. Las flechas punteadas indican relaciones teóricas para las que no existen demostraciones empíricas.

La fragmentación del hábitat genera cambios en la cobertura arbórea que alteran la calidad del hábitat en términos de estructura y composición de la vegetación, lo cual reduce la disponibilidad de árboles grandes y de alimento (Fig. 3). Para enfrentar la escasez de alimento en fragmentos, los monos araña aumentan el consumo de hojas (González-Zamora *et al.* 2009; Chaves *et al.* 2011) (Fig. 3). Como consecuencia, el porcentaje promedio de excretas sin semillas es mayor en fragmentos (Chaves *et al.* 2011), limitando la eficacia de este dispersor en términos de cantidad de semillas dispersadas (Fig. 3). Por otro lado, dado que estos animales no tienen un sistema digestivo adaptado al consumo de hojas (Milton 1981), la obtención de energía a partir de las hojas es muy limitada/ineficiente. Por tanto, probablemente como una estrategia de ahorro energético, los monos tienden a dedicar más tiempo al descanso y menos a la locomoción (González-Zamora *et al.* 2011). Además, los rangos diarios de desplazamiento de los monos tienden a ser menores en fragmentos (González-Zamora & Mandujano Rodríguez 2003), así como el tamaño de su ámbito hogareño (Asensio *et al.* 2011, 2012). Ambos factores también pueden ser consecuencia de la limitación espacial y agregación de recursos impuestos por los fragmentos más pequeños. Sea cuál sea la causa de estas adaptaciones en el comportamiento, sin duda tienen consecuencias fundamentales en el proceso de dispersión de semillas, ya que una reducción en los rangos de acción implica una disminución en las distancias de dispersión (Fig. 3). En este sentido, se espera que los árboles dormideros en paisajes fragmentados estén ubicados más cerca entre sí que en áreas de bosque continuo, pero ningún trabajo hasta la fecha ha evaluado esta predicción.

1.7 Los monos araña en la selva Lacandona

La región mexicana de la Selva Lacandona se ubica en Chiapas, y representa la mayor porción remanente de bosque tropical húmedo del país (Medellín 1994). Esta selva es uno de los principales reservorios (*hotspot*) de biodiversidad en Mesoamérica. Sin embargo, se encuentra seriamente amenazada por los cambios de uso de suelo y, por la perdida y fragmentación del hábitat (Myers 1993; Mendoza & Dirzo 1999; Díaz Gallegos *et al.* 2008). La gran variedad de topoformas y tipos de vegetación que existen en esta región, le permite mantener una gran diversidad de flora y fauna, favoreciendo una gran cantidad de interacciones ecológicas. La diversidad de especies en esta región es una de las más importantes de México (Medellín 1994). Por ejemplo, alberga el 35% de las aves residentes de México (González García 1993), el 27% de mamíferos (Medellín 1994; Lira Torres *et al.* 2012), el 9% de las especies de anfibios y 12% de las especies de reptiles (Lazcano-Barrero *et al.* 1992). Desafortunadamente, la colonización de la región durante los últimos 40 años y la continua pérdida y fragmentación del hábitat en las últimas dos décadas, han originado que hasta un 50% de la cobertura arbórea original haya sido transformada en pastizales para ganado y campos de cultivo (De Jong *et al.* 2000; Díaz Gallegos *et al.* 2008). Así la región es altamente vulnerable a la pérdida de biodiversidad (Myers *et al.* 2000; Sader *et al*. 1990).

En la selva Lacandona los monos araña han sido descritos como dispersores de semillas altamente eficaces, ya que más del 72% de su dieta consiste en frutos maduros y carnosos, y rara vez depredan las semillas (Chaves *et al.* 2011). Por ejemplo, dispersan 71 especies de 23 familias (Chaves *et al.* 2012), y en particular, es un importante dispersor para especies de semilla grande como *Pouteria, Spondias* y *Virola* entre otras (González-Zamora *et al.* 2009; Chaves *et al.* 2011). Dado que ingieren frutos enteros, más del 80% de las semillas ingeridas son defecadas sin daños y su germinación se ve favorecida (Chaves *et al.* 2011). Además, dispersan cientos de semillas a distancias mayores a 100 m (Chaves *et al.* 2011, 2012). No obstante, Chaves *et al.* (2011) señala que la eficacia de este primate como dispersor de semillas puede ser limitada en fragmentos, ya que aquí ingieren una proporción menor de semillas (Chaves *et al.* 2011). De hecho, se ha demostrado que en los fragmentos donde los monos araña han desaparecido, la composición de plántulas en el sotobosque está siendo alterada, ya que se reduce la abundancia y riqueza de especies de semilla grande, mientras que la riqueza de especies dispersadas por vertebrados pequeños se favorece, así como la abundancia de especies dispersadas por medios abióticos (Chaves *et al.* 2011; Arroyo Rodríguez *et al.* 2011).

2. CAPÍTULO II: OBJETIVOS E HIPÓTESIS

El principal objetivo de este estudio fue caracterizar la dispersión de semillas por monos araña en letrinas y probar si este tipo de dispersión puede verse alterado en paisajes fragmentados. Para ello, primero se evaluó la distribución espacial, densidad y características de los sitios dormideros y las letrinas de *Ateles geoffroyi* en bosque continuo y fragmentos en la selva Lacandona (Capítulo III). En segundo lugar, se examinó la diversidad y abundancia de semillas dispersadas por este primate en las letrinas, y se probó si la comunidad de semillas difiere entre bosque continuo y fragmentos (Capítulo IV). Finalmente, se probó si la frecuencia de uso de los árboles dormidero (i.e., fidelidad) difiere entre ambos tipos de bosque, y se evaluó el papel que juega la fidelidad sobre los patrones de lluvia de semillas (Capítulo V).

En particular, en la primera publicación (González-Zamora *et al.* 2012; Capítulo III) se probó la hipótesis de que la escasez de árboles grandes en fragmentos podría limitar la disponibilidad, lo que podría resultar en una menor densidad de árboles dormidero y letrinas en fragmentos. Alternativamente, los monos podrían seleccionar árboles dormidero de menor tamaño en fragmentos. Además, se probó la hipótesis de que los sitios dormideros mantienen una distribución espacial variable en bosque continuo y fragmentos debido a que la distribución y disponibilidad de frutos varía en espacio y tiempo. Alternativamente, puesto que en fragmentos, la baja disponibilidad de frutos puede "forzar" a los monos araña a aumentar el consumo de hojas, se probó la hipótesis de que las distancias entre letrinas podrían ser menores en fragmentos que en bosque continuo.

En el cuarto capítulo (González-Zamora *et al.* 'en revisión'), se evaluaron la abundancia de semillas y los patrones de diversidad α, β y γ, así como la equitatividad de la comunidad de semillas a diferentes escalas espaciales (letrinas, sitios y condición de bosque) para probar la hipótesis de que la escasez de alimento en fragmentos puede forzar a los monos araña a dedicar más tiempo al consumo de los parches de frutos disponibles (Chapman 1987). De ser así, la lluvia de semillas en fragmentos estará dominada por pocas especies, lo cual podría aumentar la abundancia de semillas de unas pocas especies, pero reducirá la diversidad α, β y γ, así como la equitatividad de la comunidad.

Finalmente, en el quinto capítulo (González-Zamora *et al.* ‘en revisión’), se analiza la fidelidad de árboles dormidero y su relación con la lluvia de semillas para probar la hipótesis de que la escasez de árboles grandes en fragmentos y la reducción en el área de actividad de los monos en fragmentos podrían resultar en el aumento de la fidelidad por los árboles dormidero. Además, dado que se espera que los árboles dormidero más frecuentemente usados estén asociados a sitios con mayor disponibilidad de recursos, se espera que en todos los sitios la fidelidad esté positivamente asociada con la abundancia y diversidad de especies en letrinas. Sin embargo, dado que estos monos son altamente selectivos y enfocan su dieta a pocas especies preferidas, se espera que la equitatividad de la comunidad de semillas esté negativamente asociada con la fidelidad.

Referencias

Aide TM, Clark ML, Grau HR, Lopéz-Carr D, Levy MA, Redo D, Bonilla-Moheno M, Riner G, Andrade-Nuñez MJ, Muñiz M .(2013). Deforestation and reforestation of Latin America and the Caribbean (2001–2010). *Biotropica* 45: 262–271.

Arroyo-Rodríguez V, Mandujano S .(2006). Forest fragmentation modifies habitat quality for *Alouatta palliata*. *International Journal of Primatology* 27: 1079–1096.

Arroyo-Rodrıíguez V, Mandujano S, Benítez-Malvido J, Cuende-Fanton C .(2007). The influence of large tree density on howler monkey (*Alouatta palliata mexicana*) presence in very small rain forest fragments. *Biotropica* 39: 760–766.

Arroyo Rodríguez V, Chaves MO, Guzmán Romero B, Avila FE, Stoner KE .(2011). Dispersión de semillas por monos araña y sus implicaciones para la regeneración de las selvas. In: Dias PA, Rangel Negrin A, Canales Espinosa D (eds). La conservación de los primates mexicanos. Consejo Veracruzano de Ciencia y Técnología, Xalapa, Veracruz. Pp. 125–145.

Asensio N, Schaffner CM, Aureli F .(2011). Variability in core areas of spider monkeys (*Ateles geoffroyi*) in a tropical dry forest in Costa Rica. *Primates* 53: 147–156.

Asensio N, Lusseau D, Schaffner CM, Aureli F .(2012). Spider monkeys use high-quality core areas in a tropical dry forest. *Journal of Zoology* 287: 250–258.

Augspurger CK. (1984). Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps and pathogens. *Ecology* 65: 1705–1705.

Augspurger CK, Kitajima K . (1992). Experimental studies of seedling recruitment from contrasting seed distributions. *Ecology* 73: 1270–1284.

Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, Chapman CA, Connor R, Di Fiore A, Dunbar RIM, Henzi PS, Holekamp K, Korstjens AH, Layton R, Lee P, Lehmann J, Manson JH, Ramos-Fernandez G, Strier KB, van Schaik CP .(2008). Fission–fusion dynamics: new research frameworks. *Current Anthropology* 49: 627–654.

Balcomb SR, Chapman CA .(2003). Bridging the gap: influence of seed deposition on seedling recruitment in a primate-tree interaction. *Ecological Monographs* 73: 625–642.

Beaune D, Bretagnolle F, Bollache L, Hohmann G, Surbeck M, Bourson CH, Fruth B .(2013). The Bonobo–*Dialium* positive interactions: seed dispersal mutualism. *American Journal of Primatology* 75: 394–403.

Boudreau S, Lawes MJ .(2008). Density- and distance-dependent seedling survival in a ballistically dispersed subtropical tree species *Philenoptera sutherlandii*. *Journal of Tropical Ecology* 24:1–8.

Bravo SP .(2012). The impact of seed dispersal by black and gold howler monkeys on forest regeneration. *Ecological Research* 27: 311–321.

Bravo SP, Zunino GE .(2000). Germination of three arboreal seeds dispersed by black howler monkeys (*Alouatta caraya*). *Folia Primatologica* 71: 342–345.

Bueno RS, Guevara R, Ribeiro MC, Culot L, Bufalo FS, Galetti M .(2013). Functional redundancy and complementarities of seed dispersal by the last neotropical megafrugivores. *PLoS ONE* 8(2): e56252. doi:10.1371/journal.pone.0056252.

Burkey TV .(1994). Tropical tree species diversity: a test of the Janzen-Connell model. *Oecologia* 97: 533–540.

Campos-Arceiz A, Blake S .(2011). Megagardeners of the forest e the role of elephants in seed dispersal. *Acta Oecologica* 37: 542–553.

Cant JGH .(1990). Feeding ecology of spider monkeys (*Ateles geoffroyi*) at Tikal, Guatemala. *Human Evolution* 5: 269–281.

Cestari C, Pizo MA .(2013). Seed dispersal by the lekforming whitebearded manakin (*Manacus manacus*, Pipridae) in the Brazilian Atlantic forest. *Journal of Tropical Ecology* 29: 385–389.

Chapman CA .(1987). Flexibility in diets of three species of Costa Rican primates. *Folia Primatologica* 49: 90–105.

Chapman CA .(1989a). Primate seed dispersal: the fate of dispersed seeds. *Biotropica* 21: 148–154.

Chapman CA .(1989b). Spider monkey sleeping sites: use and availability. *American Journal of Primatology* 18: 53–60.

Chapman CA .(1995). Primate seed dispersal: Coevolution and conservation implications. *Evolutionary Anthropology* 4: 74–82.

Chapman CA, Wrangham RW, Chapman LJ .(1995). Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology* 36: 59–70.

Chapman CA, Chapman LJ .(1996). Frugivory and the fate of dispersed and non-dispersed seeds in six African tree species. *Journal of Tropical Ecology* 12: 491–504.

Chapman CA, Onderdonk DA .(1998). Forests without primates: primate/plant codependency. *American Journal of Primatology* 45: 127–141.

Chapman CA, Russo SE .(2006). Primate seed dispersal: Linking behavioral ecology with forest community structure. In: Campbell CJ, Fuentes A, Mackinnon KC, Panger M, Bearder K (eds). Primates in perspective. Oxford University Press. Oxford. Pp. 510–525.

Charles-Dominique P .(1986). Inter-relations between frugivorous vertebrates and pioneer plants: *Cecropia,* birds and bats in French Guyana. In: Estrada A, Fleming TH (eds). Frugivores and seed dispersal. Dr. W. Junk Publishers, Dordrecht, The Netherlands. Pp. 119–135.

Chaves OM, Stoner KE, Arroyo-Rodríguez V, Estrada A .(2011). Effectiveness of spider monkeys (*Ateles geoffroyi vellerosus*) as seed dispersers in continuous and fragmented rain forests in southern Mexico. *International Journal of Primatology* 32: 177–192.

Chaves OM, Stoner KE, Arroyo-Rodriguez V .(2012). Differences in diet between spider monkey groups living in forest fragments and continuous forest in Lacandona, Mexico. *Biotropica* 44: 105–113.

Clark DA, Clark DB .(1984). Spacing dynamics of a tropical rain forest tree: elevation of the Janzen-Connell model. *The American Naturalist* 124: 769–789.

Clark CJ, Poulsen JR, Connor EE, Parker VT .(2004). Fruiting trees as dispersal foci in a semi-deciduous tropical forest. *Oecologia* 139: 66–75.

Clark CJ, Poulsen JR, Bolker BM, Connor EF, Parker VT .(2005). Comparative seed shadow of bird-, monkey-, and wind dispersed trees. *Ecology* 86: 2684–2694.

Condit R, Ashton PS, Baker PJ, Bunyavejchewin S, Gunatillek N, Hubbell SP, Foster RB, Itoh A, LaFrrankie JV, Hua Sen Lee L, Manokoran N, Sukumar R, Yamakura R .(2000). Spatial patterns in the distribution of tropical tree species. *Science* 288: 1414–1418.

Connell JH .(1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: den Boer PJ, Gradwell GR (eds). Dynamics of populations. Center for Agricultural Publication and Documentation, Wageningen. The Netherlands. Pp. 298–312.

Cordeiro NJ, Howe HF .(2003). Low recruitment of trees dispersed by animals in African forest fragments. *Conservation Biology* 15: 1733–1741

Corlett RT, Lucas PW .(1990). Alternative seed-handling strategies in primates: seed-spitting by long-tailed macaques (*Macaca fascicularis*). *Oecologia* 82: 166–171.

Crawley MJ .(2000). Seed predators and plant population dynamics. In: Fenner M (ed). Seeds: The ecology of regeneration in plant communities. CABI Publishing, Wallingford, U.K. Pp. 166–181.

Davies G .(1991). Seed-eating by red leaf monkeys (*Presbytis rubicunda*) in dipterocarp forest of northern Borneo. *International Journal of Primatology* 12: 119–144.

De Jong B, Ochoa-Gaona S, Castillo-Santiago MA, Ramírez-Marcial N, Cairos A .(2000). Carbon flux and patterns of land-use/land-cover change in the Selva Lacandona Mexico. *Ambio* 29: 504–511.

Dew JL .(2001). Synecology and seed dispersal in woolly monkeys (*Lagothrix lagotricha poeppigii*) and spider monkeys (*Ateles belzebuth belzebuth*) in Parque Nacional Yasuni, Ecuador. Tesis doctoral. University of California, Davis. E.U.A.

Dew JL .(2008). Spider monkeys as seed dispersers. In: Campbell CJ (ed). Spider monkeys. The biology, behavior and ecology of the genus *Ateles*.. Cambridge University Press, New York. Pp. 155–182.

Díaz Gallegos JR, Mas JF, Velázquez Montes A .(2008). Monitoreo de los patrones de deforestación en el Corredor Biológico Mesoamericano, México. *Interciencia* 12: 882–890.

Di Fiore A, Campbell CJ .(2007). The Atelines: Variation in ecology, behavior, and social organization. In: Campbell C, Fuentes A, Mackinnon KC, Panger M, Bearder S (eds). Primates in perspective, Oxford University Press, Oxford, U.K. Pp. 155–185.

Di Fiore A, Link A, Dew JL .(2008). Diets of wild spider monkeys. In: Campbell CJ (ed). Spider monkeys: behavior, ecology and evolution of the genus *Ateles*. Cambridge University Press. New York. Pp. 81–137.

Dinerstein E, Wemmer CM .(1988). Fruits rhinoceros eat–dispersal of *Trewia nudiflora*. *Ecology* 69: 1768–1774.

Estes JM, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, Essington TE, Holt RD, Jackson JBC, Marquis RJ, Oksanen L, Oksanen T, Paine RT, Pikitch EK, Ripple WJ, Sandin SA, Scheffer M, Schoener TW, Shurin JB, Sinclair ARE, Soulé ME, Virtanen R, Wardle DA .(2011). Trophic downgrading of planet earth. *Science* 333: 301–306.

Estrada A, Coates-Estrada R .(1984). Fruit eating and seed dispersal by howling monkeys (*Alouatta palliata*) in the tropical rain forest of Los Tuxtlas, Mexico. *American Journal of Primatology* 6: 77–91.

Estrada A, Coates-Estrada R .(1986). Frugivory in howling monkeys (*Alouatta palliata*) at Los Tuxtlas, Mexico: dispersal and fate of seeds. In: Estrada A, Fleming TH (eds). Frugivores and seed dispersers. Dr. W. Junk Publishers, Dordrecht. Pp. 94–104.

FAO .(2011). Situación de los bosques del mundo 2007. Food and Agriculture Organization Roma. 143 pp.

Fahrig L .(2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics* 34: 487–515.

Feeley K .(2005). The role of clumped defecation in the spatial distribution of soil nutrients and the availability of nutrients for plant uptake. *Journal of Tropical Ecology* 21: 99–102.

Fragoso JM, Silvius VKM, Correa LA .(2003). Long-distance seed dispersal by tapirs increases seed survival and aggregates tropical trees: Long-distance dispersal. *Ecology* 84: 1998–2006.

Galetti M, Dirzo R .(2013). Ecological and evolutionary consequences of living in a defaunated world. *Biological Conservation* 163: 1–6.

Garber PA .(1986). The ecology of seed dispersal in two species of callitrichid primates (*Saguinus mystax* and *Saguinus fuscicollis*). *American Journal of Primatology* 10: 155–170.

Gautier-Hion A .(1984). La dissemination des graines par les cercopithecides forestiers Africains. *Terre Vie* 39:159–165.

Gautier-Hion A, Duplantier JM, Quris R, Feer F, Sourd C, Decoux JP, Dubost G, Emmons L, Erard C, Hecketsweiler P, Moungazi A, Roussilhon C, Thiollay JM .(1985). Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65: 324–337.

Gentry AH .(1988). Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* 75: 1–34.

Gibbs AS, Rueschb F, Achardc MK, Claytond P, Holmgrene N, Ramankuttyf JA, Foleyg HK .(2010). Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proceedings of the National Academy of Sciences of the USA* 107: 16732–16737.

Gibson L, Lee T, Koh M, Brook LP, Gardner BW, Barlow TA, Peres CA, Bradshaw CJA, Laurance WF, Lovejoy TE .(2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478: 378–381.

González DiPierro AM, Benítez Malvido J, Méndez Toribio M, Zermeño I, Arroyo Rodríguez V, Stoner KE .(2011). Effects of the physical environmental primate gut passage on early establishment of *Ampelocera hottlei* Standley in rain forest fragments. *Biotropica* 43: 459–466.

González García F .(1993). Avifauna de la reserva de la biosfera “Montes Azules” selva Lacandona, Chipas, México. *Acta Zoologica Mexicana* 55: 1–86.

González Varo P, López Bao JV, Guitián J .(2012). Functional diversity among seed dispersal kernels generated by carnivorous mammals. *Journal of Animal Ecology* 82: 562–571.

González-Zamora A, Mandujano Rodríguez S .(2003). Uso de fragmentos por *Ateles geoffroyi* en el sureste de México. *Neotropical Primates* 11: 172-175.

González-Zamora A, Arroyo-Rodríguez V, Chavez O, Sánchez-López S, Stoner KE, Riba-Hernández P .(2009). Diet of spider monkeys (*Ateles geoffroyi*) in Mesoamerica: current knowledge and future directions. *American Journal of Primatology* 71: 8–20.

González-Zamora A, Arroyo-Rodríguez V, Chavez O, Sánchez-López S, Aureli F, Stoner KE .(2011). Influence of climatic variables, forest type, and condition on activity patterns of Geoffroyi's spider monkeys throughout Mesoamerica. *American Journal of Primatology* 73: 1189–1198.

Jansen PA, Bongers F, van der Meer PJ .(2008). Is farther seed dispersal better? Spatial patterns of offspring mortality in three rainforest tree species with different dispersal abilities. *Ecography* 31: 43–52.

Janson CH .(1983). Adaptation of fruit morphology to dispersal agents in a Neotropical forest. *Science* 219: 187–189.

Janzen DH .(1970). Herbivores and the number of tree species in tropical forests. *The American Naturalist* 104: 501–528.

Janzen DH, Miller GA, Hackforth-Jones J, Pond CM, Hooper K, Janos DP .(1976). Two Costa Rican bat-generated seed shadows of *Andira inermis* (Leguminosae). *Ecology* 57: 1068–1075

Jordano P, Godoy JA .(2002). Frugivore-mediated seed shadows: a landscape view of demographic and genetic effects. In: Levey DJ, Silva WR, Galetti M (eds). Seeds dispersal and frugivory. CABI Publishing, Wallingford, U.K.Pp. 305–321.

Julliot C .(1996). Seed dispersal by red howling monkeys (*Alouatta seniculus*) in the tropical rain forest of French Guiana. *International Journal of Primatology* 17: 239–258.

Harms KE, Wright SJ, Calderon O, Hernandez A, Herre EA .(2000). Pervasive density dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404: 493–495.

Heithaus ER .(1982). Coevolution between bats and plants. In: Kunz TH (ed). Ecology of bats. Plenum Press, New York. Pp. 327–367

Hoppes WG .(1988). Seedfall pattern of several species of bird-dispersed plants in an Illinois woodland. *Ecology* 69: 320–329.

Howe HF, vande Kerckhove GA .(1981). Removal of wild nutmeg *Virola surinamensis* crops by birds. *Ecology* 62: 1093–1106.

Howe HF, Smallwood J .(1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201–228.

Howe HF, Richter WM .(1982). Effects of seed size on seedling size in *Virola surinamensis*: a within and between tree analysis. *Oecologia* 53: 347–351.

Howe HF, Schupp EW, Westley LC .(1985). Early consequences of seed dispersal for a Neotropical tree (*Virola surinamensis). Ecology* 66: 781–791.

Howe HF .(1989). Scatter- and clump-dispersal and seedling demography: hypothesis and implications. *Oecologia* 79: 417–426.

Hubbell SP .(1980). Seed predation and the coexistence of tree species in tropical forests. *Oikos* 35: 214–229.

Kaplin BA, Moermond TC .(1998). Variation in seed handling by two species of forest monkeys in Rwanda. *American Journal of Primatology* 45: 83–101.

Kaplin BA, Lambert JE .(2002). Effectiveness of seed dispersal by *Cercopithecus* monkeys: implications for seed input into degraded areas. In: Levey DJ, Silva WR, Galetti M (eds). Seed dispersal and frugivory: ecology, evolution, and conservation. CABI Publishing, New York. Pp. 351–364.

Karubian J, Duraes R .(2009). Effects of seed disperser social behavior on patterns of seed movement deposition. *Oecologia Brasileira* 13: 45–57.

Kirika JM, Bleher B, Bohning-Gaese K, Chira R, Farwig N .(2008). Fragmentation and local disturbance of forests reduce frugivore diversity and fruit removal in *Ficus thonningii* trees. *Basic and Applied Ecology* 9: 663–672.

Lambert JE, Garber PA .(1998). Evolutionary and ecological implications of primate seed dispersal. *American Journal of Primatology* 45: 9–28.

Lambert JE .(1999). Seed handling in chimpanzees (*Pan troglodytes*) and redtail monkeys (*Cercopithecus ascanius*): implications for understanding hominoid and cercopithecine fruit-processing strategies and seed dispersal. *American Journal of Physical Anthropology* 109: 365–386.

Lambert JE .(2011). Primate seed dispersers as umbrella species: a case study from Kibale National Park, Uganda, with implications for Afrotropical forest conservation. *American Journal of Primatology* 73: 9–24.

Lazcano-Barrero AM, Gongora-Arones E, Vogt RC .(1992) Anfibios y reptiles en la selva Lacandona. In: Vásquez-Sánchez MA, Ramos MA (eds). Reserva de la Biosfera Montes Azules, Selva Lacandona: Investigación para su conservación. Ecosfera, Mexico City. Pp. 145–171.

Laurance WF, Delamonica P, Laurance SG, Vasconcelos HL, Lovejoy TE .(2000). Rainforest fragmentation kills big trees. *Nature* 404: 836.

Leighton M .(1993). Modeling dietary selectivity by Bornean orangutans: evidence for integration of multiple criteria in fruit selection. *International Journal of Primatology* 14: 257–313.

Levin SA, Muller-Landau HC, Nathan R, Chave J .(2003). The ecology and evolution of seed dispersal: a theoretical perspective. *Annual Review of Ecology, Evolution and Systematics* 34: 575–604.

Levey DJ .(1988). Tropical wet forest treefall gaps and distributions of understory birds and plants. *Ecology* 69: 1076–1089.

Link A, Stevenson PR .(2004). Fruit dispersal syndromes in animal disseminated plants at Tinigua National Park, Colombia. *Revista Chilena de Historia Natural* 77: 319–334.

Link A, Di Fiore A .(2006). Seed dispersal by spider monkeys and its importance in the maintenance of Neotropical rain-forest diversity. *Journal of Tropical Ecology* 22: 235–246.

Lira-Torres I, Galindo Leal C, Briones Salas M .(2012). Mamíferos de la Selva Zoque, México: riqueza, uso y conservación. *Revista de Biología Tropical* 60: 781–797.

Lucas PW, Corlett RT .(1998). Seed dispersal by long tailed macaques. *American Journal of Primatology* 45: 29–44.

Medellin RA .(1994). Mammal diversity and conservation in the Selva Lacandona, Chiapas, Mexico. *Conservation Biology* 8: 780–799.

Melo FPL, Rodriguez-Herrera B, Chazdon RL, Medellin RA, Ceballos GG .(2009). Small tent-roosting bats promote dispersal of large-seeded plants in a Neotropical Forest. *Biotropica* 41: 737–743.

Melo FPL, Arroyo Rodríguez V, Fahrig L, Martínez Ramos M, Tabarelli M. (2013). On the hope for biodiversity-friendly tropical landscapes. *Trends in Ecology and Evolution* 1649: 1–7.

Mendoza E, Dirzo R .(1999). Deforestation in Lacandonia (southeast Mexico): evidence for the declaration of the northernmost tropical hot-spot. *Biodiversity and Conservation* 8: 1621–1641.

McConkey KR .(2000). Primary seed shadow generated by gibbons in the rain forests of Barito Ulu, central Borneo. *American Journal of Primatolology* 52: 13–29.

Milton K .(1981). Food choice and digestive strategies of two sympatric primate species. *American Naturalist* 117: 476–495.

Morris RJ .(2010). Anthropogenic impacts on tropical forest biodiversity: a network structure and ecosystem functioning perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 3709–3718.

Morrison, D. W .(1978). Foraging ecology and energetics of the frugivorous bat *Artibeus jamaicensis. Ecology* 59: 716–723.

Muñoz Lazo FJ, Culot L, Huynen MC, Hymann EW .(2011). Effect of resting patterns of tamarins (*Saguinus fuscicollis* and *Saguinus mystax*) on the spatial distribution of seeds and seedling recruitment. *International Journal of Primatology* 32: 223–237.

Myers N .(1993). Tropical forests: the main deforestation fronts. *Environmental Conservation* 20: 9–16.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GA, Kent J .(2000). Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.

Nathan R, Muller-Landau HC .(2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* 15: 278–285.

Neves DSN, Feer F, Samlo S, Chateil C, Ponge JF .(2010). The impact of red howler monkeys latrines on the distribution of main nutrients and on topsoil profiles in a tropical rain forest. *Austral Ecology* 35: 549–559.

Nunes A .(1998). Diet and feeding ecology of *Ateles belzebuth* at Maracá ecological station, Roraima, Brasil. *Folia Primatologica* 69: 61–76.

Orians GH, Pearson NE .(1979). On the theory of central place foraging. In: Horn DJ, Mitchell RD, Stairs GR (eds). Analysis of ecological system. Ohio: Ohio University Press. Pp.155–177.

Peres CA .(1994). Diet and feeding ecology of gray woolly monkeys (*Lagothrix lagothrica cana*) in central Amazonia: comparison with other Atelines. *International Journal of Primatology* 15: 333–372.

Peres CA, Dolman PM .(2000). Density compensation in neotropical primate communities: evidence from 56 hunted and nonhunted Amazonian forests of varying productivity. *Oecologia* 122: 175–189.

Peres CA, van Roosmalen M .(2002). Primate frugivory in two species-rich Neotropical forests: implications for the demography of large-seeded plants in overhunted areas. In: Levey DJ, Silva WR, Galetti M (eds). Seed dispersal and frugivory: ecology, evolution and conservation. CABI Publishing, New York. Pp. 407–421.

Peres CA, Palacios E .(2007). Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: implications for animal-mediated seed dispersal. *Biotropica* 39: 304–315.

Pouvelle S, Jouard S, Feer F, Tully T, Ponge JF .(2009). The latrine effect: Impact of howler monkeys on the distribution of small seeds in a tropical rain-forest soil. *Journal of Tropical Ecology* 25: 239–248.

Ramos-Fernández G, Smith Aguilar SE, Schaffner CM, Vick LG, Aureli F .(2013). Site fidelity in space use by spider monkeys (*Ateles geoffroyi*) in the Yucatan Peninsula, Mexico. *PLoS ONE* 8: e62813. doi:10.1371/journal.pone.0062813.

Revilla E, Palomares F .(2002). Spatial organization, group living and ecological correlates in low-density populations of Eurasian badgers, *Meles meles*. *Journal of Animal Ecology* 71: 497–512.

Robertson AW, Trass A, Ladley JJ, Kelly D .(2006). Assessing the benefits of frugivory for seed germination: The importance of the deinhibition effect. *Functional Ecology* 20: 58–66.

Rogers ME, Voysey BC, McDonald KE, Parnell RJ, Tutin CEG .(1998). Lowland gorillas and seed dispersal: The importance of nest sites. *American Journal of Primatology* 45: 45–68.

Rowell TE, Mitchell BJ .(1991). Comparison of seed dispersal by guenons in Kenya and capuchins in Panama. *Journal of Tropical Ecology* 7: 269–274.

Russo SE .(2003). Responses of dispersal agents to tree and fruit traits in *Virola calophylla* (Myristicaceae): implications for selection. *Oecologia* 136: 80–87.

Russo SE, Augspurger CK .(2004). Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. *Ecology Letters* 7: 1058–1067.

Russo SE, Chapman CA .(2006). Primate seed dispersal: Linking behavioral ecology with forest community structure. In: Campbell CJ, Fuentes AF, MacKinnon KC, Panger M, Bearders S (eds). Primates in Perspective. Oxford University Press, Oxford. Pp. 523–534.

Russo SE, Campbell CJ, Dew L, Stevenson PR, Suarez SA .(2005). A multi-forest comparison of dietary preferences and seed dispersal by *Ateles* spp. *International Journal of Primatology* 26: 1017–1037.

Rylands AB, Groves CP, Mittermeier RA, Cortéz-Ortíz L, Hines JJ .(2006). Taxonomy and distributions of Mesoamerican primates. In: Estrada A, Garber PA, Pavelka M, Luecke L (eds). New perspectives in the study of Mesoamerican primates: distribution, ecology, behaviour, and conservation. New York: Kluwer Academic/Plenum Publishers. Pp. 29–79.

Sader SA, Stone TA, Joyce AT .(1990). Remote sensing of tropical forest: an overview of research and implications using non-photographic sensors. *Photogrammetric Engineering and Remote Sensing 55*: 1343–1351.

Schupp EW .(1993). Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* 107/108: 15–29.

Schupp EW, Milleron T, Russo SE .(2002). Dissemination limitation and the origin and maintenance of species-rich tropical forests. In: Levey DJ, Silva WR, Galetti M (eds). Seed dispersal and frugivory: ecology, evolution and conservation. CABI Publishing, New York. Pp. 19–33.

Schupp EW, Jordano P, Gómez JM .(2010). Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist* 188: 333–353.

Shimooka Y, Campbell CJ , DiFiore A, Felton AMF, Izawa K, Link A, Nishimura A, Ramos-Fernández G, Wallace RB .(2008). Demography and group composition of *Ateles*. In: Campbell CJ (ed). Spider monkeys: behavior, ecology and evolution of the genus *Ateles*. Cambridge University Press, Cambridge, U.K. Pp. 329–348.

Silva JMC, Tabarelli M .(2000). Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. *Nature* 404: 72–73.

Stevenson PR .(2000). Seed dispersal by woolly monkeys (*Lagothrix lagothricha*) at Tinigua National Park, Colombia: dispersal distance, germination rates, and dispersal quantity. *American Journal of Primatology* 50: 275–289.

Stevenson PR, Pineda M, Samper T .(2005). Influence of seed size on dispersal patterns of woolly monkeys (*Lagothrix lagothricha*) at Tinigua Park, Colombia. *Oikos* 110: 435–440.

Stevenson PR, Aldana A .(2008). Potential effects of Ateline extinction and forest fragmentation on plant diversity. *International Journal of primatology* 29: 365–377.

Stiles EW .(2000). Animals as seed dispersers. In: Fenner M (ed). Seeds: The ecology of regeneration in plant communities. CABI Publishing, Wallingford, U.K. Pp. 111–124.

Stoner KE, Riba-Hernández P, Vulinec K, Lambert JE .(2007). The role of mammals in creating and modifying seeds hadows in tropical forests and some possible consequences of their elimination. *Biotropica* 39: 316–327.

Suarez SA .(2006). Diet and travel costs for spider monkeys in a nonseasonal, hyperdiverse environment. *International Journal of Primatology* 27: 411–436.

Terborgh JG, Nunez-Iturri NC, Pitman A, Valverde FHC, Alvarez P, Swamy V, Pringle EG, Paine CET .(2008). Tree recruitment in an empty forest. *Ecology* 89: 1757–1768.

Traveset A, Robertson AW, Rodríguez-Pérez J .(2007). A review on the role of endozoochory in seed germination. In: Dennis AJ, Schupp EW, Green RJ, Westcott DA (eds). Seed dispersal. Theory and its application in a changing world. CABI Publishing, Wallingford, U.K. Pp. 78–103.

van der Pijl L .(1982). *Principles of dispersal in higher plants*. Springer, Berlin.

van Roosmalen MGM .(1985). Habitat preferences, diet, feeding strategy and social organization of the black spider monkey (*Ateles paniscus paniscus* Linnaeus 1758) in Surinam. *Acta amazonica* 15: 1–238.

Vidal M, Pires MM, Guimarães PR .(2013). Large vertebrates as the missing components of seed-dispersal networks. *Biological Conservation* 163: 42–48.

Voysey BC, McDonald KE, Rogers ME, Tutin CEG, Parnell RJ .(1999a). Gorillas and seed dispersal in the Lope Reserve, Gabon. I: Gorilla acquisition by trees. *Journal of Tropical Ecology* 15: 23–38.

Voysey BC, McDonald KE, Rogers ME, Tutin CEG, Parnell, RJ .(1999b). Gorillas and seed dispersal in the Lope Reserve, Gabon. II: Survival and growth of seedlings. *Journal of Tropical Ecology* 15: 39–60.

Wallace RB .(2008). Factors influencing spider monkey habitat use and ranging patterns. In: Campbell CJ (ed). Spider monkeys. The biology, behavior and ecology of the genus *Ateles*. Cambridge University Press, New York, Pp. 38–154.

Wang BC, Smith TB .(2002). Closing the seed dispersal loop. *Trends in Ecology and Evolution* 17: 379–385.

Webb CO, Peart DR .(2000). Habitat associations of trees and seedlings in a Bornean rain forest. *Journal of Ecology* 88: 464–478.

Wenny DG .(2001). Advantages of seed dispersal: A re-evaluation of directed dispersal. *Evolutionary Ecology Research* 3: 51–74.

Wenny DG, Levey DJ .(1998). Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Sciences of the USA* 95: 6204–6207.

White F .(1983). The vegetation of Africa. UNESCO, Paris.

Willson M, Traveset A .(2000). The ecology of seed dispersal. The ecology of regeneration in plant communities. Fenner M (ed). CABI Publishing, Wallingford, U.K. Pp. 85–110

Wrangham RW, Chapman CA, Chapman LJ .(1994). Seed dispersal by forest chimpanzees in Uganda. *Journal of Tropical Ecology* 10: 355–368.

Wronski T, Plath M .(2010). Characterization of the spatial distribution of latrines in reintroduced mountain gazelles: do latrines demarcate female group home ranges?. *Journal of Zoology* 280: 92–101.

Yumoto T, Kimura K, Nishimura A .(1999). Estimation of the retention times and distances of seed dispersed by two monkey species, *Alouatta seniculus* and *Lagothrix lagothricha*, in a Colombian forest. *Ecological Research* 14: 179–191.

Zhang SY, Wang LX .(1995). Fruit consumption and seed dispersal of *Ziziphus cinnamomum* (Rhamnaceae) by two sympatric primates (*Cebus apella* and *Ateles paniscus*) in French Guiana. *Biotropica* 27: 397–401.

CAPÍTULO III:

SLEEPING SITES AND LATRINES OF SPIDER MONKEYS IN CONTINUOUS AND FRAGMENTED RAINFORESTS: IMPLICATIONS FOR SEED DISPERSAL AND FOREST REGENERATION

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Sleeping Sites and Latrines of Spider Monkeys in Continuous and Fragmented Rainforests: Implications for Seed Dispersal and Forest Regeneration

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Abstract

Spider monkeys (*Ateles geoffroyi*) use sites composed of one or more trees for sleeping (sleeping sites and sleeping trees, respectively). Beneath these sites/trees they deposit copious amounts of dung in latrines. This behavior results in a clumped deposition pattern of seeds and nutrients that directly impacts the regeneration of tropical forests. Therefore, information on the density and spatial distribution of sleeping sites and latrines, and the characteristics (i.e., composition and structure) of sleeping trees are needed to improve our understanding of the ecological significance of spider monkeys in influencing forest composition. Moreover, since primate populations are increasingly forced to inhabit fragmented landscapes, it is important to assess if these characteristics differ between continuous and fragmented forests. We assessed this novel information from eight independent spider monkey communities in the Lacandona rainforest, Mexico: four continuous forest sites and four forest fragments. Both the density of sleeping sites and latrines did not differ between forest conditions. Latrines were uniformly distributed across sleeping sites, but the spatial distribution of sleeping sites within the areas was highly variable, being particularly clumped in forest fragments. In fact, the average inter-latrine distances were almost double in continuous forest than in fragments. Latrines were located beneath only a few tree species, and these trees were larger in diameter in continuous than fragmented forests. Because latrines may represent hotspots of seedling recruitment, our results have important ecological and conservation implications. The variation in the spatial distribution of sleeping sites across the forest indicates that spider monkeys likely create a complex seed deposition pattern in space and time. However, the use of a very few tree species for sleeping could contribute to the establishment of specific vegetation associations typical of the southeastern Mexican rainforest, such as *Terminalia-Dialium*, and *Brosimum-Dialium*.

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Introduction

There is ample evidence that several mammal species defecate in latrines [1]. This behavior is often related to olfactory communication among individuals or groups as part of their reproduction, territory marking, and resource defense [2,3]. This is evident in several carnivore [4,5] and primate species [2,6,7]. Nevertheless, in some cases latrines are simply the result of animal social behaviors leading to aggregation (e.g., lek formation, repeated perch use, and sleeping sites [8,9,10]). Regardless of the function that latrines serve for animals, it is increasingly recognized that latrines may have critical ecological consequences, especially those of frugivorous species, as latrines result in a clumped deposition pattern of seeds for many species (e.g., primates, *Alouatta seniculus:*[6]; *Lagothrix lagothricha and A. seniculus:*[11]; *Alouatta caraya:*[12]; rhinoceros, *Rhinocerus unicornis:*[13]*;* badgers, *Meles meles:*[14]*;* tapirs, *Tapirus terrestris:*[15]*;* elephants, *Loxodonta africana and Elephas maximus*: [16]) and are accompanied by a large amount of dung and nutrients [17,18,19]. Therefore, as a form of spatially contagious seed dispersal (*sensu* [20]), latrines may affect the recruitment, spatial distribution, abundance, and regenerative potential of plant populations, directly impacting vegetation dynamics [7,20,21,22].

The impact of latrines on plant assemblages may be particularly relevant in highly frugivorous mammals, such as spider monkeys (*Ateles* spp.) [23,24,25,26]. These Neotropical primates live in social systems with a high degree of fission–fusion dynamics, adjusting their subgroup size to local food availability [27]. Individuals forage in different subgroups during the day, whereas they regularly form larger subgroups in the evening congregating in sites (sleeping sites, hereafter) composed of one or several closely spaced large trees to sleep (sleeping trees, hereafter) located near available food resources [7,28,29]. These sleeping sites can vary in size depending on the number of monkeys using them on a particular day [7,28]. Thus spider monkey ranging behavior results in a mixed seed deposition pattern, with a fraction of seeds deposited during the day in individual scats distributed across the forest and the remaining seeds deposited at night or early morning in one or more latrines beneath sleeping sites [7,28]. This mixed seed deposition pattern has important implications for seed dispersal and seedling recruitment, as both deposition patterns may result in different areas of seedling recruitment [7,22].

Despite the potential importance of latrines of spider monkeys for forest regeneration, to our knowledge no study has assessed the density and spatial distribution of latrines or sleeping sites, nor the composition, preferences, or the characteristics of sleeping trees. Furthermore, because of the serious conservation threat to spider monkeys, they are increasingly forced to inhabit fragmented forests [25,30], where both the availability of food resources and large trees are scarce [31,32]. Thus, it is necessary to evaluate if the characteristics of sleeping trees and the density and spatial distribution of both sleeping sites and latrines differ between continuous and fragmented forests as this may contribute to the altered tree community dynamics of forest fragments. Overall, this information may have critical ecological and conservation implications for understanding the dynamics of tropical forests [22].

In this paper, we present novel information on the density and spatial distribution of sleeping sites and latrines of spider monkey in continuous and fragmented tropical rainforest in Lacandona, Mexico. We describe the arboreal composition, preferences, and structure of principal sleeping trees used by this species, and assess if these characteristics differ between forest conditions. Because of a lower availability of large trees and a limited home range size in forest fragments [31,32,33], we predicted a lower density of sleeping sites and latrines in forest fragments than in continuous forests. Additionally, the spatial distribution of sleeping sites and latrines will be highly variable, depending on the distribution of fruits in space and time [8]. Finally, since the lower availability of fruits in fragments can 'force' spider monkeys to spend more time consuming leaves [25,34,35] that are more widely available throughout the forest than fruit, we predicted that the inter-latrine distances will be lower in fragments than in continuous forest. Moreover, in forest fragments spider monkeys will use smaller sleeping trees (i.e., with lower diameter at breast height, DBH) from fewer tree species than in continuous forest.

Materials and Methods

Ethics Statement

All necessary permits were obtained for the described field studies. This study was also approved by the Mexican Office for the Environment and Natural Resources (SEMARNAT), the Office for the Biological Reserve of Montes Azules (BRMA), and the Consejo Nacional de Ciencia y Tecnología (CONACYT) from Mexico (Projects CB-2005-51043 and CB-2006-56799). Moreover, we conducted this study with the authorization of the owner of forest fragments of the Reforma and Zamora Pico de Oro communities. Since our research involved an observational field study and did not involve any contact with the animals, we met all ethical and legal requirements established by the American Society of Primatologists (ASP), Animal Care and Use Committee, and Ethical Committee of the Zoological Society of London for work on primates.

Study Area

The Mexican Lacandona rainforest constitutes the southwestern sector of the Maya forest in Mexico, and it is one of the most important rainforest remnants in Mesoamerica [36]. The area is located in the northeastern portion of the state of Chiapas, and is delimited by the Guatemalan border on the south and east, and by the Chiapas Highlands on the north and west. The predominant climate in the region is warm and humid with abundant summer rainfall [37]. Average monthly temperatures range from 24°C to 26°C, and mean annual rainfall is 2500–3500 mm, with roughly 80% of the rains falling between June and November. The area was originally covered by over one million ha of rainforest, of which about half remain today [38,39].

We worked in two adjacent areas separated by the Lacantún River (>150 m wide): the Marqués de Comillas region (MCR, eastern side of the river) encompassing ca. 176,200 ha of fragmented forest, human settlements, and agricultural lands [40], and the Montes Azules Biosphere Reserve (MABR, western side) comprising ca. 331,000 ha of undisturbed old-growth forest [41]. The original predominant vegetation type is tropical rainforest [42], but human colonization and deforestation of MCR since the 1960s resulted in the rapid disappearance and fragmentation of the forest [40]. Approximately 50% of the land surface of MCR is now used for cattle ranching and agriculture, but several forest fragments (0.5–1500 ha) remain.

We assessed latrines and sleeping sites used by eight independent spider monkey communities: four sites in continuous forest of the MABR separated by at least 5 km, and four sites in different forest fragments (ranging from 17 to 1125 ha) within the MCR (Table 1). We chose these sites because previous studies had been conducted here and we had information on the home ranges of each community (previously identified in a 16-month study [32,34,35]). All fragments in MCR were isolated ≥24 yrs ago, are immersed in an anthropogenic matrices (pastures, cocoa plantations, agricultural lands, and rural settlements), and their distances to continuous forest ranged from 200 to 1200 m. The isolation distance among fragments ranged from 50 m to 450 m. Spider monkey communities ranged from 25 to 44 individuals, and their home ranges varied from 32 to 90 ha [32,34,35].

Data Collection

We recorded all sleeping sites, the principal sleeping trees, and latrines located in a continuous 30-ha area of each community's home range, which totaled 240 ha of sampling area across the eight communities. We performed two surveys in all sites, one during March 2010 (i.e., dry season, with lower availability of fruit sources), and another during August and September 2010 (i.e., rainy season, with higher availability of fruit sources). In each survey, two people (i.e., the first author and an experienced local field assistant) walked slowly and in parallel (separated approximately 5 m) through the entire area looking for latrines. When a tree with a DBH ≥30 cm was located in the trek, we made a careful search in the ground taking into account the surface of tree crown. Depending on weather and terrain conditions, we spent between 2 and 4 days per site.

In general, latrines were easily identified in the field due to their characteristic odor and appearance, which are notably different from those of the feces of the black howler monkeys (*Alouatta pigra*) the other primate species present in the region. In the study area, the latrines are usually located below one of the main lateral branches of a sleeping tree near the crown edge (Figure 1a). They are on the ground and have a semicircular shape, ranging between 1 and 3 m of diameter (Figure 1b). They can be covered by a carpet of new and old multispecies seeds, seedlings, litter, and fresh

Table 1. Sites studied in the Lacandona rainforest, Mexico.

Sites	Area (ha)	Coordinates	DNF	DCF	YSF	CS
Continuous forest						
CF1	331,000	16°06′25.01″N 90°59′16.61″O	n/a	n/a	n/a	44
CF2	331,000	16°06′08.62′′N 90°58′05.29′′O	n/a	n/a	n/a	–
CF3	331,000	16°06′50.25′′N 90°56′24.46′′O	n/a	n/a	n/a	36
CF4	331,000	16°09′31.84′′N 90°54′17.56′′O	n/a	n/a	n/a	44
Forest fragments						
FF1	1,125	16°15′10.83′′N 90°49′53.82′′O	100	1100	27	41
FF2	33	16°16′54.15′′N 90°50′19.91′′O	100	3150	25	25
FF3	30	16°19′54.85′′N 90°51′10.71′′O	450	200	29	35
FF4	35	16°10′51.61′′N 90°52′26.50′′O	50	470	25	20

[a] DNF = distance to nearest forest fragments; DCF = distance to continuous forest; YSF = years since fragmentation; CS = community size of spider monkeys. (n/a) not applicable; (–) unavailable data.

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and old feces (Figures 1c-f). Latrines are also easily recognized by the presence of spots of feces on the leaves of vegetation that are surrounded and superimposed over the latrine (Figure 1e).

After locating a latrine, we positioned in its center (i.e., with higher amount of feces and seeds) and looked perpendicularly for the lateral branch in the canopy that could be used by spider monkeys to sleep and defecate. We recorded the tree species used (sleeping tree), its DBH, and location (with GPS). In the few cases that more than one branch was above the latrine's location, we assumed that the principal sleeping tree was the one with a branch above the latrine that, through their particular structure (e.g., large and horizontal tree branch bifurcations), could accommodate the individuals to defecate. This assumption was based on qualitative comparisons with the cases in which we only observed one large lateral branch above the latrines (Figure 1a). Although, it is possible that a few individuals slept in other neighboring sleeping trees, they did not form distinct latrines detectable during the field search. This can be possible if the number of individuals was very low and/or if the neighboring sleeping trees were smaller, and hence, the subgroups sleeping in them were smaller than the subgroups sleeping in the tree we recorded.

We also determined the inter-latrine distances with ArcGIS 9.0. This measure was used to identify different sleeping sites. Based on Russo & Augspurger [29], the average (± SD) size of a sleeping site is 89.3 ± 37.4 m^2. Therefore, we considered all latrines located at ≤ 10 m among each other as belonging to the same sleeping site. We are confident that this method was accurate in identifying different sleeping sites, as excluding these latrines, the average (± SD) inter-latrine distance was 425 ± 370 m, indicating that they most probably belonged to different sleeping sites [29]. After identifying each sleeping site, we calculated the number of sleeping trees and latrines within each sleeping site.

To estimate preferences of monkeys for certain sleeping trees, we also evaluated the density of trees with DBH ≥ 30 cm in ten 100×2-m plots (0.2 ha) randomly located within each 30-ha sampled area. This vegetation sampling was only performed in the sites with a higher density of sleeping sites and latrines (Figure 2).

Data Analysis

To test for differences in the density of latrines, species richness, and DBH of sleeping trees, and inter-latrine distances between continuous forest and forest fragments we used analyses of deviance (ANODE) with generalized linear models (GLM). As suggested for count dependent variables (i.e., richness of sleeping tree species), we used a Poisson error and a log link function [43]. However, the differences in density of latrines, DBH of sleeping trees, and inter-latrine distances between both forests conditions were analyzed by used a Normal error and an identity link function, after verifying that the errors of these dependent variables fit normal distributions (Shapiro-Wilk test).

To evaluate the spatial distribution of sleeping sites (i.e., uniform, clumped, or random) within the sampling areas, we plotted in x and y axes the UTM coordinates of each sleeping site. We divided the 30 ha of sampling area in 1-ha plots and counted the number of sleeping sites that fell within each 1-ha plot. Then, we assessed the distribution pattern of sleeping sites with the Morisita index of dispersion (I_d) [44] using the following formula:

$$I_d = n\left(\frac{\sum_{i=1}^{n} x_i^2 - \sum_{i=1}^{n} x_i}{\left(\sum_{i=1}^{n} x_i\right)^2 - \sum_{i=1}^{n} x_i}\right)$$

where n is the total number of plots in the sample, and x_i is the number of sleeping sites in the i-th plot. The value of the index $I_d = 1.0$ for randomly distributed sleeping sites, >1.0 for clumped sleeping sites and <1.0 for uniformly distributed sleeping sites, ranging from zero to the total number of plots. This index has the advantages of being relatively independent of plot size, density, and sample size [45]. The statistical significance of the departure of each I_d from 1.0 was tested with the statistic χ^2 ($\mathrm{df} = Q - 1) = (Q-1)s^2/\bar{x}$ [46], where Q in the number of plots in the sample and s^2 and $\bar{x}$ are the variance and mean of the number of latrines per plot in the sample, respectively. As the degree of clumping in nature is frequently strongly influenced by the spatial scale considered [47], we also calculated I_d and the significance of its departure from 1.0 for the whole region, i.e., considering each sampling area as a large plot (n = 8 plots). Thus, we evaluated the spatial distribution of the abundance of sleeping sites across sampling areas.

To analyze the degree to which spider monkeys are selective in their choice of sleeping trees, we used the Manly's standardized index. This index is based on the selection ratio w_i, which is the proportional use divided by the proportional availability of each resource: $w_i = o_i/\pi_i$; where: o_i is the proportion of the sample of used resource units in category i, and π_i is the proportion of available resource units in category i. Because sampling efforts for "use" versus "availability" were different (30 ha and 0.2 ha, respectively), we calculated the proportional use of each sleeping tree and its proportional availability considering the density of trees per hectare; i.e., number of trees used/30 ha, and number of trees available/0.2 ha. A w_i value larger than 1 indicates a positive selection for the resource (i.e., sleeping trees in our case), and a value less than 1 indicates avoidance of the resource. A value around 1 indicates that the resource was used proportionally to its availability and no selection was noted. The preference/avoidance of each tree species was calculated from the selection ratio w_i, and

Figure 1. Lateral branches of a *Dialium guianense* sleeping tree (a), and different characteristics of latrines of spider monkeys (*Ateles geoffroyi*) in the Lacandona rainforest, Mexico: form of latrine (b), carpet of seedlings (c), seeds and fresh dung (d), spots of feces on the leaves of understory palms (e), and seeds and seedlings (f).
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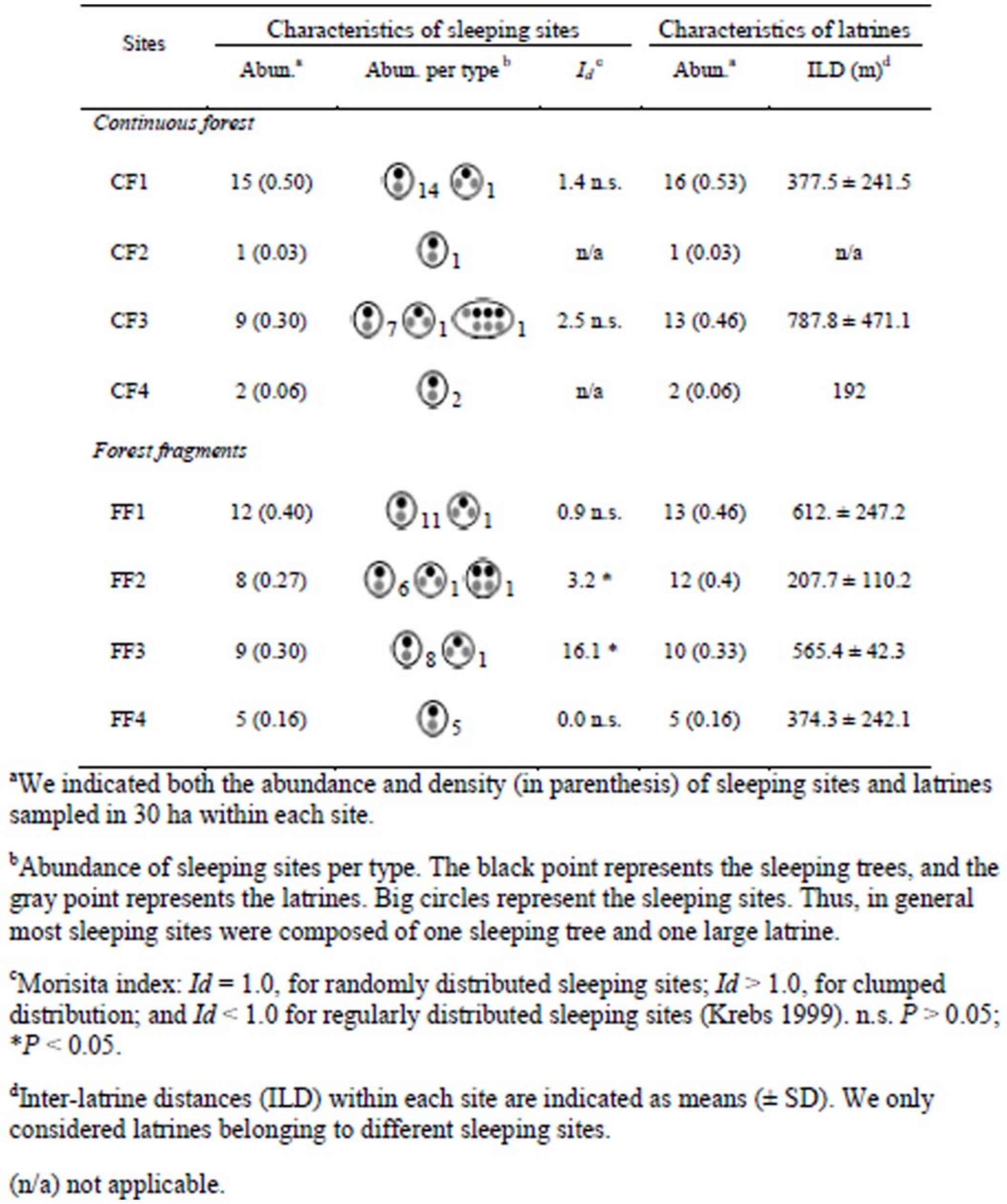

Sites	Characteristics of sleeping sites			Characteristics of latrines	
	Abun.[a]	Abun. per type[b]	I_d[c]	Abun.[a]	ILD (m)[d]
Continuous forest					
CF1	15 (0.50)	◉$_{14}$ ◉$_{1}$	1.4 n.s.	16 (0.53)	377.5 ± 241.5
CF2	1 (0.03)	◉$_{1}$	n/a	1 (0.03)	n/a
CF3	9 (0.30)	◉$_{7}$ ◉$_{1}$ ◉$_{1}$	2.5 n.s.	13 (0.46)	787.8 ± 471.1
CF4	2 (0.06)	◉$_{2}$	n/a	2 (0.06)	192
Forest fragments					
FF1	12 (0.40)	◉$_{11}$ ◉$_{1}$	0.9 n.s.	13 (0.46)	612. ± 247.2
FF2	8 (0.27)	◉$_{6}$ ◉$_{1}$ ◉$_{1}$	3.2 *	12 (0.4)	207.7 ± 110.2
FF3	9 (0.30)	◉$_{8}$ ◉$_{1}$	16.1 *	10 (0.33)	565.4 ± 42.3
FF4	5 (0.16)	◉$_{5}$	0.0 n.s.	5 (0.16)	374.3 ± 242.1

[a] We indicated both the abundance and density (in parenthesis) of sleeping sites and latrines sampled in 30 ha within each site.

[b] Abundance of sleeping sites per type. The black point represents the sleeping trees, and the gray point represents the latrines. Big circles represent the sleeping sites. Thus, in general most sleeping sites were composed of one sleeping tree and one large latrine.

[c] Morisita index: *Id* = 1.0, for randomly distributed sleeping sites; *Id* > 1.0, for clumped distribution; and *Id* < 1.0 for regularly distributed sleeping sites (Krebs 1999). n.s. $P > 0.05$; $^{*}P < 0.05$.

[d] Inter-latrine distances (ILD) within each site are indicated as means (± SD). We only considered latrines belonging to different sleeping sites.

(n/a) not applicable.

Figure 2. Sleeping sites and latrines of spider monkeys (*Ateles geoffroyi*) in four continuous forest sites and four forest fragments in the Lacandona rainforest, Mexico.

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the statistical significance was assessed with a chi-square test [48]. With this test we compared the observed number of sleeping trees used per species with the expected number under the hypothesis of no selection (i.e., considering that the tree species *i* was used proportionally to its availability) [48]. Additionally, to evaluate if spider monkeys selected larger trees to sleep, for each tree species, we tested for differences in the average DBH of sleeping trees versus the average DBH of the trees available within the home range using Student's t-tests. In those cases in which we compared a single observation with the mean of a sample, we used the Student's t-test [49]: $t\ (\mathrm{df} = n - 1) = y - \overline{x}/SD * \sqrt{((n+1)/n)}$; where y is the single tree DBH, $\overline{x}$ and SD are the mean and standard deviation of the trees' DBH in the sample, respectively and n is the number of trees in the sample.

Results

Density and Spatial Distribution of Latrines and Sleeping Sites

Overall we found 72 latrines in 61 sleeping sites (Figure 2). Considering the total sampled area (240 ha), the density of latrines and sleeping sites were 0.3 latrines/ha and 0.25 sleeping sites/ha, respectively. The density of latrines did not differ between the continuous forest (0.27 latrines/ha, n = 32 latrines) and forest fragments (0.33 latrines/ha, n = 40 latrines) (GLM, $\chi^2 = 0.28$, df = 1, $P = 0.59$), nor did the density of sleeping sites differ between the continuous forest (0.23 sleeping trees/ha) and forest fragments (0.28 sleeping trees/ha) ($\chi^2 = 0.32$, df = 1, $P = 0.57$) (Figure 2).

In general, latrines were uniformly distributed across sleeping sites, as most sleeping sites (89%) had only one latrine beneath one single sleeping tree (Figure 2). Five sleeping sites (8%) had two latrines beneath one single sleeping tree, and these sleeping sites were located in both continuous and fragmented sites. We only found one large sleeping site within the continuous forest with three different sleeping trees and four latrines, and one sleeping site within a forest fragment composed of two different sleeping trees and two latrines (one latrine per sleeping tree) (Figure 2).

The spatial distribution of sleeping sites within the 30-ha sampled areas was highly variable, being significantly clumped only in two forest fragments, particularly in the smallest one ($Id = 16.1$; $\chi^2 = 134.5$, df = 29, $P < 0.0001$; Figure 2). At a regional scale, sleeping sites showed a clumped distribution ($Id = 1.23$; $\chi^2 = 20.97$, df = 7, $P = 0.004$), indicating that sleeping sites are particularly abundant in some fragments and areas within the continuous forest, but very scarce in others (Figures 2, 3). Interestingly, the average distance among latrines was almost double in continuous forest (mean ± SD, 585.0±286.7 m) compared to the fragments (296.7±283.6 m), but the difference was not significant ($\chi^2 = 1.86$, df = 1, $P = 0.17$; Figure 2).

Tree Species used as Sleeping Sites

The 64 sleeping trees belonged to 9 species, 9 genera, and 9 families (Table 2). There were no significant differences in species richness of sleeping trees between continuous (5 species from 5 families) and fragmented (8 species from 8 families) forests ($\chi^2 = 0.04$, df = 1, $P = 0.85$). However, the DBH of sleeping trees was two times greater in continuous forest (62.39±36.70 cm) as compared to the forest fragments (35.17±20.75 cm) ($\chi^2 = 14.35$, df = 1, $P < 0.0001$).

Most (66%) of the sleeping trees were from *Dialium guianense* (Caesalpinaceae) and *Brosimum alicastrum* (Moraceae). Based on the w_i index, spider monkeys seem to select different species of sleeping trees in different sites (*B. alicastrum* in CF1 and FF1, *D. guianense* in CF3 and FF2, and *Guarea glabra* in FF3; $w_i > 1.5$ in all cases; Table 2). However, the chi-square tests were not significant ($P > 0.50$, in all cases), suggesting that these species were used proportionally to its availability. Similarly, testing for differences in the DBH of trees used versus available within the home range, in most cases we did not detected significant differences in DBH (Table 2), indicating that spider monkeys did not select larger trees.

Discussion

During the last decades, researchers have increasingly recognized that latrines of primates have important implications for seed dispersal and seedling recruitment [22]. However, the lack of information on the density and spatial distribution of sleeping sites and latrines and the characteristics of sleeping trees have hampered the understanding of their ecological significance. We demonstrate that in the Lacandona rainforest, Mexico: (i) both the density of sleeping sites and latrines did not differ between continuous forest and forest fragments; (ii) latrines were uniformly distributed across sleeping sites, but the spatial distribution of sleeping sites within the study areas was highly variable, being particularly clumped in forest fragments; (iii) latrines were located beneath only a few sleeping tree species; and (iv) sleeping trees were larger in continuous than fragmented forests.

Density and Distribution of Sleeping Sites and Latrines

The density of sleeping sites and latrines averaged 0.25 sleeping sites and 0.30 latrines per ha, respectively but varied greatly among sites. This large variation may be related to differences in the distribution of food resources throughout the forest, and the foraging strategy of this species. Spider monkeys are one of the largest and most frugivorous Neotropical primates [25,50,51], and the availability of fruits is highly variable in space and time [8]. For reducing inter-patch travel costs, resource competition, and increase foraging efficiency, spider monkeys [28,52,53,54] and other primate species (*Callicebus torquatus*: [55]; *Saguinus oedipus*: [56]; *Papio cynocephalus*: [57]; *Macaca nemestrina*: [58]; *Colobus vellerosus*: [59]) typically select sleeping sites located close to the available feeding areas. Moreover, because spider monkeys returns to the same sleeping trees after their foraging excursions, they have been considered typical examples of central-place foragers (*sensu* [60]) or multiple-central place foragers [8].

The higher variation of sleeping site density within the continuous forest sites (Figure 2), may be related to the larger home range in continuous forest than in fragments [61,62,63], and the fact that larger home ranges can be highly dynamic, varying in size among years and seasons depending on food availability [63,64], and/or the presence of competing groups [65,66]. Furthermore, it has been recently demonstrated that spider monkeys forage mainly in high-quality core areas (i.e., small areas of intense use within the home ranges) that tend to vary in size and spatial location along years and seasons [63]. Thus, because sleeping sites used by *Ateles* are usually located near core areas of exclusive use [63,67,68], it is quite possible that in the sites with lower density of sleeping sites (CF2 and CF4, Figure 2) the 30 ha we sampled within the home ranges we estimated for the years 2007 and 2008 [32,34,35], were temporally underused by the monkeys when we conducted the present study (2010). Thus, following the temporal and spatial variations in core areas within the home range in continuous forest, the distribution of sleeping sites within this habitat is probably more spatially and temporally dynamic in time and space than within forest fragments. Future long-term studies analyzing temporal variations in the use of sleeping trees will be valuable to accurately test this prediction.

Interestingly, the spatial distribution of latrines was particularly clumped in two forest fragments, resulting in smaller inter-latrine distances within this forest condition than within the continuous forest. Both spatial patterns can be attributed to the small home range of spider monkeys in fragments [32], and a reduced availability of large trees (and consequently overall fruit availability) in smaller fragments (e.g., Los Tuxtlas, Mexico: [31,33]; Lacandona, Mexico: [34]). Indeed, in response to lower fruit availability in fragments, spider monkeys increase the time feeding on leaves [32,34], which are generally available throughout the forest and along years [69]. Thus, monkeys need to travel shorter distances in fragments, and hence, they do not need to use distantly located sleeping sites. Furthermore, the forest fragments in which we found that the distribution of sleeping sites was significantly clumped (FF2 and FF3) were located next to a paved and dirt road, and hence, local people and the noise produced by cars could harass the monkeys forcing them to use the sleeping trees available in the interior of the patch.

Characteristics of Sleeping Trees

The choice of specific sleeping trees by primates is crucial for survival, as they spend a large proportion of their time in these trees [28,67,68]. In this sense, we found that despite the diversity of tree species present in the Lacandona rainforest [42], spider monkeys used a small number of tree species as sleeping trees (Table 2); *Dialium guianense* and *Brosimum alicastrum* were particularly used in both continuous and fragmented forests. Both species are considered top-food species for this primate [25,33] and are dominant and ecologically important tree species in the Lacandona rainforest [70,71,72]. Although spider monkeys used these

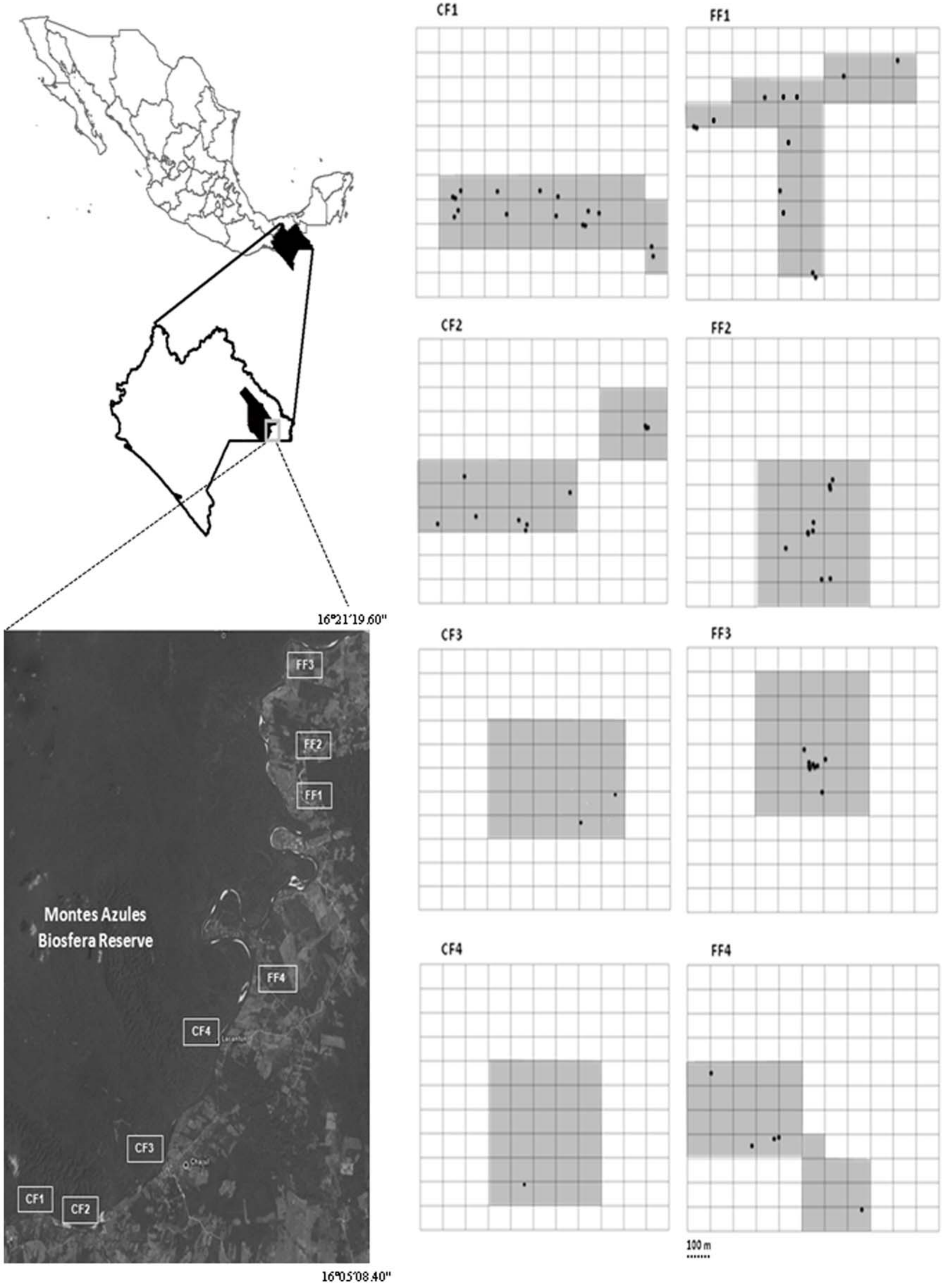
16°21′19.60″
FF3
FF2
FF1
Montes Azules
Biosfera Reserve
FF4
CF4
Lacantun
CF3
Chajul
CF1
CF2
16°05′08.40″
CF1
FF1
CF2
FF2
CF3
FF3
CF4
FF4
100 m

Figure 3. Continuous forest sites and forest fragments studied in the Lacandona rainforest, Mexico. The location of each sleeping site of spider monkeys (dots) within the 30 ha of sampling area (gray shaded areas) area indicated. These areas were divided in 1-ha plots to estimate the spatial distribution of sleeping sites within each study area.
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species proportionally to their availability, these species and other tree species that were used (e.g., *Licania platypus, Terminalia amazonica,* and *Pouteria* sp.) shared a similar tree architecture. For example, they are all trees that reach over 40 m high, and structurally have straight trunks with large and well shaped buttresses, as well as big crowns that offer abundant and very long lateral branches [71]. This kind of tree architecture can give support and comfort in the face of adverse climatic conditions [67,73,74], as well as protection against predators [67,74]. The long horizontal branches of these tree species are adequate for the locomotor suspensory pattern of spider monkeys, facilitating their movements inside and around of peripheries of crowns [75]. The

Table 2. Use and availability of sleeping trees for spider monkeys (*Ateles geoffroyi*) in continuous and fragmented forests in Lacandona, Mexico.[a]

Sites/Families	Species	Trees used	Trees available[b]	w_i	DBH used (range, cm)	DBH available[b] (range, cm)	t
Continuous forest							
CF1							
Meliaceae	*Guarea glabra*	2 (0.07)	4 (20)	0.4	23.3 (17.5–29)	36.2 (30.9–38.8)	−2.91*
Ulmaceae	*Ampelocera hottlei*	4 (0.13)	3 (15)	1.06	41.8 (16.2–55)	63.0 (54.8–76.4)	−1.65n.s
Caesalpiniaceae	*Dialium guianense*	3 (0.1)	4 (20)	0.6	51.3 (27–77)	53.2 (33.7–80.2)	−0.11n.s
Moraceae	*Brosimum alicastrum*	6 (0.2)	1 (5)	4.8	106.3 (52–138)	79.6	−0.96n.s
CF2							
Caesalpiniaceae	*Dialium guianense*	1 (0.03)	–	–	46	–	–
CF3							
Chrysobalanaceae	*Licania platypus*	2 (0.07)	4 (20)	0.67	115.3 (107.6–123)	35.8 (35.5–40.1)	2.02n.s
Caesalpiniaceae	*Dialium guianense*	4 (0.13)	4 (20)	1.35	42.8 (28–51)	61.4 (37.6–95.5)	−1.29n.s
Moraceae	*Brosimum alicastrum*	2 (0.07)	3 (15)	0.90	84.5 (70.3–98.7)	61.0 (54.7–69.7)	1.95n.s
Ulmaceae	*Ampelocera hottlei*	2 (0.07)	2 (10)	1.35	27 (25–29)	33.9 (32.1–35.7)	−2.59n.s
Meliaceae	*Guarea glabra*	1 (0.03)	2 (10)	0.67	24	35.8 (31.5–40.1)	−2.38n.s
CF4							
Caesalpiniaceae	*Dialium guianense*	2	–	–	54.27 (43.3–65.3)	–	–
Forest fragments							
FF1							
Caesalpiniaceae	*Dialium guianense*	7 (0.23)	7 (35)	0.72	32.28 (15.0–56.6)	38.6 (30.6–44.2)	−0.91n.s
Moraceae	*Brosimum alicastrum*	3 (0.1)	1 (5)	2.18	31.9 (23.3–38)	70.3	5.77*
Sapotaceae	*Pouteria sp.*	1 (0.03)	–	–	27.7	–	–
Clusiaceae	*Calophyllum brasiliense*	1 (0.03)	–	–	34.8	–	–
FF2							
Moraceae	*Brosimum alicastrum*	1 (0.03)	4 (20)	0.16	42.6	68.5 (54.1–86.6)	1.83n.s
Caesalpiniaceae	*Dialium guianense*	6 (0.3)	1 (5)	4	27.70 (19.4–39)	45.8	2.98*
Meliaceae	*Guarea glabra*	1 (0.03)	1 (5)	0.66	23.5	36	–
Combretaceae	*Terminalia amazonica*	1 (0.03)	–	–	39.5	–	–
FF3							
Meliaceae	*Guarea glabra*	4 (0.13)	1 (5)	2.22	17.6 (15.6–20.1)	34.2	8.52*
Acanthaceae	*Bravaisia integerrima*	2 (10)	2 (10)	0.55	43.0 (41.4–44.6)	39.8 (31.8–47.7)	0.39n.s
Caesalpiniaceae	*Dialium guianense*	3 (10)	2 (10)	0.83	24.3 (16.9–31.8)	34.5 (34.4–34.7)	−1.83n.s
FF4							
Chrysobalanaceae	*Licania platypus*	1	–	–	101	–	–
Caesalpiniaceae	*Dialium guianense*	4	–	–	60.31 (27.6–99.3)	–	–

[a] We indicated: (i) total number (and density, in parentheses) of trees used and available, along with the index of preference (w_i); and (ii) diameter at breast height (DBH, cm) of trees used and available, along with the Student t-test for comparing differences in DBH between trees used and available. A w_i value >1 indicates a positive selection; <1 indicates avoidance; and a value around 1 indicates that the sleeping trees are used proportionally to their availability. n.s. ($P>0.05$), * $P<0.05$.
[b] Tree availability was estimated in 0.2 ha per site (see Methods).
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fact that spider monkeys did not select larger trees for sleeping in both forest conditions could actually represent a protection strategy against adverse climatic conditions.

Implications for Seed Dispersal and Forest Regeneration

Latrines of spider monkeys receive hundreds of seeds from a large number of plant species ([23], A. González-Zamora et al. unpublished data). In spite of potential negative effects of density-dependent mortality factors (e.g., seed/seedling predators) [76], evidence indicates that seedlings and saplings of some plants dispersed by primates recruit well at or near latrines [77,78,79]. Although seed/seedling aggregation in latrines can reduce the *per capita* seed-to-seedling survival [29], the large and constant arrival of seeds can produce a saturation of some biotic mortality agents (e.g., rodents, insects) [79,80,81,82], permitting the recruitment and survival of seedlings and saplings within latrines [29,79]. In fact, saplings can have higher growth rates in latrines [79]. This is probably related to the fact that latrines are enriched in nutrients compared to surrounding areas [17,19]. Furthermore, not all seeds removed by rodents are predated, as seeds in fecal clumps may be secondarily dispersed by rodents and dung beetles, reducing the negative effects of clumping [83]. Dung can disappear quickly due to dung beetles (<3 hours: [84]; <7 hours: [83]), reducing the effect of dung on seed predation and, at the same time, potentially increasing the probability of seed burial, secondary seed dispersal by dung beetles, and seedling establishment [23,83,84,85,86].

Therefore, assuming that latrines may represent hotspots of seedling recruitment within the forest [23,29], our results have important implications for seed dispersal and forest regeneration. First, the large variation in the spatial distribution of sleeping sites across the forest indicates that spider monkeys may create a complex seed deposition pattern in space and time. In fact, evidence indicates that this species can create a highly structured seed shadow, with a fraction of seeds deposited in individual scats distributed across the forest (scattered pattern), and a fraction deposited in sleeping sites (spatially contagious pattern) [7,28]. This mixed seed deposition pattern can result in different areas of seedling recruitment within the forest [7,23].

Second, because seed dispersal distance may be critical for some tree species to escape areas of high mortality ('escape hypothesis', see [76]), our results suggest that the effectiveness of spider monkeys as seed dispersers (*sensu* [87]) may be lower in forest fragments, in which the inter-latrine distances were notably shorter than in continuous forest, and hence, seed/seedling survival could be lower in latrines located in forest fragments. Although this hypothesis needs to be adequately tested by comparing seed/seedling/sapling survival in latrines located in continuous versus fragmented sites, Chaves et al. [32,34] also suggests that the effectiveness of spider monkeys as seed dispersers may be limited in fragments of Lacandona forest, in which spider monkeys swallow a lower proportion of seeds and spend a higher proportion of time consuming leaves, resulting in a lower number of fecal samples containing seeds than in continuous forests.

Finally, botanists have traditionally classified tropical rainforests based on specific vegetation associations (e.g., *Terminalia-Dialium, Brosimum-Dialium* in southeastern Mexican rainforest [72,88]). If as discussed above, seeds deposited in latrines by spider monkeys regenerate well [77,78,79], our results support the idea that seed dispersal by spider monkeys could contribute to creating these types of vegetation associations, as this primates consistently used trees of *Dialium, Brosimum,* and *Terminalia* to sleep in different sites, depositing copious amounts of seeds from different top fruit species such as *Dialium* and *Brosimum* (A. González-Zamora *et al.* unpublished data). However, because seeds must go through many subsequent filters to reach adulthood, further long-term studies evaluating seed germination and seedling and sapling establishment and survival are needed to accurately test this hypothesis.

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Author Contributions

Conceived and designed the experiments: AG-Z VA-R KES KO VS. Performed the experiments: AG-Z KES. Analyzed the data: AG-Z VA-R. Contributed reagents/materials/analysis tools: AG-Z VA-R KES KO VS. Wrote the paper: AG-Z VA-R KO VS CAC KES.

References

1. Miller KE, Lazlo K, Dietz JM (2003) The role of scent marking in the social communication of wild golden lion tamarins, *Leontopithecus rosalia*. Animal Behaviour 65: 95–803.
2. Irwin MT, Samons KE, Raharison JC, Wright PC (2004) Lemur latrines: Observations of latrine behavior in wild primates and possible ecological significance. Journal of Mammalogy 85: 420–427.
3. Ralls K, Deborah AS (2004) Latrine use by San Joaquin kit foxes (*Vulpes macrotis*) and coyotes (*Canis latrans*). Western North American Naturalist 64: 544–547.
4. Brown RE, Macdonald W (1985) Social odours in mammals. Oxford: Clarendon Press.
5. Gorman ML, Trowbridge BJ (1989) Role of odor in the social lives of carnivores. In: Gittleman JL, ed. Carnivore Behavior, Ecology and Evolution. Vol. 1. New York: Cornell University Press. 57–88.
6. Julliot C (1996) Seed dispersal by red howling monkeys (*Alouatta seniculus*) in the tropical rain forest of French Guiana. International Journal of Primatology 17: 239–258.
7. Russo E, Portnoy S, Augspurger CK (2006) Incorporating animal behavior into seed dispersal models: Implications for seed shadows. Ecology 87: 3160–3174.
8. Chapman CA, Chapman LJ, McLaughlin RL (1989) Multiple central place foraging by spider monkeys: travel consequences of using many sleeping sites. Oecologia 79: 506–511.
9. Wenny DG (2000b) Seed dispersal of a high quality fruit by specialized frugivores: High quality dispersal? Biotropica 32: 327–337.
10. Karubian J, Duraes R (2009) Effects of seed disperser social behavior on patterns of seed movement deposition. Oecologia Brasileira 13: 45–57.
11. Yumoto T, Kimura K, Nishimura A (1999) Estimation of the retention times and distances of seed dispersed by two monkey species, *Alouatta seniculus* and *Lagothrix lagothricha*, in a Colombian forest. Ecological Research 14: 179–191.
12. Bravo SP, Zunino GE (2000) Germination of three arboreal seeds dispersed by black howler monkeys (*Alouatta caraya*). Folia Primatologica 71: 342–345.
13. Dinerstein E, Wemmer CM (1988) Fruits rhinoceros eat–dispersal of *Trewia nudiflora*. Ecology 69: 1768–1774.
14. Revilla E, Palomares F (2002) Spatial organization, group living and ecological correlates in low-density populations of Eurasian badgers, *Meles meles*. Journal of Animal Ecology 71: 497–512.
15. Fragoso JM, Silvius VKM, Correa LA (2003) Long-distance seed dispersal by tapirs increases seed survival and aggregates tropical trees: Long-distance dispersal. Ecology 84: 1998–2006.
16. Campos-Arceiz A, Blake S (2011) Megagardeners of the forest e the role of elephants in seed dispersal. Acta Oecologica 37: 542–553.
17. Feeley K (2005) The role of clumped defecation in the spatial distribution of soil nutrients and the availability of nutrients for plant uptake. Journal of Tropical Ecology 21: 99–102.
18. Pouvelle S, Jouard S, Feer F, Tully T, Ponge JF (2009) The latrine effect: Impact of howler monkeys on the distribution of small seeds in a tropical rain-forest soil. Journal of Tropical Ecology 25: 239–248.
19. Neves DSN, Feer F, Samlo S, Chateil C, Ponge JF (2010) The impact of red howler monkeys latrines on the distribution of main nutrients and on topsoil profiles in a tropical rain forest. Austral Ecology 35: 549–559.

20. Schupp EW, Milleron T, Russo SE (2002) Dissemination limitation and the origin and maintenance of species-rich tropical forests. In: Levey DJ, Silva WR, Galetti M, eds. Seed Dispersal and Frugivory: Ecology, Evolution, and Conservation. New York: CABI Publishing. 19–34.
21. Herrera CM (1989) Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics, in undisturbed Mediterranean habitats. Oikos 55: 250–262.
22. Russo SE, Chapman CA (2011) Primate seed dispersal: Linking behavioural ecology and forest community structure. In: Campbell CJ, Fuentes AF, MacKinnon KC, Panger M, Bearder S, eds. Primates in Perspective. Oxford: Oxford University Press. 523–534.
23. Chapman CA (1989) Primate seed dispersal: The fate of dispersed seeds. Biotropica 21: 148–153.
24. Di Fiore A, Link A, Dew JL (2008) Diets of wild spider monkeys. Spider monkeys: behavior, ecology and evolution of the genus *Ateles*. In: Campbell CJ, ed. Cambridge: Cambridge University Press. 81–137.
25. González-Zamora A, Arroyo-Rodríguez V, Chaves OM, Sánchez-López S, Stoner KE, et al. (2009) Diet of spider monkeys (*Ateles geoffroyi*) in Mesoamerica: current knowledge and future directions. American Journal of Primatology 71: 8–20.
26. Stevenson PR, Link A (2010) Fruit preferences of *Ateles belzebuth* in Tinigua Park, Northwestern Amazonia. International Journal of Primatology 31: 393–407.
27. Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, et al. (2008) Fission–fusion dynamics: new research frameworks. Current Anthropology 49: 627–654.
28. Chapman CA (1989) Spider monkey sleeping sites: use and availability. American Journal of Primatology 18: 53–60.
29. Russo SE, Augspurger CK (2004) Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. Ecology Letters 7: 1058–1067.
30. Ramos-Fernández G, Wallace RB (2008) Spider monkey conservation in the twenty-first century: recognizing risks and opportunities. In: Campbell CJ, ed. Spider monkeys. The biology, behavior and ecology of the genus *Ateles*. New York: Cambridge University Press. 351–372.
31. Arroyo-Rodríguez V, Mandujano S (2006) Forest fragmentation modifies habitat quality for *Alouatta palliata*. International Journal of Primatology 27: 1079–1096.
32. Chaves OM, Stoner KE, Arroyo-Rodríguez V (2012) Differences in diet between spider monkey groups living in forest fragments and continuous forest in Lacandona, Mexico. Biotropica 44: 105–113.
33. Cristóbal-Azkarate JC, Arroyo-Rodríguez V (2007) Diet and activity pattern of howler monkeys (*Alouatta palliata*) in Los Tuxtlas, Mexico: Effects of habitat fragmentation and implications for conservation. American Journal of Primatology 69: 1013–1029.
34. Chaves OM, Stoner KE, Arroyo-Rodriguez V (2011) Effectiveness of spider monkeys (*Ateles geoffroyi vellerosus*) as seed dispersers in continuous and fragmented rainforests in southern Mexico. International Journal of Primatology 32: 177–192.
35. Chaves OM, Stoner KE, Campos SA, Arroyo-Rodríguez V (2011) Wood consumption by Geoffroyi's spider monkeys and its role in mineral supplementation. PLoS ONE 6: e25070.
36. Vásquez-Sánchez MA, March IJ, Lazcano-Barrero MA (1992) Características socioeconómicas de la Selva Lacandona. In: Vásquez-Sánchez MA, Ramos MA, eds. Reserva de la biósfera de Montes Azules, Selva Lacandona: investigación para su conservación. Mexico city: Ecosfera. 287–323.
37. García-Gil JG, Lugo-Hupb J (1992) Las formas del relieve y los tipos de vegetación de la Selva Lacandona. In: Vásquez- Sánchez MA, Ramos MA, eds. Reserva de la Biosfera Montes Azules, Selva Lacandona: Investigación para su Conservación. San Cristóbal de las Casas: Centro de Estudios para la Conservación de los Recursos Naturales, A.C. 34–39.
38. Medellin R (1994) Mammal diversity and conservation in the Selva Lacandona, Chiapas. Conservation Biology 8: 780–799.
39. Naranjo EJ (2002) Population Ecology and Conservation of Ungulates in the Lacandon Forest, Mexico. PhD Thesis. Gainesville: University of Florida.
40. Marquez-Rosano C (2006) Environmental policy and dynamics of territorial appropriation: The tensions between the conservation of tropical forests and the expansion of cattle ranching in the Mexican tropics. iasc2008 website. Available: http://iasc2008.glos.ac.un/conference%20papers/pappers/M/Marquez-Rosano_110701.pdf. Accessed 2011 Nov 3.).
41. Gómez-Pompa A, Dirzo R (1995) Atlas de las áreas naturales protegidas de México. Mexico city: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad- Instituto Nacional de Ecología.
42. Martínez E, Ramos CH, Chiang F (1994) Lista florística de la Lacandona, Chiapas. Boletin de la Sociedad Botánica de México 54: 99–177.
43. Crawley M (2002) Statistical computing: An introduction to data analysis using S-Plus. Chichester: John Wiley & Sons.
44. Morisita M (1962) Id-index, a measure of dispersion of individuals. Researches in Population Ecology 4: 1–7.
45. Krebs JC (1999) Ecological methodology. New York: Addison Wesley Longman Inc.
46. David F & Moore PG (1954) Notes on contagious distributions in plants populations. Annals of Botany 18: 47–53.
47. Souza AF, Martins FR (2002) Spatial distribution of an undergrowth palm in fragments of the Brazilian Atlantic Forest. Plant Ecology 164: 141–155.
48. Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) Resource selection by animals: statistical design and analysis for field studies. Second edition. Massachusetts: Kluwer Press.
49. Sokal RR, Rohlf FJ (1995) Biometry. The principles and practice of statistics in biological research, 3rd edition. New York: W. H. Freeman WH & Co.
50. Link A, Di Fiore A (2006) Seed dispersal by spider monkeys and its importance in the maintenance of neotropical rain-forest diversity. Journal of Tropical Ecology 22: 235–246.
51. Stevenson PR (2011) The abundance of large Ateline monkeys is positively associated with the diversity of plants regenerating in Neotropical forests. Biotropica 43: 512–519.
52. Symington MM (1988) Demography, ranging patterns, and activity budgets of black spider monkeys (*Ateles paniscus chamek*) in the Manu National Park, Peru. American Journal of Primatology 15: 45–67.
53. Symington MM (1990) Fission–fusion social organization in *Ateles* and *Pan*. International Journal of Primatology 11: 47–61.
54. Suarez SA (2006) Diet and travel costs for spider monkeys in a nonseasonal, hyperdiverse environment. International Journal of Primatology 27: 411–436.
55. Kinzey WG, Rosenberg AL, Heisler PS, Prowse DL, Trilling JS (1977) A preliminary field investigation of the yellow handed titi monkey, *Callicebus torquatus torquatus*, in northern Peru. Primates 18: 15–181.
56. Neyman PF (1978) Aspects of the ecology and social organization of free-ranging cotton-top tamarins (*Saguinus oedipus*) and the conservation status of the species. In: Klein DG, ed. The biology and conservation of the Callitrichidae. Washington: Smithsonian Institution Press. 39–71.
57. Rasmussen DR (1979) Correlates patterns of range use of a troop of yellow baboons (*Papio cynocephalus*). Sleeping sites, impregnable females, births, and male emigrations and immigrations. Animal Behaviour 27: 1098–1112.
58. Caldecott JO (1986) An ecological and behavioural study of the pig-tailed macaque. In: Szalay FS, ed. Contributions to primatology, Vol. 21. Basel (Switzerland): Karger.
59. Teichroeb JA, Holmes JA, Sicotte P (2012) Use of sleeping trees by ursine colobus monkeys (*Colobus vellerosus*) demonstrates the importance of nearby food. Primates (early view, doi:10.1007/s10329-012-0299-1).
60. Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Mitchell RD, Stairs GR, eds. Analysis of ecological system. Ohio: Ohio University Press. 155–177.
61. Fedigan LM, Fedigan L, Chapman C, Glander KE (1988) Spider monkey home ranges: a comparison of radio telemetry and direct observation. American Journal of Primatology 16: 19–29.
62. Ramos-Fernández G, Ayala-Orozco B (2003) Population size and habitat use of spider monkeys in Punta Laguna, Mexico. In: Marsh LK, ed. Primates in fragments: ecology and conservation. New York: Kluwer/Plenum Press. 191–209.
63. Asensio N, Schaffner CM, Aureli F (2012) Variability in core areas of spider monkeys (*Ateles geoffroyi*) in a tropical dry forest in Costa Rica. Primates 53: 147–156.
64. Burt WH (1943) Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24: 346–352.
65. Aureli F, Schaffner CM, Verpooten J, Slater K, Ramos-Fernandez G (2006) Raiding parties of male spider monkeys: insights into human warfare? American Journal of Physical Anthropology 131: 486–497.
66. Spehar SN, Link A, DiFiore A (2010) Male and female range use in a group of white-bellied spider monkeys (*Ateles belzebuth*) in Yasuní National Park, Ecuador. American Journal of Primatology 72: 129–141.
67. Heymann EW (1995) Sleeping habits of tamarins, *Saguinus mystax* and *Saguinus fuscicollis* (Mammalia: Primates: Callitrichidae), in north-eastern Peru. Journal of Zoology 237: 211–226.
68. Ramirez M (1989) Feeding ecology of the moustached tamarin *Saguinus mystax* in northeastern Peru. PhD Thesis. New York: City University of New York.
69. Milton K (1980) The foraging strategy of howler monkeys: A study in primate economics. New York: Columbia University Press.
70. Boege K, Dirzo R (2004) Intraspecific variation in growth, defense and herbivory in *Dialium guianense* (Caesalpinaceae) mediated by edaphic heterogeneity. Plant Ecology 175: 59–69.
71. Pennington TD, Sarukhán J (2005) Árboles tropicales de México. Manual para la identificación de las principales especies. Mexico city: Universidad Nacional Autónoma de México and Fondo de Cultura Económica.
72. Sarukhán J (1968) Análisis sinecológico de las selvas de *Terminalia amazonia* en la planicie costera del Golfo de México. MSc Thesis. Chapingo: Colegio de Posgraduados.
73. Cui LW, Xiao W (2006) Sleeping sites of black-and white snub-nosed monkeys (*Rhinopithecus bieti*) at Baima Snow Mountain, China. Journal of Zoology 270: 192–198.
74. Smith AC, Knogge C, Huck M, Löttker P, Buchanan-Smith HM, Heymann EW (2007) Long-term patterns of sleeping site use in wild saddleback (*Saguinus fuscicollis*) and mustached tamarins (*S. mystax*): Effects of foraging, thermoregulation, predation, and resource defense constraints. American Journal of Physical Anthropology 134: 340–353.
75. Cant JGH, Youlatos D, Rose M (2003) Suspensory locomotion of *Lagothrix lagothricha* and *Ateles belzebuth* in Yasuní National Park, Ecuador. Journal of Human Evolution 44: 685–699.
76. Howe HF, Smallwood J (1982) Ecology of seed dispersal. Annual Review Ecology and Systematics 13: 201–228.

77. Pacheco LF, Simonetti JA (2000) Genetic structure of a Mimosoid tree deprived of its seed disperser, the spider monkey. Conservation Biology 14: 1766–775.
78. Marsh L, Loiselle BA (2001) Recruitment of black howler fruit trees in fragmented forest of northern Belize. International Journal of Primatology 24: 65–86.
79. Bravo SP (2012) The impact of seed dispersal by Black and Gold Howler Monkeys on forest regeneration. Ecological Research 27: 311–321.
80. Janzen DH (1971) Seed predation by animals. Annual Review Ecology and Systematics 2: 465–492.
81. Howe HF (1989) Scatter- and clump-dispersal and seedling demography: hypothesis and implications. Oecologia 79: 417–426.
82. Chauvet SF, Feer F, Forget PM (2004) Seed fate of two Sapotaceae species in a Guaianan rain forest in the context of escape and satiation hypotheses. Journal of Tropical Ecology 20: 1–9.
83. Andresen E (1999) Seed dispersal by monkeys and the fate of dispersed seeds in a Peruvian rain forest. Biotropica 31: 145–158.
84. Estrada A, Coates-Estrada R (1991) Howler monkeys (*Alouatta palliata*), dung beetles (Scarabaeidae) and seed dispersal: ecological interactions in the tropical rain forest of Los Tuxtlas, Mexico. Journal of Tropical Ecology 7: 459–474.
85. Wehncke EV, Valdez CN, Dominguez CA (2004) Seed dispersal and defecation patterns of *Cebus capucinus* and *Alouatta palliata*: Consequences for seed dispersal effectiveness. Journal of Tropical Ecology 20: 535–543.
86. Santos-Heredia C, Andresen E, Zarate DA (2010) Secondary seed dispersal by dung beetles in a Colombian rain forest: Effects of dung type and defecation pattern on seed fate. Journal of Tropical Ecology 26: 355–364.
87. Schupp EW (1993) Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio 107/108: 15–29.
88. Rzedowski J (2006) Vegetación de México. 1ra. Edición digital. Mexico city: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad.

Capítulo IV:

CONTAGIOUS DEPOSITION OF SEEDS IN SPIDER MONKEYS' SLEEPING TREES LIMITS EFFECTIVE SEED DISPERSAL IN FRAGMENTED LANDSCAPES

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En: **PLoS ONE** (en revisión)

Contagious Deposition of Seeds in Spider Monkeys' Sleeping Trees Limits Effective Seed Dispersal in Fragmented Landscapes

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Abstract

The repeated use of sleeping sites by frugivorous vertebrates promotes the deposition and aggregation of copious amounts of seeds in these sites. This spatially contagious pattern of seed deposition has key implications for seed dispersal, particularly because such patterns can persist through recruitment. Assessing the seed rain patterns in sleeping sites thus represents a fundamental step in understanding the spatial structure and regeneration of plant assemblages. We evaluated the seed rain produced by spider monkeys (*Ateles geoffroyi*) in latrines located beneath 60 sleeping trees in two continuous forest sites (CFS) and three forest fragments (FF) in the Lacandona rainforest, Mexico. We tested for differences among latrines, among sites, and between forest conditions in the abundance, diversity (α-, β- and, γ-components) and evenness of seed assemblages. We recorded 45,919 seeds ≥ 5 mm (in length) from 68 species. The abundance of seeds was 1.7 times higher in FF than in CFS, particularly because of the dominance of a few plant species. As a consequence, community evenness tended to be lower within FF. β-diversity of common and dominant species was two times greater among FF than between CFS. Although mean α-diversity per latrine did not differ among sites, the greater β-diversity among latrines in CFS increased γ-diversity in these sites, particularly when considering common and dominant species. Our results support the hypothesis that fruit scarcity in FF can 'force' spider monkeys to deplete the available fruit patches more intensively than in CFS. This feeding strategy can limit the effectiveness of spider monkeys as seed dispersers in FF, because (i) it can limit the number of seed dispersers visiting such fruit patches; (ii) it increases seed dispersal limitation; and (iii) it can contribute to the floristic homogenization (i.e., reduced β-diversity among latrines) in fragmented landscapes.

Introduction

Seed dispersal processes link the reproductive cycle of adult plants with the establishment of their offspring [1]. Assessing the patterns of seed rain thus represents a fundamental step to understand the spatial structure and regeneration of plant populations, and is critical in understanding patterns of species richness [2]. In the tropics, more than 60% and up to 94% of woody plant species have their seeds dispersed through endozoochory [3] and primates are among the most prominent taxa of seed-dispersing frugivores [4]. Although many primates deposit copious amounts of seeds in latrines beneath sleeping trees, little is known about the ecological implications of this spatially contagious pattern of seed deposition [4].

Schupp et al. [5] argue that contagious seed dispersal can reduce the quality of dispersal because it creates dissemination limitation for other potential plant recruitment sites, and consequently recruitment limitation. Furthermore, based on the Janzen–Connell hypothesis [6,7], seed/seedling mortality could be higher in latrines, since the aggregation of seeds can attract predators and/or pathogens that act in a density-dependent fashion. Nevertheless, growing empirical evidence demonstrates that primate latrines are enriched in nutrients compared to surrounding areas [8,9] and such soil enrichment can positively affect the establishment, growth, and survival of seedlings arising from primate-dispersed seeds [4,10,11]. Thus, consistent with the ‘directed dispersal hypothesis’ [12], primate latrines can represent non-random habitats, where survival of seeds and seedlings could be relatively high. Therefore, assessing the seed rain patterns in primate latrines is a fundamental task for understanding the potential impacts that latrines have on the spatial distribution of plant populations, as well as on emerging properties, such as community structure and diversity [4,13].

In terms of seed dispersal quantity (sensu Schupp [14]), spider monkeys (*Ateles* spp.) likely represent one of the most effective seed dispersers in Neotropical rainforests, as there is no other mammal dispersing higher quantities of seeds per kilogram of biomass [15,16]. Spider monkeys are specialized frugivores that incorporate a diverse array of fruit species in their diets (e.g., 152 plant species by *A. belzebuth* [17]; 165 species by *A. geoffroyi* [18]). The seeds of most of these plant species are swallowed [17,19], and are then defecated following a mixed seed deposition pattern. A fraction of these seeds are deposited during the day in individual scats distributed across the forest and the remaining seeds are deposited at night or early morning in one or more latrines beneath sleeping sites [19-21]. Although a few studies have described the use, availability, and spatial distribution of spider monkey latrines [20,22,23], to our knowledge no study to date has assessed the abundance, species diversity, and/or composition of seeds that fall within these sites. Furthermore, spider monkeys are increasingly forced to inhabit fragmented landscapes [24,25], but it is virtually unknown how the seed rain patterns produced by these primates will alter the future tree composition of these fragments.

Based on a hierarchically nested sampling design (Figure 1), we assessed the seed rain produced by spider monkeys (*Ateles geoffroyi*) in 60 latrines located in two continuous forest sites and three forest fragments in the Lacandona rainforest, Mexico. Using a multiplicative diversity partitioning approach, we assessed variations among latrines, among sites and between forest conditions in the abundance, diversity (α-, β- and γ-components), and evenness of seed assemblages (Figure 1). The species diversity was evaluated using true diversity measures (i.e., numbers equivalents); an analytical approach that has been recently recognized as the most appropriate for diversity evaluations [26,27]. We considered true diversities ^0D (species richness), ^1D (exponential of Shannon's entropy) and ^2D (inverse Simpson concentration). ^0D is not sensitive to species abundances and so gives disproportionate weight to rare species [26]. ^1D weights each species according to its abundance in the community, and hence, it can be interpreted as the number of ‘common’ species in the community [28]. Finally, ^{2}D favors abundant species, and can be actually interpreted as the number of ‘very abundant’ or ‘dominant’ species in the community [28]. Thus, we identified the abundance level, from rare to common to dominant species, at which we observed higher variations in seed species diversity across different spatial scales.

Because fruit availability can vary widely among sites, and spider monkeys can adapt their diet to food availability within each site [16,18,30], we hypothesized that patterns of abundance, diversity, and evenness of seed assemblages will be highly variable among latrines. In particular, fruit availability is typically lower in fragments than in continuous forest because of the combination of both smaller home range sizes [30] and a lower density of big (dbh > 60 cm) food trees (i.e., larger fruit patches [31]) in fragments [32,30,33]. Thus, the abundance and species diversity of seeds within latrines is expected to be lower in fragments where spider monkeys usually spend more time consuming leaves [18,30], and the number of feces without seeds is usually higher than in continuous forests [19]. However, we also predict that fruit scarcity in fragments will ‘force’ spider monkeys to spend more time consuming the available fruit patches; i.e., they will deplete the available patches more intensively than in continuous forest sites [34,35]. As consequence, the seed rain in fragments will be dominated by a few plant species, reducing the number of common (^{1}D) and dominant species (^{2}D), as well as the seed community evenness in forest fragments.

Materials and Methods

Ethics Statement

This study adhered to the laws of the Mexican Government (SEMARNAT, Secretaría de Medio Ambiente y Recursos Naturales) to work with wild animals and plants in Lacandona (permit no. SGPA/DGVS/09606). Since our work is not invasive, only observational, we meet all ethical and legal requirements established by the American Society of Primatologists (ASP), Animal Care and Use Committee, and Ethical Committee of the Zoological Society of London for work on primates. Although our institution, Universidad Nacional Autónoma de Mexico (UNAM), does not yet have an Institutional Review Board (IRB) or a similar governing body of ethics, this project was approved by the Consejo Nacional de Ciencia y Tecnología (project CB-2006-56799). We thank the owners of the forest patches for giving us the permission to perform the research in the study sites.

Study Site

The Lacandona rainforest constitutes the southwestern sector of the Mayan forest in Mexico, and it is one of the most important rainforest remnants in Mesoamerica. The area is located in the northeastern portion of the state of Chiapas, and is delimited by the Guatemalan border on the south and east, and by the Chiapas highlands on the north and west. Average monthly temperatures range from 24 °C to 26 °C, and mean annual rainfall is 2,500–3,500 mm, with roughly 80% of the rains falling between June and November. The area was originally covered by over 1.4 million ha of rainforest, but human settlement and deforestation between 1960 and 1990 resulted in the loss of 70% of the original forest cover.

We worked in two adjacent areas separated by the Lacantún River (> 150 m wide): the Marqués de Comillas region (MCR, eastern side of the river) encompassing ca. 176,200 ha of fragmented forest, human settlements, and agricultural lands. Approximately 50% of the land surface of MCR is now used for cattle ranching and agriculture, but several fragments (0.5–1,500 ha) remain. The second area was the Montes Azules Biosphere Reserve (MABR, western side) comprising ca. 331,000 ha of undisturbed old-growth forest.

Experimental Design and Indicators of Food Availability

Based on a recent study on the density and spatial distribution of sleeping sites and latrines of spider monkeys (*Ateles geoffroyi*) in four continuous forest sites within MABR and four forest fragments in MCR [23], we selected sites with more than 12 latrines (i.e., three fragments and two continuous forest sites) to control for sampling effort (i.e., we sampled 12 latrines per site, see details below). The continuous forest sites were separated by at least 5 km from each other (CF1: 16°06´25.01” N – 91°59´16.61” O; CF2: 16°06´50.25” N – 90°56´24.46” O). The fragments were isolated ≥ 24 yrs ago, are immersed in an anthropogenic matrix, and their distances to continuous forest ranged from 200 to 1,200 m (FF1: 16°15´10.83” N – 90°49´53.82” O; FF2: 16°16´54.15” N – 90°50´19.91” O; FF3: 16°19´54.85” N – 90°51´10.71” O). The average isolation distance among fragments is 4,200 m (a detailed map of the sites is located in [23]).

Tree species diversity was similar in continuous and fragmented forests, both when considering the whole tree community (i.e., trees with diameter at breast height, dbh ≥ 10 cm) and when considering the top spider monkey food tree species (i.e., those contributing to > 80% of total feeding time in a recent review of spider monkey diet in Mesoamerica [18]; Figure S1 in Supporting Information). However, the density (stems/1,000 m^2) and basal area of top food species were significantly higher in continuous than fragmented forest sites (Appendix S1 and

Table S1 in Supporting Information). Thus, as previously reported for this [30] and other Mexican rainforests [32], food availability can be limited in fragments, as the lack of large food trees can limit the availability of fruits [31].

Seed Collection

Within each site we randomly selected 12 latrines (60 in total). We measured the seed rain within each latrine for 13 months (February 1, 2011 to February 28, 2012) by placing one seed trap in the center of each latrine. Each seed trap consisted of a circular 1.5-m diameter PVC frame supporting a 0.5-m depth, open-topped, 0.5-mm nylon mesh bag suspended 1 m above the ground on three thin steel posts to prevent predation by terrestrial vertebrates. The continuous falling of leaves and dung also contributed to hide seeds, thus further reducing the probability of seeds being removed by animals. In fact, we did not detect signs of seed predation (e.g., open husks, seeds with teeth marks) within the traps. Traps were emptied once a month and the seeds located within the spider monkeys' feces were collected, washed, counted, and identified to species level based on (i) our experience with the local flora [19,30]; (ii) the knowledge of local parataxonomists; and (iii) information from seed catalogs [36]. Only seeds ≥ 5 mm in length were recorded. Although seed traps also captured some fruits and seeds dispersed by wind or gravity, we only considered seeds immersed within monkeys' feces. These were identified in the field based on their typically "stained" appearance and characteristic adhesion of fecal matter.

Data Analyses

We first evaluated sample completeness within each latrine in the following manner [29]:

$$C_n = 1 - \frac{f_1}{n}\left[\frac{(n-1)f_1}{(n-1)f_1 + 2f_2}\right]$$

where f_1 and f_2 are the number of species represented by one (singletons) and two (doubletons) individuals in the sample, respectively, and n is the total number of individuals in the sample. Sample coverage did not differ between sites (Kruskal-Wallis test, $H = 6.7$, $P = 0.14$), averaging (± SD) 99% ± 1% (range = 93-100%) per latrine, indicating that the seed inventory was accurate with our sampling effort, and that our results are not biased by differences in sample completeness among sites.

Based on our hierarchically nested sampling design (i.e., 60 latrines in 5 sites within two forest conditions in one landscape; Figure 1), we analyzed patterns of seed species diversity across multiple spatial scales using Hill numbers (^qD). These metrics represent true diversities because they obey the replication principle [27]. They are in units of 'species', which facilitates comparison between samples. It is thus possible to plot them all on a single graph to compare diversity profiles as a continuous function of the parameter q. This 'diversity profile' characterizes the species–abundance distribution of a community and provides complete information about its diversity [27]. For S species and $q \neq 1$, Hill numbers of order q are defined as:

$$^qD = \left(\sum_{i=1}^{S} \overline{p_i}^{\,q}\right)^{1/(1-q)}$$

where p_i indicates the relative abundance of the ith species, and q is an exponent that determines the sensitivity of the measure to the relative abundances. Because the Hill number is undefined for q = 1, the diversity of order 1 can be estimated as:

$$^{1}D = \exp\left(-\sum_{i=1}^{S} \overline{p_i} \log \overline{p_i} \right)$$

We considered three orders for q (0, 1, and 2) in its unweighted form [27]. ^{0}D is the species richness, ^{1}D is equivalent to the exponential of Shannon's entropy, and ^{2}D is equivalent to the inverse Simpson concentration [26]. When considering several communities, alpha and gamma components of diversity can be analyzed following Jost [27]:

$$^{q}D_{\alpha} = \left(\frac{1}{N} \sum_{i=1}^{S} p_{i1}{}^{q} + \frac{1}{N} \sum_{i=1}^{S} p_{i2}{}^{q} + \ldots \right)^{1/(1-q)}$$

where p_i denotes the relative abundance of the ith species in each of the N communities. Again, for the particular case of q = 1, α-diversity can be estimated as:

$$^{1}D_{\alpha} = \exp\left\{ -\frac{1}{N} \left(\sum_{i=1}^{S} (p_{i1} \ln p_{i1}) + \sum_{i=1}^{S} (p_{i2} \ln p_{i2}) + \ldots \right) \right\}$$

Then, using a multiplicative partitioning of Hill numbers, beta (between group) component of diversity can be calculated as: $^{q}D_{\beta} = {}^{q}D_{\gamma}/{}^{q}D_{\alpha}$. This beta can be interpreted as the 'effective number of completely distinct communities' [27], which ranges from one (when all communities are identical) to N (when all communities are completely distinct).

To evaluate changes in different components of diversity (γ, α, and β) at multiple spatial scales, we partitioned species diversity into within- (α) and between- (β) components considering three spatial scales (Figure 1): (i) the diversity of the landscape (γ_{land}) was partitioned into mean alpha and beta diversities in the two forest conditions ($^{q}\gamma_{\text{land}} = {}^{q}\alpha_{\text{forest}} \times {}^{q}\beta_{\text{forest}}$); (ii) the diversity within each forest condition (γ_{forest}) was partitioned into mean alpha and beta diversities in the sites (${}^{q}\gamma_{forest} = {}^{q}\alpha_{site} \times {}^{q}\beta_{site}$); and (iii) the diversity within each site (γ_{site}) was partitioned into mean alpha and beta diversities in the 12 sampling latrines (${}^{q}\gamma_{site} = {}^{q}\alpha_{latrine} \times {}^{q}\beta_{latrine}$). To assess if the magnitude in β-diversity differed between forest conditions, we compared the relative compositional dissimilarity between communities using the transformation of beta (${}^{q}D_{\beta}$) proposed by Jost [26] for communities with different numbers of samples (i.e., continuous forest: n = 2; fragments: n = 3): ${}^{q}DS = 1 – [(1/{}^{q}D_{\beta}-1/N)/(1-1/N)]$, where N is the number of samples. ${}^{q}DS = 1$, when all the samples are completely distinct, and ${}^{q}DS = 0$, when all are identical.

We also calculated changes in species dominance across spatial scales using the evenness factor proposed by Jost [28]: $EF_{0,2} = {}^{2}D/{}^{0}D$. This measure was used because it: (i) is calculated from true diversity measures; (ii) is independent of the number of species in the sample; and (iii) is very easy to interpret. This index ranges between 1 (when all species are equally common) and nearly 1/S (when the community is totally dominated by one species) [28]. Roughly speaking, EF can be interpreted as the proportion of dominant species in the community [28].

To assess if seed species diversity and abundance differed among forest conditions, we used generalized linear models. As suggested for count dependent variables (i.e., ${}^{0}D$ and abundance of seeds), we used a Poisson error and a log link function. For EF, ${}^{1}D$ and ${}^{2}D$ we used normal error and an identity link function [37]. To assess if latrines can be considered independent samples, we applied a Mantel test using the XLSTAT program (version 2012.6.08) to correlate the compositional similarity among latrines (Bray-Curtis index) with the inter-latrine isolation distances (ln-transformed). The Mantel-test detected a significant spatial autocorrelation of data sets ($R = -0.423$, $P = 0.0001$), thus, we cannot consider the latrines as replicates for testing differences among sites. Therefore, differences in species diversity and abundance among sites were tested using general linear mixed models (GLMM) with JMP 8.0, where the fixed effect was "sites". To control for the unavoidable pseudoreplication effect of our design, we nested latrines within each site as a random effect in the models. Residual maximum likelihood method (REML) was used to separate variances of fixed from random effects in the models [38].

Results

We recorded 45,919 seeds belonging to 32 families, 49 genera, and 68 plant species (including 8 morphospecies) during the 13-mo period. The species with greater number of seeds were the palm *Sabal mexicana*, Arecaceae (13.1% of all records), the trees *Dialium guianense*, Fabaceae (12.6%), *Castilla elastica*, Moraceae (9.2%), *Spondias radlkoferi*, Anacardiaceae (6.3%), and *Trophis mexicana*, Moraceae (5.2%), and the lianas *Rourea glabra*, Connaraceae (5.1%), and *Paullinia costata*, Sapindaceae (4.7%). At the family level, most seeds were from Arecaceae (22.7%), Moraceae (15.4%), Fabaceae (15.4%), Anacardiaceae (8.8%), Sapindaceae (5.5%), and Connaraceae (5.1%), together representing 72.9% of all seeds recorded (Table S2 in Supporting Information).

Abundance of Seeds and Species Diversity across Scales

The abundance of seeds was highly variable among sites, ranging from 6,234 seeds in CF1 to 15,414 seeds in FF1. Seeds were 1.7 times more abundant in fragments (mean ± SE, 11,045 ± 3,853 seeds) than in continuous forest sites (6,393 ± 224 seeds) ($\chi^2 = 3.07$, df = 1, $P = 0.08$; Figure 2a). The mean number of seeds per latrine was 765 (ranging from 32 to 4,621 seeds), and tended to differ among sites ($F_{4,55}$ = 2.34, P = 0.06), being between 1.6 and 2.5 times higher in FF1 than in the rest of the sites (Figure 2b).

At the landscape scale, total species diversity (γ_{land}) was, on average, 1.28 times higher than mean species diversity per forest condition (α_{forest}) for any order of q, as species turnover between forest conditions (β_{forest}) was almost the same (1.26 to 1.30) for all q orders (Figures 3a-c). When analyzing each forest condition separately, mean species diversity per site (α_{site}) was similar in continuous and fragmented forests for ^0D (χ^2 = 1.05, df = 1, P = 0.30), but was significantly higher in continuous forest than in fragments in terms of ^1D (χ^2 = 8.58, df = 1, P = 0.003) and ^2D (χ^2 = 10.0, df = 1, P = 0.001; Figure 3f). Nevertheless, since species turnover (β_{site}) was two times greater among fragments than between continuous forest sites when considering ^1D and ^2D (Figure 3e), the accumulated number of species (γ_{forest}) was almost the same in continuous and fragmented forests (Figure 3d). Finally, at the site scale, mean species diversity per latrine (α_{latrine}) differed among sites for ^0D ($F_{4,55}$ = 2.73, P = 0.04), being significantly higher in the largest fragment (FF1) than in the rest of the sites; however, mean ^1D and ^2D per latrine did not differ among sites (P > 0.68 in all cases) (Figure 3i). Species turnover among latrines (β_{latrine}) was notably higher in continuous forest sites than in fragments for any order of q (Figure 3h), and as consequence, in most cases the continuous forest sites accumulated a greater number of species (γ_{site}) than fragments (Figure 3g).

Community Evenness across Spatial Scales

The evenness factor at the landscape scale (i.e., based on γ_{land}) was 0.24 (Figure 4). At the forest condition scale (i.e., based on γ_{forest}), the evenness factor was slightly higher in continuous

($EF_{0,2}$ = 0.26) than in fragmented ($EF_{0,2}$ = 0.23) forests. Based on means (± SE) per site (γ_{site}), we also found a slightly higher evenness factor in continuous forest (0.26 ± 0.02) than in fragments (0.21 ± 0.04), but this difference was not significant (χ^2 = 1.37, df = 1, P = 0.24; Figure 4). This pattern was evident when analyzing the rank-abundance curves, which showed that in fragments the seed rain was dominated by 9 species, whereas in the continuous forest it was dominated by 5 species (Figure 5). In continuous forest sites, *C. elastica* and *Ampelocera hottlei,* and the lianas *Trichostigma octandrum*, *Paullinia costata*, and *Mendoncia retusa* represented 53.4% of all seeds recorded. However, in fragments, the palm *S. mexicana*, the trees *D. guianense*, *C. elastica*, and *S. radlkoferi*, and the liana *R. glabra* represented 55.1% of all seeds recorded (Table S2). The number of rare species followed the opposite pattern, being higher in continuous (n = 11 species) than fragmented forests (n = 8 species; Figure 5).

At the latrine scale, we found significant differences in evenness among sites ($F_{4,55}$ = 3.50, P = 0.01; Figure 4), with the fragment FF1 showing lower evenness than the continuous forest CF1 (Figures 4 and 5). In CF1 the trees *A. hottlei* and *C. elastica* represented 31.3% of all seeds recorded whereas in CF2 the lianas *M. retusa*, *T. octandrum* and *P. costata* represented 44.6% of recorded seeds. Regarding the fragments, in FF1, the palm *S. mexicana* and the tree *D. guianense* represented 52.6% of all seeds recorded. In FF2, the palm *S. mexicana* and the trees *C. elastica* and *T. mexicana* represented 53.6% of all seeds recorded. Finally, in FF3, the liana *R. glabra* and the trees *C. elastica* and *Nectandra ambigens* represented 46.9% of all recorded seeds (Figure 5).

Discussion

Potential Causes of Seed Dispersal Patterns across Scales

Our results support the hypothesis that fruit scarcity in fragments (see Methods and Appendix S1) can result in spider monkeys depleting the available fruit patches more intensively than in continuous forest sites [34]. As predicted, the abundance of seeds was 1.7 times higher in fragments than in continuous forest sites. This was principally associated with the dominance of a few plant species, which tended to reduce seed community evenness in fragments. In particular, *Sabal mexicana* and *Dialium guianense* were by far the most abundant species in fragments providing seeds, which together represented 34% of all seeds at these sites (Table S2). The fruits from these species also are among the most commonly consumed by spider monkeys in these fragments [30], most likely because they are particularly abundant in fragments in this region (VAR, unpubl. data), and because they produce large amounts of fruits over long periods (i.e., March to August [39]). In fact, these two species were the most abundant in FF1 and FF2 (Table S1); the fragments in which these species were particularly common in the seed rain (Figure 5; Table S2). Therefore, in agreement with previous studies that have documented that spider monkeys can adapt their diet to resource availability [16,30], our results suggest that to cope with a lower availability of food resources in fragments, this primate spends more time feeding on fruits from a few largely available and productive plant species.

This hypothesis was also supported by the fact that, considering common (^{1}D) and dominant (^{2}D) seed species, the compositional dissimilarity (β-diversity) among fragments was two times higher than between continuous forest sites (Figure 3e). Spider monkeys in continuous forest areas can have access to a greater amount of top food trees, and hence, they can feed from preferred foods. In this sense, 50% of the top species (i.e., those representing 75% of the total seed rain within each site) were the same in both continuous forest sites. However, in fragments, where primates need to adapt their diet to the available foods [16,30,33], the percentage of top species that were shared between pairs of fragments averaged 35%. This higher species turnover among fragments may be largely due to the fact that plant species composition strongly differs among fragments [40], not only because of greater inter-fragment isolation distances that can limit the interchange of plant species in fragmented forests [41], but also because of the differences among fragments in disturbance regimes (e.g., edge effects, logging), that are known to influence plant community composition [40,42,43]. Thus, the species turnover in the seed rain is most likely associated with the species turnover in the available food plant communities, particularly in terms of common and dominant fruit species.

At smaller spatial scales, it was particularly interesting that β-diversity among latrines was notably lower in fragments than in continuous forest sites. This seed community homogenization can be related to the fact that inter-latrine distances are almost double in continuous forest than in fragments [23]. This distribution of sleeping sites limits the availability of food resources they can obtain in fragments, as these primates are multiple-central place foragers (sensu [44]); i.e., they feed on different trees located in the vicinity of sleeping sites, and return to the same sleeping sites after their foraging excursions. Thus, the probability of sharing the same foraging areas, and food trees, by different subgroups of spider monkeys is probably higher in fragments than in continuous forests. This can explain the compositional homogenization of the seed rain among latrines and the sharp increase in the abundance of a few plant species in some fragments.

Implications for Seed Dispersal and Forest Regeneration

Although these feeding strategies may allow primates to maintain their fruit diet in forest fragments, it may alter their effectiveness as seed dispersers in fragments. For example, in terms of dispersal quality (sensu [14]), spider monkeys appeared to deplete the fruit patches more intensively in fragments than in continuous forest sites. This can reduce the probability that such plant species are dispersed by other high-quality dispersers (e.g., howler monkeys, large birds, frugivorous bats). From the plant point of view, the higher the number of seed dispersers, the greater the probability of creating complex composite seed shadows and establishing seedlings in a larger number of suitable sites [13,45]. Additionally, seed dispersal limitation can also result directly from the deposition of a large number of seeds in latrines [5]. For example, spider monkeys deposited 4,868 seeds of *D. guianense* in fragment FF1, 2,539 seeds of *S. mexicana* in FF2 and 2,115 seeds of *Rourea glabra* in FF3; whereas dominant species in continuous forest sites showed a notably lower number of seeds (988 seeds of *Ampelocera hottlei* in CF1, and 1,220 seeds of *Mendocia retusa* in CF2). Although the accumulation of seeds in latrines could saturate seed predators and therefore allow some seeds to escape predation and recruit near latrines [11], this seed dispersal pattern clearly limits the dissemination to other potential plant recruitment sites [5]. Furthermore, because the distance among primates' sleeping sites can be a good indicator of seed dispersal distances [16], dispersal limitation is expected to be higher in fragments, in which sleeping sites are closer together [23]. In this sense, the combination of reduced inter-latrine distances in fragments and a higher abundance of seeds in latrines from these forest remnants can increase the incidence of density-dependent mortality factors (e.g., seed predators, pathogens) [6,7], limiting the establishment and survival of seedlings in latrines from fragments.

Finally, our results indicate that primates in fragments can contribute to plant community homogenization, limiting the total number of species (γ-diversity) that they can disperse in fragmented forests. An increasing number of studies have demonstrated that plant assemblages in fragmented tropical landscapes can experience a process of floristic homogenization [40,46,47].

This process has been associated with ecological filters related to intensive land-use changes, and to the alteration of seed dispersal, seedling recruitment, and survival in fragmented landscapes (reviewed by Tabarelli et al. [48]). Our results thus suggest that changes in feeding strategies of spider monkeys in fragments can lead to the homogenization of the seed rain, which in turn could result in more homogeneous seedling carpets. A similar phenomenon may also occur with other key dispersers in fragments, intensifying the pattern we document with spider monkeys, but this remains to be tested. As spider monkeys are one of the most important dispersers of large-seeded species in these regions [19,30], and fragmented forests continue to become more common in Neotropical landscapes, conservation and management efforts should concentrate on maintaining landscape connectivity. This action likely will help ameliorate the effects of homogenization of the seed rain and ultimately will help in assuring the maintenance of tropical ecosystems.

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References

1. Wang BC, Smith TB (2002) Closing the seed dispersal loop. Trend Ecol Evol 17:379–385.

2. Nathan R, Muller-Landau HC (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends Ecol Evol 15:278–285.

3. Jordano P (1992) Fruits and frugivory. In: Fenner M, editor. Seeds: The ecology of regeneration in plant communities. Wallingford: CAB International, pp. 105–156.

4. Russo SE, Chapman CA (2011) Primate seed dispersal: Linking behavioral ecology with forest community structure. In: Campbell CJ, Fuentes AF, MacKinnon KC, Panger M, Bearders S, editors. Primates in perspective. Oxford: Oxford University Press, pp. 523–534.

5. Schupp EW, Milleron T, Russo SE (2002) Dissemination limitation and the origin and maintenance of species-rich tropical forests. In: Levey DJ, Silva WR, Galetti MM, editors. Seed dispersal and frugivory: ecology, evolution and conservation. Wallingford: CAB International, pp. 19–33.

6. Janzen DH (1970) Herbivores and the number of tree species in tropical forests. Am Nat 104:501–528.

7. Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: den Boer PJ, Gradwell GR, editors. Dynamics of populations. The Netherlands: Center for Agricultural Publication and Documentation, Wageningen, pp. 298–312.

8. Feeley K (2005) The role of clumped defecation in the spatial distribution of soil nutrients and the availability of nutrients for plant uptake. J Trop Ecol 21:99–102.

9. Neves N, Feer F, Salmon S, Chateil C, Ponge JF (2010) The impact of red howler monkey latrines on the distribution of main nutrients and topsoil components in tropical rain forests. Austral Ecol 35:545–559.

10. Marsh L, Loiselle BA (2001) Recruitment of black howler fruit trees in fragmented forest of northern Belize. Int J Primatol 24:65–86.

11. Bravo SP (2012) The impact of seed dispersal by black and gold howler monkeys on forest regeneration. Ecol Res 27:311–321.

12. Howe HF, Smallwood J (1982) Ecology of seed dispersal. Ann Rev Ecol Syst 13:201–228.

13. Schupp EW, Jordano P, Gómez JM (2010) Seed dispersal effectiveness revisited:

14. Schupp EW (1993) Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio 107:15–29.

15. Stevenson PR (2000) Seed dispersal by woolly monkeys (*Lagothrix lagothricha*) at Tinigua National Park, Colombia: dispersal distance, germination rates, and dispersal quantity. Am J Primatol 50:275–289.

16. Dew JL (2008) Spider monkeys as seed dispersers. In: Campbell CJ, editor. Spider monkeys. The biology, behavior and ecology of the genus *Ateles*. New York: Cambridge University Press, pp. 155–182.

17. Link A, Di Fiore A (2006) Seed dispersal by spider monkeys and its importance in the maintenance of Neotropical rain-forest diversity. J Trop Ecol 22:235–246.

18. González-Zamora A, Arroyo-Rodríguez V, Chaves OM, Sánchez-López S, Stoner KE (2009) Diet of spider monkeys (*Ateles geoffroyi*) in Mesoamerica: current knowledge and future directions. Am J Primatol 71:8–20.

19. Chaves GM, Stoner KE, Arroyo-Rodríguez V (2011) Effectiveness of spider monkeys (*Ateles geoffroyi vellerosus*) as seed dispersers in continuous and fragmented rainforests in southern Mexico. Int J Primatol 32:177–192.

20. Russo SE, Augspurger CK (2004) Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. Ecol Lett 7:1058–1067.

21. Russo SE, Portnoy S, Augspurger CK (2006) Incorporating animal behavior into seed dispersal models: Implications for seed shadows. Ecology 87:3160–3174.

22. Chapman CA (1989) Spider monkey sleeping sites: use and availability. Am J Primatol 18:53–60.

23. González-Zamora A, Arroyo-Rodríguez V, Oyama K, Sork V, Chapman CA, et al. (2012) Sleeping sites and latrines of spider monkeys in continuous and fragmented rainforests: implications for seed dispersal and forest regeneration. PLoS ONE 7: e46852.

24. Garber PA, Estrada A, Pavelka MSM (2006) New perspective in the study of Mesoamerican Primates: concluding comments and conservation priorities. In: Estrada A, Garber PA, Pavelka MSN, Luecke M, editors. New perspective in the study of Mesoamerican primates: distribution, ecology, behaviour and conservation. New York: Springer, pp. 489–511.

25. Ramos-Fernández G, Wallace RB (2008) Spider monkey conservation in the twenty-first century: recognizing risks and opportunities. In: Campbell JC, editor. Spider monkeys. The biology, behavior and ecology of the genus Ateles. New York: Cambridge University Press, pp. 351–372.

26. Jost L (2006) Entropy and diversity. Oikos 113:363–375.

27. Jost L (2007) Partitioning diversity into independent alpha and beta components. Ecology 88:2427–2439.

28. Jost L (2010) The relation between evenness and diversity. Diversity 2:207–232.

29. Chao A, Jost L (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93:2533–2547.

30. Chaves OM, Stoner KE, Arroyo-Rodríguez V (2012) Differences in diet between spider monkey groups living in forest fragments and continuous forest in Lacandona, Mexico. Biotropica 44:105–113.

31. Chapman CA, Chapman LJ, Wrangham R, Hunt K, Gebo D, et al. (1992) Estimators of fruit abundance of tropical trees. Biotropica 24:527–531.

32. Arroyo-Rodríguez V, Mandujano S (2006) Forest fragmentation modifies habitat quality for *Alouatta palliata*. Int J Primatol 27:1079–1096.

33. Dunn JC, Cristóbal-Azkarate J, Vea J (2009) Differences in diet and activity pattern between two groups of *Alouatta palliata* associated with the availability of big trees and fruit of top food taxa. Am J Primatol 71:654–662.

34. Chapman CA (1987) Patch use and patch depletion by the spider and howling monkeys of Santa Rosa National Park, Costa Rica. Behaviour 105:99–116.

35. Tombak KJ, Reid AJ, Chapman CA, Rothman JM, Johnson CA, et al. (2012) Patch depletion behavior differs between sympatric folivorous primates. Primates 53:57–64.

36. Ibarra-Manríquez G, Cornejo-Tenorio G (2010) Diversidad de frutos de los árboles del bosque tropical pefennifolio de México. Acta Bot Mex 90:51–104.

37. Crawley M (2002) Statistical computing: An introduction to data analysis using S-Plus. Chichester: John Wiley and Sons, 772 p.

38. Grafen A, Hails R (2002) Modern statistics for the life sciences. Oxford University Press, Oxford. 351 p.

39. Ochoa-Gaona S, Domíngez-Vásquez G (2000) Distribución y fenología de la flora leñosa de Chajul, Selva Lacandona, Chiapas, México. Brenesia 54:1–24.

40. Arroyo-Rodríguez V, Rös M, Escobar F, Melo FPL, Santos BA, et al. (2013) Plant β-diversity in fragmented rainforests: testing floristic homogenization and differentiation hypotheses. J Ecol 101:1449–1458.

41. Hubbell SP (2001) The Unified Neutral Theory of Biodiversity and Biogeography. Princeton: Princeton University Press. 448 p.

42. Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, et al. (2002) Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conserv Biol 16:605–618.

43. Tabarelli M, Lopes AV, Peres CA (2008) Edge-effects drive tropical forest fragments towards an early-successional system. Biotropica 40:657–661.

44. Chapman CA, Chapman LJ, McLaughlin RL (1989) Multiple central place foraging by spider monkeys: travel consequences of using many sleeping sites. Oecologia 79:506–511.

45. Schupp EW (2007) The suitability of a site for seed dispersal is context-dependent. In: Dennis AJ, Schupp EW, Green RA, Wescott DA, editors. Seed dispersal. Theory and its application in a changing world. Wallingford: CAB International, pp.445–462.

46. Chapman CA, Onderdonk DA (1998) Forests without primates: Primate/plant codependency. Am J Primatol 45:127–141.

47. Lôbo D, Leao T, Melo FPL, Santos AMM, Tabarelli M (2011) Forest fragmentation drives Atlantic forest of northeastern Brazil to biotic homogenization. Divers Distrib 17:287–296.

48. Tabarelli M, Peres CA, Melo FPL (2012) The ‘few winners and many losers’ paradigm revisited: Emerging prospects for tropical forest biodiversity. Biol Conserv 155:136–140.

Figure legend

Figure 1. Hierarchically nested sampling design. The figure shows the spatial scales used to assess differences in species diversity of seeds defecated by spider monkeys (*Ateles geoffroyi*) in latrines located in continuous and fragmented forest in the Lacandona region, Mexico. Seed species diversity was partitioned into α- and β-components considering three spatial scales, from larger to smaller: (i) the diversity of the landscape (γ_{land}) was partitioned into mean alpha (α_{forest}) and beta (β_{forest}) diversities in the two forest conditions; (ii) the diversity within each forest condition (γ_{forest}) was partitioned into mean alpha (α_{site}) and beta (β_{site}) diversities in the sites; and (iii) the diversity within each site (γ_{site}) was partitioned into mean alpha (α_{latrine}) and beta (β_{latrine}) diversities in the 12 sampling latrines.

Figure 2. **Abundance of seeds deposited by spider monkeys in latrines located in continuous and fragmented forests in the Lacandona region, Mexico**. We show differences between forest conditions considering medians per site (a), and among sites based on medians per latrine (b). FF = forest fragments ordered from the largest to the smallest; CF = continuous forest sites.

Figure 3. **Seed species diversity in spider monkeys' latrines located in continuous and fragmented forests in the Lacandona region, Mexico**. From left to right, the panels show γ-, β-, and α-components of diversity at three spatial scales. The diversity of the landscape (γ_{land}; panel a) was partitioned into mean β- (b) and α- (c) diversities within the two forest conditions. The diversity within each forest condition (γ_{forest}; panel d) was partitioned into mean β- (e) and α- (f) diversities in the sites. Finally, the diversity within each site (γ_{site}; panel g) was partitioned into mean β- (h) and α- (i) diversities in latrines. Mean (± SE) α-diversities per forest condition, per site and per latrine is indicated in panels c, f and i, respectively (in panels f and i, significant differences are indicated with asterisks; * $P < 0.05$; ** $P < 0.01$; n.s. $P > 0.05$). In all cases, we evaluated true diversities of order 0 (species richness), 1 (exponential of Shannon's entropy), and 2 (inverse Simpson concentration); however, in panel e we compared the relative compositional dissimilarity between forest conditions using the transformation of beta proposed by Jost (2007) for communities with different numbers of samples (CF: $n = 2$; FF: $n = 3$) (see Materials and Methods).

Figure 4. **Species evenness in seeds deposited by spider monkeys in latrines located in continuous and fragmented forests in the Lacandona region, Mexico**. Differences across spatial scales are indicated; from the landscape scale (i.e., including both forest conditions) to the latrine scale. Means (± SE) per site and per latrine are indicated for the site and latrine spatial scales. Significant differences among sites are indicated with different letters ($P = 0.01$). The evenness factor did not differ between forest conditions (n.s., $P > 0.05$).

Figure 5. **Relative abundance of seeds deposited by spider monkeys in latrines located in each study site**. The identity of dominant species within each site is indicated: 1. *Sabal mexicana*; 2. *Dialium guianense*; 3. *Castilla elastica*; 4. *Spondias radlkoferi*; 5. *Trophis mexicana*; 6. *Rourea glabra*; 7. *Paullinia costata*; 8. *Bactris mexicana*; 9. *Trichostigma octandrum*; 10. *Ampelocera hottlei*; 11. *Mendoncia retusa*.

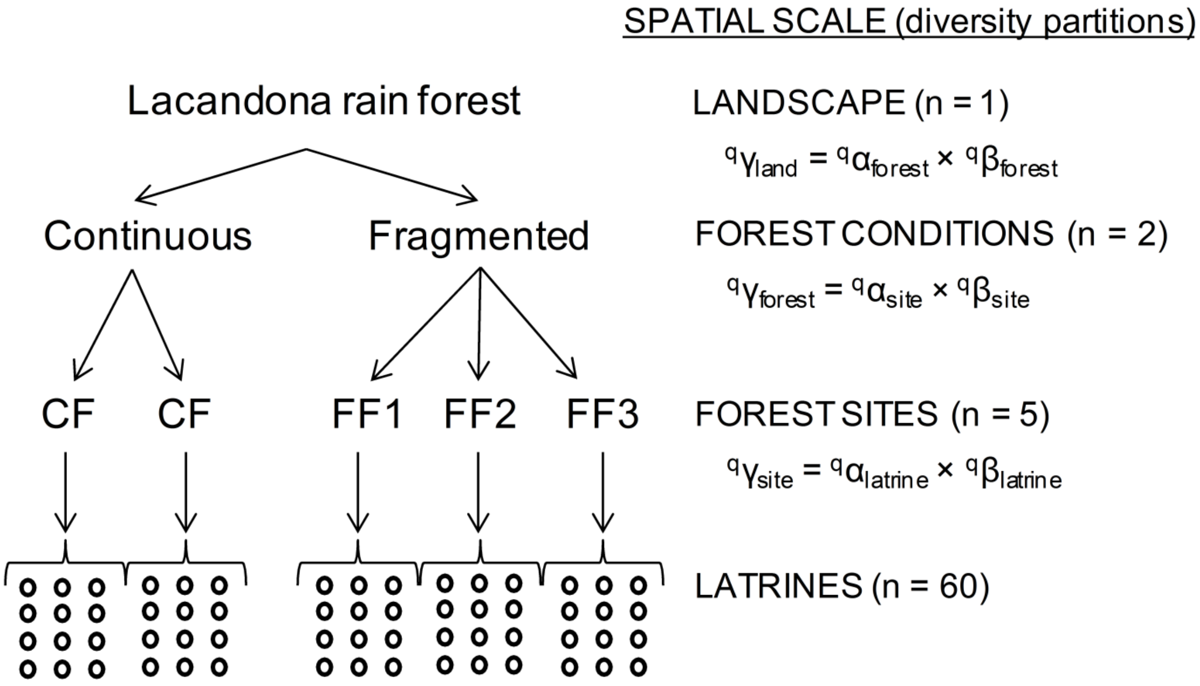

SPATIAL SCALE (diversity partitions)
Lacandona rain forest
LANDSCAPE (n = 1)
${}^{q}\gamma_{land} = {}^{q}\alpha_{forest} \times {}^{q}\beta_{forest}$
Continuous
Fragmented
FOREST CONDITIONS (n = 2)
${}^{q}\gamma_{forest} = {}^{q}\alpha_{site} \times {}^{q}\beta_{site}$
CF
CF
FF1
FF2
FF3
FOREST SITES (n = 5)
${}^{q}\gamma_{site} = {}^{q}\alpha_{latrine} \times {}^{q}\beta_{latrine}$
LATRINES (n = 60)

Figure 1

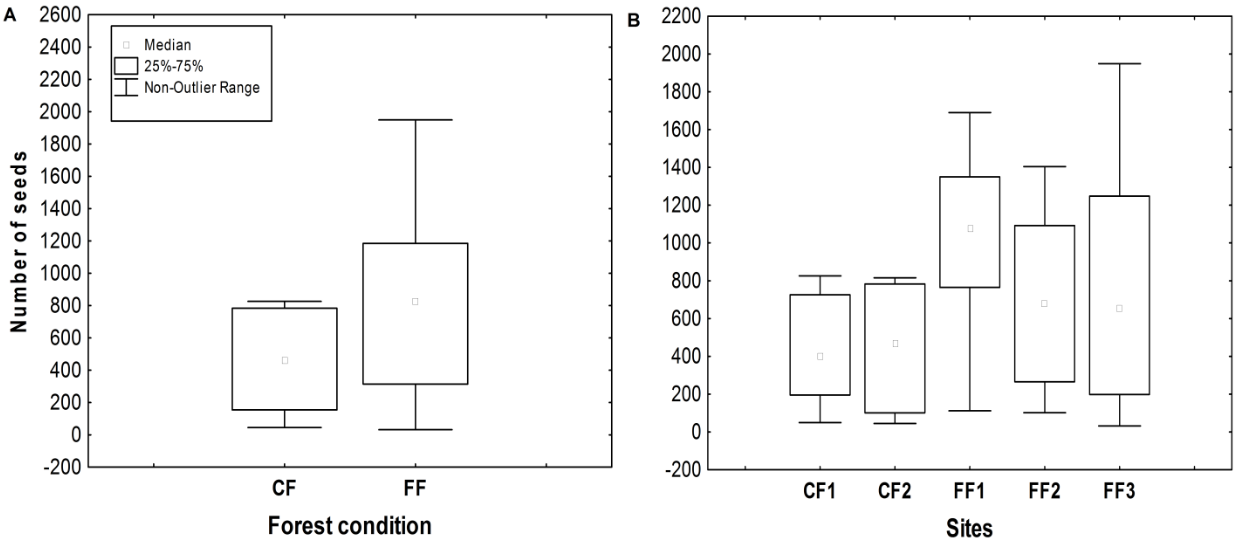

A
B
Median
25%-75%
Non-Outlier Range
Number of seeds
2600
2400
2200
2000
1800
1600
1400
1200
1000
800
600
400
200
0
-200
CF
FF
Forest condition
CF1
CF2
FF1
FF2
FF3
Sites

Figure 2

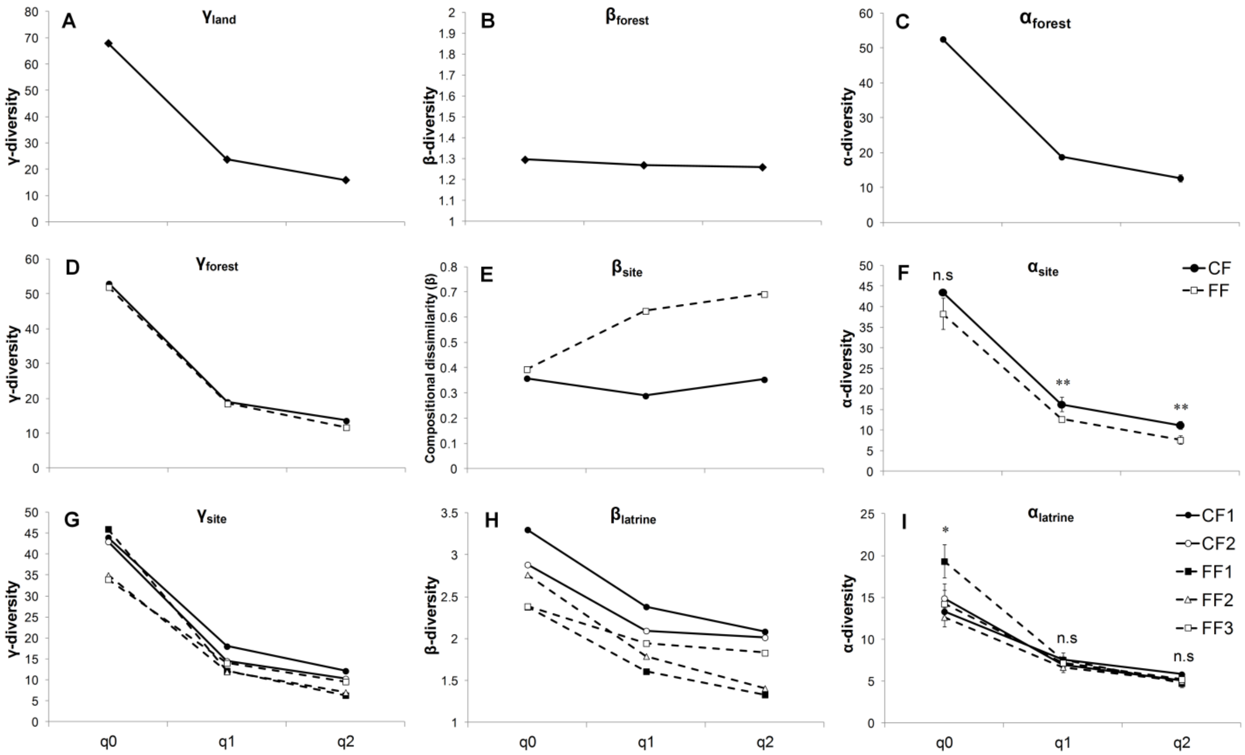
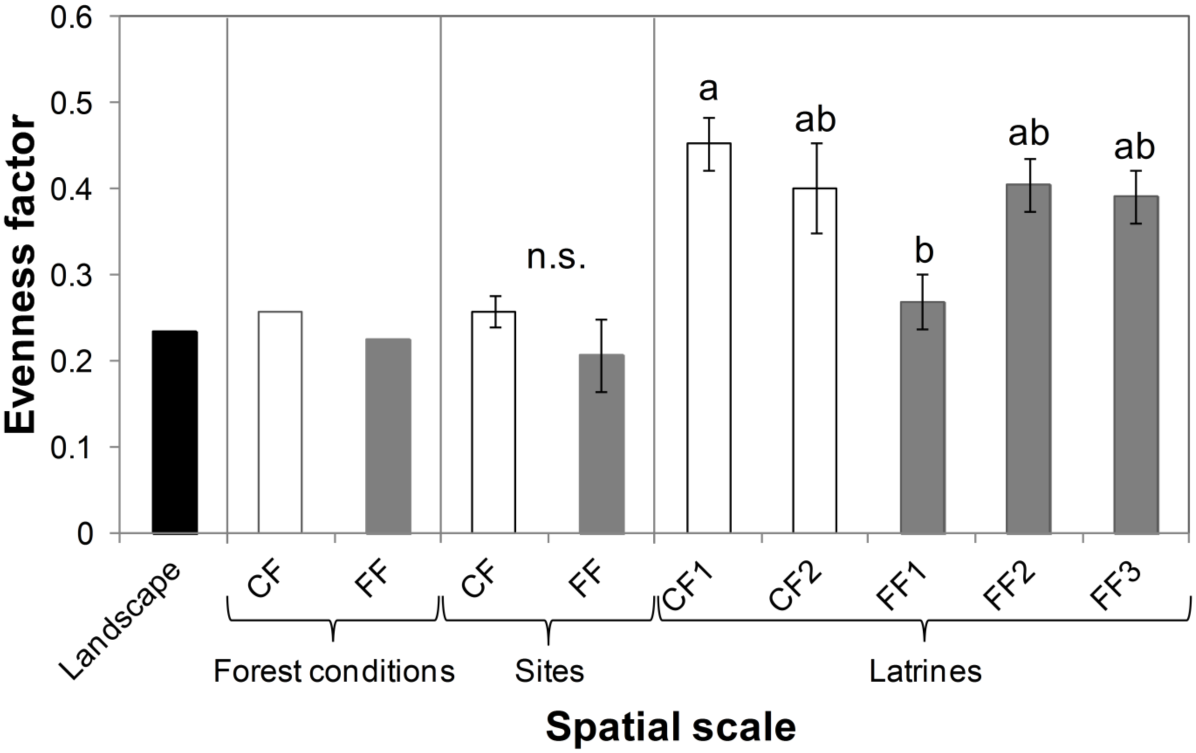

A
γland
γ-diversity
B
βforest
β-diversity
C
αforest
α-diversity
D
γforest
γ-diversity
E
βsite
Compositional dissimilarity (β)
F
αsite
α-diversity
n.s
**
**
CF
FF
G
γsite
γ-diversity
H
βlatrine
β-diversity
I
αlatrine
α-diversity
*
n.s
n.s
CF1
CF2
FF1
FF2
FF3
q0
q1
q2

Figure 3



0.6
0.5
0.4
0.3
0.2
0.1
0
Evenness factor
a
ab
ab
ab
b
n.s.
Landscape
CF
FF
CF
FF
CF1
CF2
FF1
FF2
FF3
Forest conditions
Sites
Latrines
Spatial scale

Figure 4

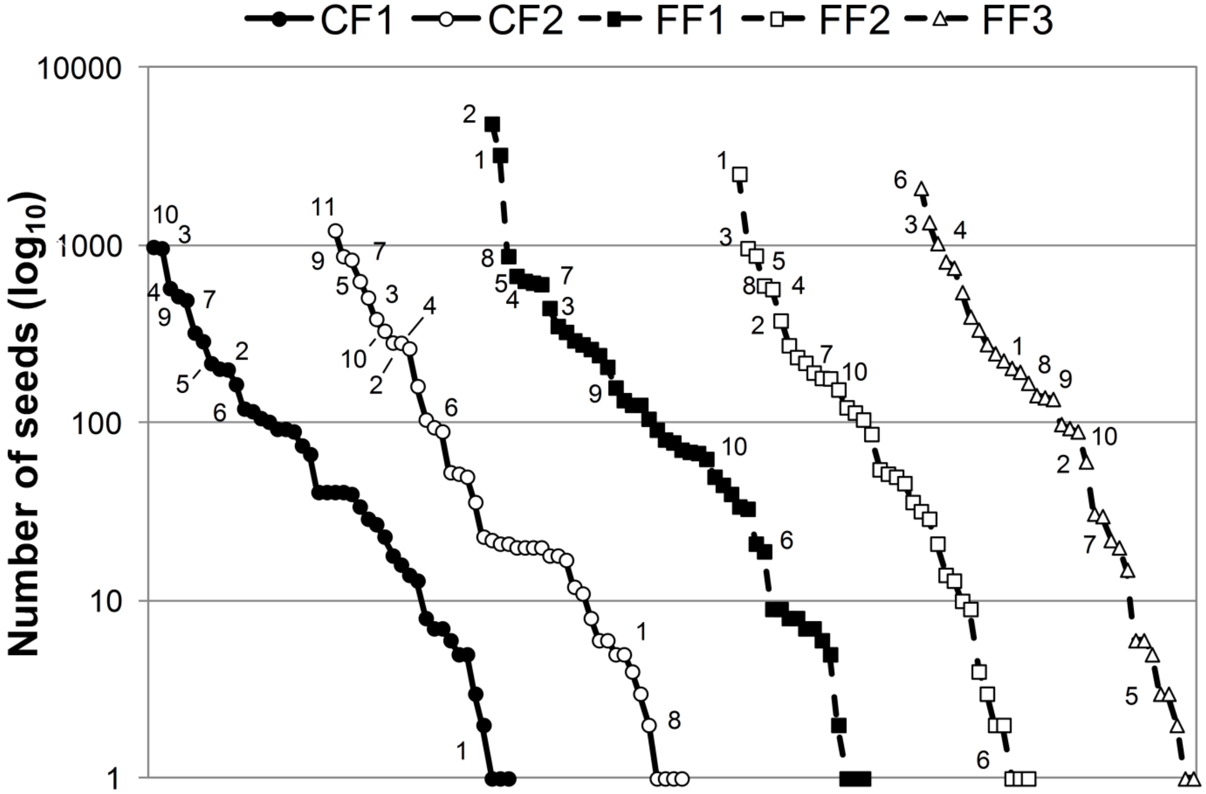

CF1
CF2
FF1
FF2
FF3
Number of seeds ($\log_{10}$)
10000
1000
100
10
1
10
3
4
7
9
5
2
6
1
11
9
7
5
3
4
10
2
6
1
8
2
1
8
5
7
4
3
9
10
6
1
3
5
8
4
2
7
10
6
6
3
4
1
8
9
10
2
7
5

Figure 5

Supplementary Information

Appendix S1. Differences among sites and between forest conditions in vegetation composition and structure.

Table S1. Availability of top food tree species in continuous forest sites and fragmented forests in the Lacandona region, Mexico. The total number of trees and total basal area (m^2, in parentheses) is indicated for each tree species.

Table S2. Seed species deposited by spider monkeys during a 13-mo period in 60 latrines located in two continuous forest sites and three forest fragments in the Lacandona region, Mexico. The total number of seeds (and percentages, in parentheses) is indicated for each forest condition and for the entire landscape (i.e., considering both forest conditions).

Figure S1. Tree species diversity in continuous and fragmented forest sites in the Lacandona region, Mexico. In panel (a) we indicate values for all trees with DBH > 10 cm, whereas in panel (b) we show values for the top food tree species. Means (± SE) per site are indicated. In all cases, differences were not significant ($P > 0.05$). In all cases, we evaluated true diversities of order 0 (species richness), 1 (exponential of Shannon’s entropy), and 2 (inverse Simpson concentration).

Appendix S1. Differences among sites and between forest conditions in vegetation composition and structure.

To assess if differences in seed species diversity between forest conditions could be related to inter-forest variations in vegetation structure, we sampled vegetation within each site following the Gentry [1] protocol. We randomly located twenty 50 x 2-m transects (2,000 m^2) and identified and measured the diameter at breast height (dbh) of all trees with dbh ≥ 10 cm. We chose this method because it has been used to describe the habitat of other Mexican primates (e.g., *Alouatta palliata* [2-4], *Ateles geoffroyi* [5]), and hence, it is possible to compare our data with other Mexican sites.

For each site (i.e., pooling the transect data for each site), we quantified tree species diversity using true diversity measures of order 0, 1 and 2 (see the text for further details on these metrics). Additionally, using data from a recent review of spider monkey's diet in Mesoamerica [6], we identified all plant species that together constituted > 80% of total feeding time (TFT) in this review paper and that were present in our study transects. We considered these species as potential top food species contributing to resource abundance, and we then calculated true diversities of order 0, 1 and 2 for these top food tree species. Additionally, we calculated total stem density and total basal area of top food species within each site.

The differences between forest conditions in tree species diversity, and in density and basal area of top food species were tested with generalized linear models. As suggested for count dependent variables (i.e., diversity of order 0 and density of top food trees), we used a Poisson error and a log link function. For the basal area of top foods and for the diversities of order 1 and 2 we used normal error and identity link function [7].

Both forest conditions showed a similar number of tree species (Figure S1a). This was evident when considering rare (i.e., ${}^0D$, species richness) ($\chi^2 = 0.08$, df = 1, $P = 0.77$), common (i.e., ${}^1D$, exponential of Shannon's entropy) ($\chi^2 = 1.02$, df = 1, $P = 0.31$), and dominant (${}^2D$, inverse Simpson concentration) tree species ($\chi^2 = 1.67$, df = 1, $P = 0.27$). When assessing the top food tree species, tree species diversity was also similar in both forest conditions when considering ${}^0D$ ($\chi^2 = 0.02$, df = 1, $P = 0.087$), ${}^1D$ ($\chi^2 = 0.09$, df = 1, $P = 0.75$) and ${}^2D$ ($\chi^2 = 0.62$, df = 1, $P = 0.43$) (Figure S1b). However, tree density of top food species was higher in continuous forest (mean ± SE, 133 ± 22 stems/2,000 m^2) than in forest fragments (90 ± 31 stems/2,000 m^2; $\chi^2 = 104.4$, df = 1, $P < 0.001$; Table S1). The basal area of top food species was also higher in continuous (15.1 ± 1.27 m^2) than in fragmented forest sites (7.26 ± 1.84 m^2) ($\chi^2 = 44.1$, df = 1, $P < 0.001$; Table S1).

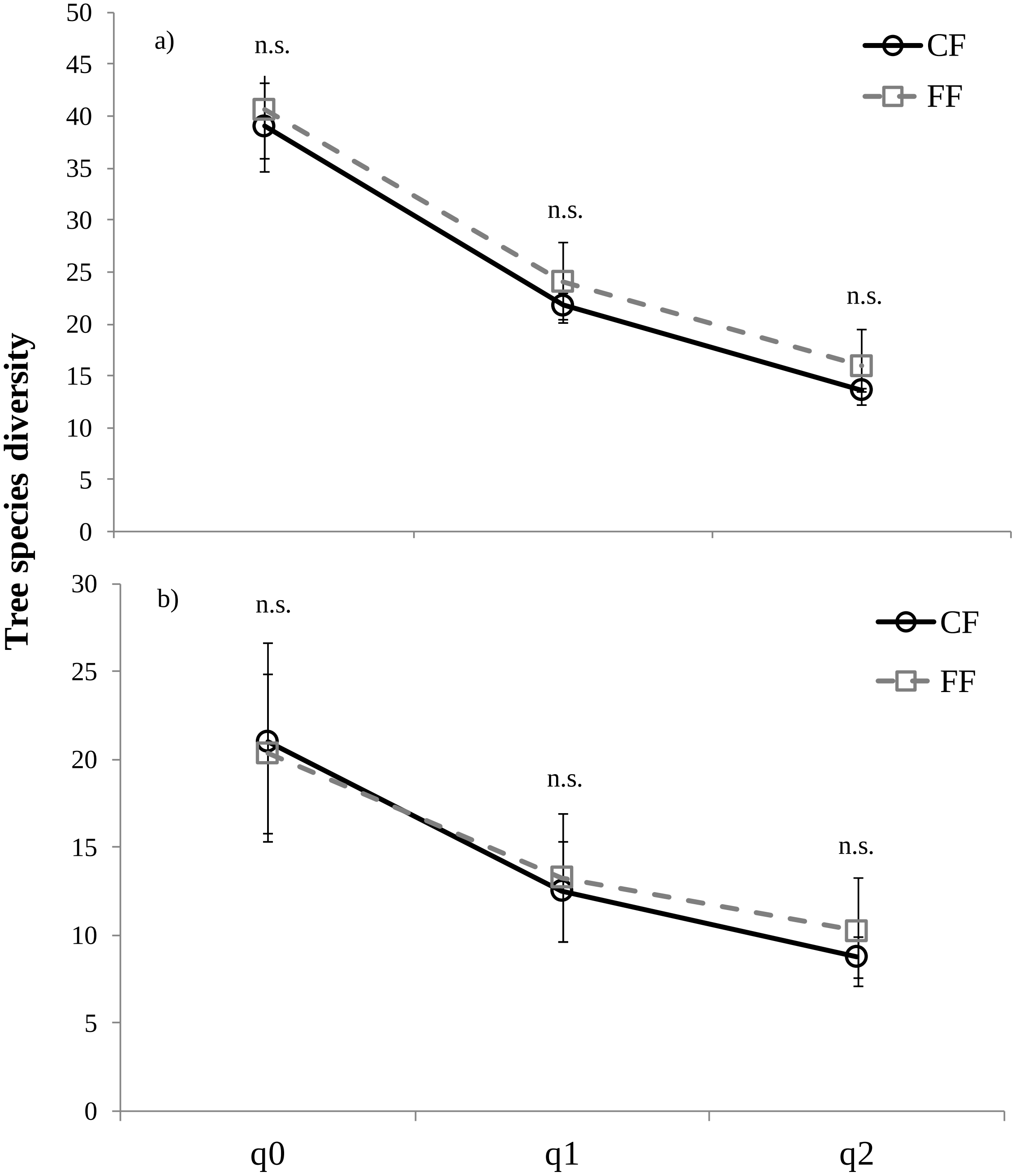


Figure 1. Tree species diversity in continuous and fragmented forest sites in the Lacandona region, Mexico. In panel (a) we indicate values for all trees with DBH > 10 cm, whereas in panel (b) we show values for the top food tree species. Means (± SE) per site are indicated. In all cases, differences were not significant ($P > 0.05$). In all cases, we evaluated true diversities of order 0 (species richness), 1 (exponential of Shannon's entropy), and 2 (inverse Simpson concentration).

Table S1. Availability of top food tree species in continuous forest sites and fragmented forests in the Lacandona region, Mexico. The total number of trees and total basal area (m^2, in parentheses) is indicated for each tree species.

Species	**Family**	**CF1**	**CF2**	**FF1**	**FF2**	**FF3**
Ampelocera hottlei	Ulmaceae	8 (1.08)	13 (0.39)	0	2 (0.11)	1 (0.04)
Attalea butyracea	Arecaceae	0	0	0	7 (0.74)	2 (0.29)
Brosimum alicastrum	Moraceae	2 (0.50)	7 (0.98)	8 (0.66)	7 (1.59)	5 (1.79)
Brosimum costaricanum	Moraceae	0	2 (0.05)	0	0	0
Brosimum lactescens	Moraceae	0	0	0	3 (0.09)	0
Bursera simaruba	Burseraceae	1 (0.00)	0	0	7 (0.41)	0
Castilla elastica	Moraceae	4 (0.29)	10 (1.92)	0	5 (0.15)	7 (0.24)
Cecropia obtusifolia	Urticaceae	1 (0.05)	4 (0.19)	0	0	1 (0.01)
Coccoloba sp.	Polygonaceae	0	1 (0.20)	0	0	0
Cojoba arborea	Fabaceae	4 (1.41)	3 (0.28)	0	0	1 (0.02)
Cupania sp.	Sapindaceae	0	1 (0.03)	0	0	0
Dialium guianense	Fabaceae	9 (1.16)	13 (1.65)	17 (1.14)	18 (0.63)	2 (0.19)
Faramea occidentalis	Rubiaceae	0	0	0	0	1 (0.02)
Ficus aurea	Moraceae	0	0	0	0	1 (0.97)
Ficus sp.	Moraceae	4 (3.35)	1 (1.99)	0	1 (0.72)	0
Guarea glabra	Meliaceae	18 (0.79)	37 (0.85)	11 (0.16)	9 (0.29)	13 (0.49)
Guarea sp.	Meliaceae	0	0	3 (0.03)	0	1 (0.01)
Guarea grandifolia	Meliaceae	2 (0.06)	0	1 (0.01)	0	0
Hirtella americana	Chrysobalanaceae	0	0	0	1 (0.01)	0
Inga sp.	Fabaceae	1 (0.01)	0	0	1 (0.15)	4 (0.13)
Inga pavoniana	Fabaceae	1 (0.02)	1 (0.01)	0	1 (0.01)	1 (0.04)
Inga punctata	Fabaceae	0	1 (0.06)	1 (0.03)	0	0
Licania sp.	Chrysobalanaceae	0	2 (0.02)	0	0	0
Licania platypus	Chrysobalanaceae	6 (0.92)	4 (2.20)	5 (1.18)	4 (0.59)	5 (2.56)
Lonchocarpus sp.	Fabaceae	0	1 (0.06)	1 (0.01)	2 (0.13)	0
Lonchocarpus cruentus	Fabaceae	0	0	0	2 (0.13)	0
Mortoniodendron guatemalense	Malvaceae	2 (0.69)	0	0	0	0
Nectandra ambigens	Lauraceae	0	3 (0.07)	1 (0.13)	0	4 (0.15)
Nectandra sp.	Lauraceae	0	2 (0.03)	0	1 (0.01)	0
Poulsenia armata	Moraceae	0	0	0	0	5 (0.19)
Pouteria sp.1	Sapotaceae	7 (0.12)	3 (0.06)	0	9 (0.19)	0
Pouteria campechiana	Sapotaceae	0	0	3 (0.09)	1 (0.01)	5 (0.22)
Protium copal	Burseraceae	2 (0.04)	6 (0.11)	1 (0.01)	0	0
Pterocarpus rohrii	Fabaceae	0	0	3 (0.80)	1 (0.14)	0
Quararibea funebris	Malvaceae	23 (0.81)	15 (0.43)	0	0	1 (0.05)

Sabal mexicana	Arecaceae	0	0	19 (0.63)	18 (0.64)	0
Spondias mombin	Anacardiaceae	24 (4.66)	0	1 (0.08)	9 (0.47)	1 (0.02)
Spondias radlkoferi	Anacardiaceae	0	9 (1.75)	2 (0.23)	11 (1.38)	6 (1.18)
Tabebuia chrysantha	Bignoniaceae	0	0	1 (0.02)	0	0
Tabebuia guayacan	Bignoniaceae	0	0	0	1 (0.07)	0
Magnolia mexicana	Magnoliaceae	0	5 (0.49)	0	0	0
Terminalia amazonia	Combretaceae	0	0	0	1 (0.13)	0
Trichospermum mexicanum	Malvaceae	0	0	0	4 (0.21)	0
Trophis mexicana	Moraceae	0	1 (0.05)	0	0	0
Virola guatemalensis	Myristicaceae	0	4 (0.35)	0	0	0
Total		117 (16.0)	149 (14.2)	78 (5.2)	126 (8.9)	67 (7.6)

Table S2. **Seed species deposited by spider monkeys during a 13-mo period in 60 latrines located in two continuous forest sites and three forest fragments in the Lacandona region, Mexico**. The total number of seeds (and percentages, in parentheses) is indicated for each forest condition and for the entire landscape (i.e., considering both forest conditions).

Species	**Family**	**Number (and percentage) of seeds**		
		Continuos forest	**Forest fragments**	**Total**
Sabal mexicana	Arecaceae	7 (0.0%)	6,011 (18.1%)	6,018 (13.1%)
Dialium guianense	Fabaceae	486 (3.8%)	5,308 (16.0%)	5,794 (12.6%)
Castilla elastica	Moraceae	1,479 (11.5%)	2,771(8.3%)	4,250 (9.2%)
Spondias radlkoferi	Anacardiaceae	861 (6.7%)	2,019 (6%)	2,880 (6.2%)
Trophis mexicana	Moraceae	835 (6.5%)	1,559 (4.7%)	2,394 (5.2%)
Rourea glabra	Connaraceae	211 (1.6)	2,150 (6.4%)	2,361 (5.1%)
Paullinia costata	Sapindaceae	1,328 (10.3%)	822 (2.4%)	2,150 (4.6%)
Bactris mexicana	Arecaceae	2 (0.01%)	1,665 (5%)	1,667 (3.6%)
Trichostigma octandrium	Phytolaccaceae	1,393 (10.8%)	267 (0.8%)	1,660 (3.6%)
Ampelocera hottlei	Ulmaceae	1,316 (10.2%)	320 (0.9%)	1,636 (3.5%)
Mendoncia retusa	Acanthaceae	1,313 (10.2%)	293 (0.8%)	1,606 (3.4%
Nectandra ambigens	Lauraceae	123 (0.9%)	1294 (3.9%)	1,417 (3.0%)
Spondias mombin	Anacardiaceae	35 (0.2%)	1162 (3.5%)	1,197 (2.6%)
Acacia cornígera	Fabaceae	33(0.2%)	856 (2.5%)	889 (1.9%)
Bactris americana	Arecaceae	1 (0%)	875 (2.6%)	876 (1.9%)
Celtis iguanea	Cannabaceae	188 (1.4%)	670 (2%)	858 (1.8%)
Arecaceae (1)	Arecaceae	42 (0.3%)	727 (2.1%)	769 (1.6%)
Virola guatemalensis	Myristicaceae	588 (4.5%)	44 (0.1%)	632 (1.3%)
Morphoespecie (3)	-	340 (2.6%)	279 (0.8%)	619 (1.3%)
Desmoncus ortacanthus	Arecaceae	49 (0.3%)	496 (1.4%)	545 (1.1%)
Guarea glabra	Meliaceae	323 (2.5%)	192 (0.5%)	515 (1.1%)
Attalea butyraceae	Arecaceae	25 (0.1%)	466 (1.4%)	491 (1.0%)
Theobroma cacao	Malvaceae	0	470 (1.4%)	470 (1.0%)
Brosimum lactescens	Moraceae	162 (1.2%)	254 (0.7%)	416 (0.9%)
Morphoespecie (2)	-	388 (3.0%)	0	388 (0.8%)
Serjania sp.	Sapindaceae	2 (0.0%)	255 (1.0%)	357 (0.6%)
Inga sp.	Fabaceae	93 (0.7%)	259 (0.7%)	352 (0.6%)
Faramea occidentalis	Rubiaceae	18(0.1%)	282 (0.8%)	300 (0.3%)
Morphoespecie (1)	-	129(1%)	129 (0.3%)	258 (0.5%)
Smilax sp.	Smilacaceae	0	252 (0.7%)	252 (0.5%)
Morphoespecie (5)	-	166 (1.2%)	0	166 (0.3%)
Abuta panamensis	Menispermaceae	142(1.1%)	20 (0.0%)	162 (0.3%)
Vitaceae	Vitaceae	0	137 (0.4%)	137 (0.2%)
Syngonium sp.	Araceae	59(0.4%)	72 (0.21%)	131 (0.2%)
Rollinia sp.	Annonaceae	123(0.9%)	0	123 (0.2%)
Strichnos tabascana	Loganiaceae	0	114 (0.3%)	114 (0.2%)
Posoqueria latifolia	Rubiaceae	27(0.2%)	81 (0.2%)	108 (0.2%)
Lauraceae	Lauraceae	0	106(0.3%)	106 (0.2%)
Morphoespecie (4)	-	0	105(0.3%)	105 (0.2%)
Cissus microcarpa	Vitaceae	77(0.6%)	25(0.07%)	101 (0.2%)
Chionantus dominguensis	Oleaceae	78(0.6%)	21(0.06%)	99 (0.2%)
Garcinia intermedia	Clusiaceae	18(0.1%)	71(0.2%)	89 (0.1%)
Hirtella americana	Chrysobalanaceae	67(0.5%)	0	67 (0.1%)
Inga punctata	Fabaceae	31(0.2%)	16(0.04%)	47 (0.1%)
Guarea grandifolia	Meliaceae	41(0.3%)	1(0.0%)	42 (0.9%)

Bursera simaruba	Burseraceae	15(0.1%)	22(0.06%)	37 (0.8%)
Chamaedorea tepejilote	Arecaceae	0	34(0.1%)	34 (0.7%)
Cupania sp.	Sapindaceae	34(0.2%)	0(0%)	34 (0.7%)
Cissus sp.	Vitaceae	26(0.2%)	0(0%)	26 (0.05%)
Arecaceae (2)	Arecaceae	23(0.1%)	0(0%)	23 (0.05%)
Araceae	Araceae	8(0.06%)	13(0.03%)	21(0.04%)
Pseudolmedia glabrata	Moraceae	21(0.1%)	0	21 (0.04%)
Arecaceae (3)	Arecaceae	16(0.1%)	0	16 (0.03%)
Trophis racemosa	Moraceae	0	13 (0.03%)	13 (0.03%)
Mollinedia sp.	Monimiaceae	12(0.09%)	0	12 (0.02%)
Guazuma ulmifolia	Malvaceae	0	10 (0.03%)	10 (0.02%)
Clarisia racemosa	Moraceae	8(0.06%)	0	8 (0.01%)
Monstera sp.	Araceae	0	8(0.02%)	8 (0.01%)
Psichotrya chiapensis	Rubiaceae	0	8(0.02%)	8 (0.01%)
Tetracera sp.	Dilleniaceae	0	7(0.02%)	7 (0.01%)
Myrtaceae	Myrtaceae	6(0.04%)	0	6 (0.01%)
Anturio sp.	Araceae	5(0.03%)	0	5 (0.01%)
Calatola sp.	Icacinaceae	5(0.03%)	0	5 (0.01%)
Licaria hipoleuca	Lauraceae	5(0.03%)	0	5 (0.01%)
Passiflora helleri	Passifloraceae	0	2(0.0%)	2 (0%)
Magnolia mexicana	Magnoliaceae	2(0.01%)	0	2 (%)
Cymbopetalum pendiflorum	Annonaceae	0	1(0.0%)	1 (%)
Pouteria sp.	Sapotaceae	0	1(0.0%)	1 (%)

References

1. Gentry AH (1982) Patterns of Neotropical plant species diversity. Evol Biol 15:1–84.

2. Arroyo-Rodríguez V, Mandujano S (2006) Forest fragmentation modifies habitat quality for *Alouatta palliata*. Int J Primatol 27:1079–1096.

3. Arroyo-Rodríguez V, Mandujano S, Benítez-Malvido J, Cuende Fanton C (2007) The influence of large tree density on howler monkey (*Alouatta palliata mexicana*) presence in very small rain forest fragments. Biotropica 39:760–766.

4. Dunn JC, Cristóbal-Azkarate J, Vea J (2009) Differences in diet and activity pattern between two groups of *Alouatta palliata* associated with the availability of big trees and fruit of top food taxa. Am J Primatol 71:654–662.

5. Chaves OM, Stoner KE, Arroyo-Rodríguez V (2012) Differences in diet between spider monkey groups living in forest fragments and continuous forest in Lacandona, Mexico. Biotropica 44:105–113.

6. González-Zamora A, Arroyo-Rodríguez V, Chaves OM, Sánchez S, Stoner KE, Riba-Hernández P (2009) Diet of spider monkeys (*Ateles geoffroyi*) in Mesoamerica: Current knowledge and future directions. Am J Primatol 71:8–20.

7. Crawley M (2002) Statistical computing: An introduction to data analysis using S-Plus. Chichester: John Wiley and Sons, 772 p.

CAPÍTULO V:

SLEEPING TREE FIDELITY OF SPIDER MONKEYS SHAPES COMMUNITY-LEVEL SEED RAIN PATTERNS IN CONTINUOUS AND FRAGMENTED RAINFORESTS

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Sleeping tree fidelity of spider monkeys shapes community-level seed rain patterns in continuous and fragmented rainforests

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Abstract

The repeated use of sleeping sites by frugivorous vertebrates can promote the deposition and aggregation of copious amounts of seeds in these sites, thus having key implications for seed dispersal and forest regeneration. Seed rain patterns produced by this behavior are expected to depend on the frequency of use of these sites (site fidelity); yet this hypothesis has been poorly tested. We evaluated community-level seed rain patterns produced by spider monkeys (*Ateles geoffroyi*) during a 13-mo period in latrines located beneath 60 sleeping trees in the Lacandona rainforest, Mexico. Because these primates are increasingly 'forced' to inhabit fragmented landscapes, we first tested if the frequency of use of sleeping trees, STF (i.e., as the number of months each sleeping tree was used during the study period) differed among study sites and between continuous and fragmented forests. We then tested if the seed rain patterns beneath sleeping trees were associated to STF within each site and forest condition. STF was highly variable among sleeping trees, but did not differ among study sites or between forest conditions. As predicted, STF was positively associated with the abundance of seeds, seed species diversity and seed species turnover (β-diversity) in most sites. Nevertheless, STF tended to be negatively related to seed community evenness. These novel findings can be explained by the fact that the sleeping trees most frequently used are located in core areas of the home range with greater density of available food trees. Our results demonstrate that site fidelity shapes community-level seed rain patterns and thus has key ecological and conservation implications.

Keywords

Ateles · Contagious seed dispersal · Frugivory · Lacandona · Sleeping site.

Introduction

Animal seed dispersal has key ecological, evolutionary and conservation implications for both the animal and plant species involved, as well as for ecosystem functioning (Herrera 2002; Schupp et al. 2010). The initial pattern of seed deposition affects the number of seedlings and saplings present in a given area, and determines both the spatial distribution of individuals in a given population and the species composition and structure of plant communities (Wang and Smith 2002; Schupp et al. 2010), particularly because such patterns can persist through recruitment (see Russo and Augspurger 2004). Assessing patterns of seed rain thus represents a fundamental step to understand the spatial structure and regeneration of plant assemblages (Nathan and Muller-Landau 2000). Although seed deposition is usually spatially aggregated (Schupp et al. 2002), the impact that this component of seed dispersal may have at the community level is poorly understood, as most studies have been focused on only a few plant populations (e.g., Herrera et al. 1994; Julliot 1997; Fragoso 1997; Russo and Augspurger 2004).

The repeated use of perches, roosting sites, reproductive sites and sleeping sites by frugivorous vertebrates promote the deposition and aggregation of copious amounts of seeds in these sites (Wenny 2001; Russo and Augspurger 2004; Melo et al. 2009; Karubian and Duraes 2009; González-Zamora et al. 2012). These behaviors have key implications for seed dispersal and forest regeneration (Jordano and Schupp 2000; Schupp et al. 2002, 2010), particularly in tropical forests where up to 94% of woody plant species are dispersed by frugivorous animals (Jordano 1992). The importance of this spatially aggregated seed deposition pattern for seed dispersal is, however, largely dependent on site fidelity, (i.e., the frequency of use of these sites: Wenny 2001; Schupp et al. 2010) yet, empirical evidence on this relation is scarce.

Site fidelity is particularly common in territorial animals (e.g., Börger et al. 2008), such as the Geoffroyi's spider monkey (*Ateles geoffroyi*) (Chapman et al. 1995; Asensio et al. 2012a; Ramos-Fernández et al. 2013). This primate is a highly specialized frugivore (González-Zamora et al. 2009) that defends stable home ranges (Wallace 2008; Asensio et al. 2012a). As multi-central place foragers (sensu Chapman et al. 1989), they feed on several plants located near sleeping trees, and return to the same sleeping trees after their feeding excursions. Nevertheless, because they concentrate their activities in particular regions of their home ranges (i.e., core areas) that are known to be of higher quality (Asensio et al. 2012b), sleeping trees located within core areas are more frequently used than sleeping trees located outside of these areas because they are used occasionally during exploratory excursions and territory defense (Chapman 1990a; Shimooka 2005; Wallace 2008; Spehar et al. 2010; Asensio et al. 2012b; Ramos-Fernández et al. 2013). An important fraction of seeds swallowed by these primates are defecated in latrines located beneath these sleeping trees (Russo and Augspurger 2004; Russo et al. 2006; González-Zamora et al. 2012), and hence, variation in STF is expected to alter patterns of seed rain within latrines. Only one study has assessed the abundance, species diversity and composition of seeds that fall within latrines of spider monkeys (González-Zamora et al. submitted), but no study to date has associated these community-level seed rain patterns with STF.

STF of spider monkeys is expected to be higher in forest fragments (González-Zamora et al. 2012), as the home ranges of these primates in fragments are smaller than in continuous forest sites (Chaves et al. 2011; 2012). Nevertheless, potential variation between continuous and fragmented forests in STF has not been evaluated; similarly the impact of STF on seed rain patterns is unknown. This information has critical ecological implications, as spider monkeys are increasingly forced to inhabit fragmented landscapes (Michalski and Peres 2005; Garber et al. 2006; Ramos-Fernández and Wallace 2008).

Here, we evaluated the frequency of use of 60 sleeping trees by *A. geoffroyi* and the seed rain patterns produced by this primate during a 13-mo period in two continuous forest sites (CF) and three forest fragments (FF) in the fragmented Lacandona rainforest, Mexico. We first tested whether STF differed among sites and between forest conditions. For each sampling site and forest condition, we then assessed the association between STF and six community-level attributes of seed assemblages that are known to provide complementary information on community composition and structure (Jost 2006; 2007; Tuomisto 2010; Chiarucci et al. 2011; Chao et al. 2012): abundance of seeds, seed species diversity (i.e., species richness, exponential of Shannon's entropy, and inverse Simpson concentration), community evenness, and seed species turnover (β-diversity) between sleeping trees.

Because the sleeping trees most frequently used are expected to be located in core areas with greater density of available food trees (Asensio et al. 2012b), we predicted that STF is positively associated with the abundance of seeds and with all diversity metrics. Thus, differences in STF (Δ STF) is expected to result in significant differences in seed species turnover (i.e., increasing β-diversity) between sleeping trees. Moreover, because spider monkeys show high selectivity towards the consumption of a few species (Milton 1980; Chapman 1988; McFarland Symington 1988; Estrada and Coates-Estrada 1981) and a large number of species are used opportunistically (Nunes 1998; Dew 2008; Link et al. 2012; González-Zamora et al. 2009), we predicted that STF is negatively associated with seed community evenness.

Because site fidelity is highly variable (Asensio et al. 2012a; Ramos-Fernández et al. 2013), our analyses contributes to improve our understanding of the potential impacts that changes in site fidelity may have on seed dispersal patterns due to spider monkeys. This contribution is particularly relevant in the context of habitat fragmentation, as shifts in the distribution and abundance of food resources in fragmented landscapes (Arroyo-Rodríguez and Mandujano 2006; Chaves et al. 2012) can promote changes in the sizes of home ranges and core areas of spider monkeys (Wallace 2008), potentially altering STF and seed dispersal.

Material and methods

Study site

The Lacandona rainforest constitutes the southwestern sector of the Mayan forest in Mexico, and represents a priority area for biodiversity conservation in Mexico and Mesoamerica (Myers et al. 2000). The area is located in the northeastern portion of the state of Chiapas, and is delimited by the Guatemalan border on the south and east, and by the Chiapas highlands on the north and west. The climate is hot and humid, with an annual precipitation average of 2,850 mm, and average monthly temperatures of 24 ºC to 26 °C. This region was originally covered by over 1.4 million hectares of rainforest, but deforestation between 1960 and 1990 resulted in the loss of 70% of the original forest cover (Arizpe and Velázquez 1993).

Within this region the Montes Azules Biosphere Reserve (MABR) was created in 1978 to protect biodiversity. Adjacent to the southern extreme of MABR, the Marqués de Comillas Region (MCR) was colonized about 40 years ago and since then MCR has suffered the rapid loss and fragmentation of the original rainforest (Mora 2008). Currently, MCR is dominated by different-sized rainforest patches, embedded in a matrix of cattle pastures, agricultural lands (e.g., corn, oil palm, rubber) and human settlements. The study was conducted in MCR (eastern side of the Lacantún river; 2,039 km^2) and the MABR (western side; 3,312 km^2).

Experimental design

Based on a recent study on the density and spatial distribution of sleeping sites, sleeping trees and latrines of spider monkeys (*Ateles geoffroyi*) in the region (González-Zamora et al. 2012), we selected 60 sleeping trees in two continuous forest sites within MABR and three forest fragments in MCR (12 sleeping trees per study site). To increase the independence between the two continuous forest sites, they were separated by 5 km from each other. The forest fragments FF1, FF2 and FF3 have an area of 125, 33 and 30 ha, respectively and were isolated ≥ 24 yrs ago and were immersed in an anthropogenic matrix of pastures and agricultural lands. The average distance between two fragments was 4.2 km (see further details in Gonzalez-Zamora et al. 2012).

Seed rain patterns

All selected sleeping trees had a single latrine (Gonzalez-Zamora et al. 2012), and we placed one seed trap in the center of each latrine. Traps consisted of a circular 1.5-m diameter PVC frame supporting a 0.5-m depth open-topped nylon mesh bag suspended 1 m above the ground on three steel posts. Each trap was emptied once monthly during a 13-mo period (1-Feb- 2011 to 28-Feb-2012), and the seeds located within the spider monkeys' feces were collected and afterwards washed for subsequent identification in the laboratory. All seeds were counted and identified to the species level based on (i) our own experience with the local flora (from seeds to adults) (Chaves et al. 2011; 2012; González-Zamora et al. 2012); (ii) botanical expert familiar with the flora of the region (G. Ibarra-Manríquez, Universidad Nacional Autónoma de México, Morelia, Mexico) and a local parataxonomist; and (iii) information from seed catalogs (Ibarra-Manríquez and Cornejo-Tenorio 2010). Only seeds ≥ 5 mm in length were recorded. Although seed traps also captured some fruits and seeds dispersed by wind or gravity, only seeds immersed within monkey feces were considered. These were identified in the field based on their typically "stained" appearance and characteristic adhesion of fecal matter.

Sleeping tree fidelity

Following Reichard (1998), STF was defined as the number of months each sleeping tree was used during the study period. Given that all traps were checked at the end of each month, the presence of fresh feces defecated lat least one week before in the traps or in the understory floor was used as an indicator of sleeping tree use by spider monkeys.

Sample completeness

We first evaluated sample completeness (within each latrine using the formula suggested by Chao and Jost (2012) for calculating sample completeness :

$$\hat{C}_n = 1 - \frac{f_1}{n}\left[\frac{(n-1)f_1}{(n-1)f_1 + 2f_2}\right]$$

where f_1 and f_2 are the number of species represented by one (singletons) and two (doubletons) individuals in the sample, respectively, and n is the total number of individuals in the sample. Sample coverage did not differ between sites (Kruskal-Wallis test, $H = 6.7$, $P = 0.14$), averaging (± SD) 99% ± 1% (range = 93%-100%) per latrine. This indicates that the seed inventory was accurate with our sampling effort, and that our results are not biased by differences in sample completeness among sites (Chao and Jost 2012).

Composition and structure of seed assemblages

Based on our hierarchically nested sampling design (i.e., 60 sleeping trees in 5 sites within two forest conditions), we calculated the total abundance of seeds and seed species diversity within each sleeping tree during the 13-mo period. Patterns of seed species diversity were analyzed using true diversity measures (i.e., number equivalents, ${}^{q}D$). This analytical approach has been recognized as the most appropriate for diversity evaluations (Jost 2006, 2007; Tuomisto 2010; Chao et al. 2012). The formulas are detailed elsewhere (e.g., Jost 2006; Chao et al. 2012). We considered true diversities ${}^{0}D$ (species richness), ${}^{1}D$ (exponential of Shannon's entropy) and ${}^{2}D$ (inverse Simpson concentration), which were calculated using the R statistical software (v. 2.15.2) (R Core Team Development). ${}^{0}D$ is not sensitive to species abundances and so gives disproportionate weight to rare species (Jost 2006; Tuomisto 2010). ${}^{1}D$ weights each species according to its abundance in the community, and can be therefore interpreted as the number of 'common' species in the community (Chao et al. 2012). Finally, ${}^{2}D$ favors abundant species, and can be interpreted as the number of 'dominant' species in the community (Jost 2010; Chao et al. 2012).

We also assessed differences in species dominance among latrines using the evenness factor proposed by Jost (2010): $EF_{0,2} = {}^{2}D/{}^{0}D$. We used this measure because: (i) it is calculated from true diversity measures; (ii) is independent of the number of species in the sample; and (iii) is very easy to interpret. It ranges between 1 (when all species are equally common) and nearly $1/{}^{0}D$ (when the community is totally dominated by one species). In other words, EF can be interpreted as the proportion of dominant species in the community (Jost 2010).

Statistical analyses

To assess if sleeping trees can be considered independent samples, we used Mantel tests to correlate the distance between two sleeping trees with the difference in STF between the same two trees. The *P*-values were calculated using the distribution of the *R* coefficients obtained from 10,000 permutations. Because the Mantel tests did not detect a significant spatial autocorrelation of data sets within the continuous forest sites (CF1: $r = -0.23$, $P = 0.05$; CF2: $r = -0.16$, $P = 0.17$), nor within the forest fragments (FF1: $r = -0.14$, $P = 0.24$; FF2: $r = -0.02$, $P = 0.87$; FF3: $r = 0.10$, $P = 0.41$), we considered the sleeping trees as replicates in the following analyses.

We first tested for differences in STF among sites and between forest conditions using generalized linear models (GLM). As suggested for count dependent variables (i.e., number of months), we used a Poisson error and a log link function, and corrected for data overdispersion (Crawley 2002). We then assessed the association between STF as the dependent variable and the abundance of seeds, D^0, D^1, D^2, and *EF* with linear Pearson correlation tests. These analyses were done for each sampling site and each forest condition. We used Mantel tests to evaluate the association between ΔSTF and seed species turnover (Bray Curtis index) between sleeping trees within each sampling site.

Results

Sleeping tree fidelity in continuous and fragmented forests

Overall, the STF of spider monkeys was highly variable among sites. It ranged from 3 to 10 months in continuous forest sites, and from 1 to 12 months in forest fragments, but it did not differ among sites (GLM; $\chi^2 = 5.55$, d.f. = 4, $P = 0.23$, Fig. 1a) or between forest conditions ($\chi^2 = 0.56$, d.f. = 1, $P = 0.45$, Fig. 1b).

Association between STF and seed rain patterns

The correlations between STF and seed rain attributes varied among sites, but in general, STF was positively associated with the abundance of seeds and seed species diversity in most sites (Table 1). Nevertheless, STF tended to be negatively related to seed community evenness. These patterns remained at the forest condition scale (Fig. 2).

The Mantel tests showed that seed β-diversity between sleeping trees increased with increasing inter-tree differences in STF. This association was significant in the two continuous forest sites (CF1: r = 0.26, P = 0.02; CF2: r = 0.25, P = 0.03) and all forest fragments (FF1: r = 0.36, P = 0.002; FF2: r = 0.39, P = 0.02; FF3: r = 0.49, P = 0.001), indicating that differences in STF between sleeping trees were associated with significant differences in seed species composition.

Discussion

Sleeping tree fidelity in continuous and fragmented forests

Contrary to our prediction, STF was similar in all study sites and did not differ between continuous and fragmented forests. This was due to the large variation among sleeping trees. Although sleeping trees were used by spider monkeys on average for 7 out of 13 months, there was a substantial variation across trees (range: 1-12 months). Previous studies on spider monkeys (Chapman 1989) and other primate species (*Gorilla gorilla*: Rogers et al. 1998; *Hylobates lar*: Reichard 1998; *Lagothrix lagothricha*: Stevenson 2000; *A. paniscus*: Russo and Augspurger 2004; *Brachyteles arachnoides*: Bueno et al. 2013) also indicate that the use of sleeping trees can be highly variable, with some trees used for long periods, while others are only used occasionally (Anderson 1984; 2000; Reichard 1998; Teichroeb et al. 2012). In the case of spider monkeys, this pattern results from their foraging in several core areas within the home range that contain a higher availability of food resources (Asensio et al. 2012b; Ramos-Fernández et al. 2013), and then routinely returning at night to the same sleeping trees located within these core areas (i.e., multiple central place foraging; *sensu* Chapman 1989). This behavior allows the monkeys to monitor the spatial and temporal distribution of their resources (Asensio et al. 2012a; Ramos-Fernández et al. 2013) and to move back to their sleeping trees more easily using recognized travel routes (Orians and Pearson 1979; Chapman 1989), minimizing the costs associated with traveling (Chapman 1989; Wallace 2006; Asensio et al. 2012a, Teichroeb et al. 2012). Yet, during foraging explorations to locate new food resources (Ramos- Fernández et al. 2004; Valero and Byrne 2007; Wallace 2008; Asensio et al. 2012a), *A. geoffroyi* can use sleeping trees for short periods, thus explaining the low fidelity found for some sleeping trees in our study. Therefore, as reported for other primate species (Sigg and Stolba 1981; Heymann 1995; Reichard 1998; Pontes and Soares 2005; Smith et al. 2007; da Silva Júnior et al. 2009), the high variation in STF in the Lacandona rainforest is most likely related to the spatial and temporal variations in the distribution of food resources.

Although STF did not differ significantly between continuous and fragmented forests, as expected, monkeys tended to use sleeping trees more frequently in fragments. For example, we recorded 24 sleeping trees (67%) that were used above the general mean (7 months) in fragments, whereas in the continuous forest only 13 trees (54%) were used more than the general mean. In fact, in the continuous forest all trees were used less than 10 months, while in fragments, 5 trees (13.8%) were used > 10 months. This result can be associated with the spatial limits imposed by the fragments, particularly in the two smaller fragments FF2 and FF3. This spatial limit can reduce the home range, and thus increase the accessibility of available food resources (Wallace 2008; Boyle et al. 2009; Link et al. 2012; Chaves et al. 2012). Also, these primates preferentially use larger trees to sleep in (DBH > 60 cm: Chapman 1989; da Silva Júnior et al. 2009; González-Zamora et al. 2012), and the density of big trees is often reduced in forest fragments (Arroyo Rodríguez and Mandujano 2006; Chaves et al. 2012) due to logging and increasing rates of tree mortality (Laurance et al. 2000; 2006). In fact, the density of big trees (DBH > 60 cm) in the fragmented sites is significantly lower than within the continuous forest sites (González-Zamora et al. submitted). In summary, the scarcity of big trees and the reduction of the home range in fragments can 'force' these primates to use the available sleeping trees more frequently than in continuous forest sites.

Association between STF and seed rain patterns

In agreement with our predictions, STF was positively related to the abundance and diversity of seeds in all sites. Such associations can be explained because the more often a sleeping tree is used, the more seeds are deposited under it. As a result of the spatial location of the sleeping trees in relation to the areas of high concentration of resources (Sigg and Stolba 1981; Heymann 1995; Pontes and Soares 2005; Smith et al. 2007; da Silva Júnior et al. 2009). Previous studies demonstrated that spider monkeys' core areas are located in forest areas with higher availability of food resources (Chapman 1989; Nunes 1998, Shimooka 2005; Spehar et al.2010; Asensio et al. 2012b). Thus, since sleeping trees located within core areas are used more frequently (McFarland Symington 1988; Wallace 2006, 2008; Spehar et al. 2010; Asensio et al. 2012b), this results in an increase in STF and consequently an increase in the abundance and diversity of seeds. In contrast, sleeping trees used for short time periods are probably associated with exploration events in areas with lower availability of food resources, thus explaining the lower abundance and diversity of seeds deposited below these sleeping trees. In conclusion, our results suggest that the spatial configuration of seed communities deposited in latrines depends on the spatial and temporal variations in the availability of food resources within their home range, but this hypothesis remains to be further tested.

STF was negatively related to community evenness in all study sites. As expected, this finding can be related to the fact that the sleeping trees that are more frequently used reflect the common feeding pattern of the species, i.e., there is a high selectivity towards the consumption of a few plant species, and the opportunistic use of a large number of other fruit species (Milton 1980; Estrada and Coates-Estrada 1981; Chapman1987b; 1988; McFarland Symington 1988; Nunes 1998; Dew 2008; González-Zamora et al. 2009; Link et al. 2012). This feeding pattern results in the reduction of community evenness of the seeds that are deposited in sleeping trees more frequently used.

Association between seed species turnover and STF

In all sites, seed species turnover between sleeping trees increased with increasing inter-tree differences in STF. This finding supports our expectations, because differences in STF are most probably associated with differences in the availability of food resources in the vicinity of sleeping trees (see above). Thus, differences in STF are expected to lead to significant differences in seed species composition between sleeping trees. Also, the positive association between STF and seed species richness implies that with increasing differences in STF, the compositional differentiation of seed communities also increases.

Implications for seed dispersal

Our study demonstrates that STF is a key factor shaping the seed rain patterns produced by spider monkeys below their sleeping trees. Therefore, changes in STF associated with climate change or anthropogenic disturbances could have important implications for seed dispersal. For example, climate change models for the region predict an increase in ambient temperatures and a decrease in annual rainfall during the coming decades (Anderson et al. 2008). Under this scenario, recent evidence suggests that spider monkeys will probably increase their resting time, limiting the time monkeys can devote to other critical activities, such as feeding and traveling and one of the probably consequences is the increase of STF (González-Zamora et al. 2011). The day range and the size of the home ranges and core areas also are expected to decrease with such climate changes (Asensio et al. 2012b; Ramos-Fernández et al. 2013), potentially altering the patterns of STF. Indeed, some studies already have demonstrated that in the 21st century the interactions between plants and their seed dispersers are negatively affected by climate change and habitat fragmentation (Pereira et al. 2010; McConkey et al. 2012). Changes in plant distributions and community composition are expected in response to climate change (McConkey et al. 2012).

Since in fragmented landscapes seed dispersal has a major influence on both plant species persistence (Farwig et al. 2006; Herrera and Garcia 2010; Sansevero et al. 2011) and vegetation recovery (Howe and Miriti 2004), large-bodied animal seed dispersers, such as spider monkeys, are especially important in facilitating seed movement of a larger number of plant species that depend on them as key dispersal (Dew 2008). As the Lacandona rain forest becomes warmer and less wet in the near future (Anderson et al. 2008; Wiederholt and Post 2010) we can expect direct effects of climate change on spider monkeys' activity (González-Zamora et al. 2011), spatial behavior (Asensio et al. 2012b; Ramos-Fernández et al. 2013), sleeping site densities (González-Zamora et al. 2012), and ultimately in the STF. Such effects may be most notable in the magnitude of spatial and temporal aggregated seed dispersal of spider monkeys because more seeds could be deposited within more reduced areas increasing seeds aggregations.

Because changes in phenological patterns, food availability and fruit production is expected in response to climate change (Wiederholt and Post 2010), we hypothesized that one on the possible effects of climate change on spider monkeys' seed dispersal may be determined by drastics changes in fruit productions and food availability as a consequences of changes in phenological patterns. For example, it has recently been documented that a cycle of high then low fruit production occurs during El Niño and La Niña years, respectively; the latter can cause famine in frugivorous mammals (Wright et al. 1999; Milton et al. 2005). Thus, because changes in phenological patterns can alter fruit production are expected in the Lacandona rain forest, we can expect changes in fruit productions that affects the quantity component of seed dispersal effectiveness of spider monkeys by La Niña (e.g., Schupp 1993), in the spatial aggregation of seed dispersal and ultimately in the spatial configuration of the seed community. Insight into the behavioural responses of spider monkey populations to climatic stochasticity and fruit foraging strategy is essential in view of current and future climate change, especially for populations living in fragmented landscapes.

The reduction in community evenness with increasing levels of STF indicates that a few seed species dominate the seed rain in frequently used areas. From the perspective of the quantity of seed dispersal (Schupp 1993), as a result of the high density of seeds in latrines (Howe 1989), by the emergence of regulatory effects of mortality (i.e., fungi, pathogens and competition between conspecific seedlings: Janzen 1970; Connell 1971), we expect higher seed predation of the most dominant species, which could reduce predation pressure on less abundant species allowing the recruitment of rare species (i.e., escape hypothesis: Howe and Smallwood 1982). By contrast, in sleeping trees where fidelity was lower, the possible arrival of a poor community seed species but with similar relative abundances could reduce the degree of aggregation (Good et al. 2013), levels of predation (Janzen 1970; Connell 1971) and, consequently, favor a similar probability of recruitment between species (Bravo 2012). Since the seed community structure and composition can be decisive for the initial stages of recruitment (Wang and Smith 2002; Russo and Augspurger 2004; Schupp et al. 2010), further studies are required to assess the persistence of seeds and recruitment of seedlings under different levels of evenness in the seed bank of latrines to test this hyphotesis.

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References

Anderson JR .(1984). Ethology and ecology of sleep in monkeys and apes. Advances in the Study of Behavior 14: 166–229.

Anderson JR. (2000). Sleep-related behavioural adaptations in freeranging anthropoid primates. Sleep Medicine Reviews 4: 355–373.

Anderson ER, Cherrogton EA, Flores AI, Perez JB, Carrillo R, Sempris E. (2008). Potential impacts of climate change on biodiversity in Central America, Mexico, and the Dominican Republic. Panama City: CATHALAC/USAID.

Arizpe LPF, Velázquez M. (1993). Cultura y cambio global: percepciones sociales sobre la deforestación en la Selva Lacandona. In: A. P. Miguel (ed) Centro Regional de Investigaciones Multidisciplinarias. Universidad Nacional Autónoma de México, Porrúa, Mexico City.

Arroyo-Rodríguez V, Mandujano S. (2006). Forest fragmentation modifies habitat quality for *Alouatta palliata*. International Journal of Primatology 27: 1079–1096.

Asensio N, Schaffner CM, Aureli F. (2012a). Variability in core areas of spider monkeys (*Ateles geoffroyi*) in a tropical dry forest in Costa Rica. Primates 53:147– 156

Asensio N, Lusseau D, Schaffner CM, Aureli F. (2012b). Spider monkeys use high-quality core areas in a tropical dry forest. Journal of Zoology 287: 250–258.

Börger L, Dalziel BD, Fryxell JM. (2008). Are there general mechanisms of animal home range behaviour? A review and prospects for future research. Ecology Letters 11: 637–650.

Boyle SA, Lourenc¸o WA, da Silva LR, Smith AT (2009) Travel and spatial patterns change when northern bearded saki monkeys (Chiropotes satanas chiropotes) inhabit forest fragments. International Journal of Primatology 30:515–531.

Bravo SP. (2012). The impact of seed dispersal by black and gold howler monkeys on forest regeneration. Ecological Research 27: 311–321.

Bueno RS, Guevara R, Ribeiro MC, Culot L, Bufalo FS, Galetti M. (2013) Functional Redundancy and Complementarities of Seed Dispersal by the Last Neotropical Megafrugivores. PLoS ONE 8(2): e56252. doi:10.1371/journal.pone.0056252.

Chapman CA. (1988). Patterns of foraging and range use by three species of neotropical primates. Primates 29: 177–194.

Chapman CA. (1989). Spider monkey sleeping sites: use and availability. American Journal of Primatology 18: 53–60.

Chapman CA. (1990). Ecological constraints on group size in three species of neotropical primates. Folia primatologica 55: 1-9.

Chapman CA, Chapman LJ, McLaughlin RL. (1989). Multiple central place foraging by spider monkeys: travel consequences of using many sleeping sites. Oecologia 79: 506–511.

Chapman CA, Wrangham RW, Chapman, LJ. (1995). Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. Behavioral Ecology and Sociobiology 36: 59–70.

Chao A, Chiu CH, Hsieh T. (2012). Proposing a resolution to debates on diversity partitioning. Ecology 93: 2037–2051.

Chaves GM, Stoner KE, Arroyo-Rodríguez V. (2011). Effectiveness of spider monkeys (*Ateles geoffroyi vellerosus*) as seed dispersers in continuous and fragmented rainforests in southern Mexico. International Journal of Primatology 32:177–192.

Chaves OM, Stoner KE, Arroyo-Rodríguez V. (2012). Differences in diet between spider monkey groups living in forest fragments and continuous forest in Lacandona, Mexico. Biotropica 44: 105–113.

Chiarucci A, Bacaro G, Scheiner SM .(2011) .Old and new challenges in using species diversity for assessing biodiversity. Phil. Trans. R. Soc. B 366:2426–2437.

Crawley M. (2002). Statistical computing: An introduction to data analysis using S-Plus. Chichester: John Wiley & Sons.

Connell JH. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: den Boer PJ, Gradwell GR (eds) Dynamics of populations. Center for Agricultural Publication and Documentation, Wageningen, The Netherlands, pp. 298–312.

Dew JL. (2008). Spider monkeys as seed dispersers. In: Campbell CJ (ed). Spider monkeys. The biology, behavior and ecology of the genus *Ateles*. Cambridge University Press, New York, pp. 155–182.

Estrada A, Coates-Estrada R. (1981). Some observations on the present distribution and conservation of *Alouatta* and *Ateles* in southern Mexico. American Journal of Primatology 7:133–137.

Farwig, N., Bohning-Gaese, K., Bleher, B., 2006. Enhanced seed dispersal of Prunus africana in fragmented and disturbed forests. Oecologia 147: 238–252.

Fragoso JMV. (1997). Tapir-generated seed shadows: Scale-dependent patchiness in the Amazon rain forest. Journal of Ecology 85: 519–529.

Garber PA, Estrada A, Pavelka MSM. (2006). New perspective in the study of Mesoamerican Primates: concluding comments and conservation priorities. In: A. Estrada, P.A. Garber, M.S.N. Pavelka, M. Luecke (eds) New perspective in the study of Mesoamerican primates: distribution, ecology, behaviour and conservation, Springer, New York, pp 489–511.

González-Zamora A, Arroyo-Rodríguez V, Chaves OM, Sánchez-López S, Stoner KE. (2009). Diet of spider monkeys (*Ateles geoffroyi*) in Mesoamerica: current knowledge and future directions. American Journal of Primatology 71: 8–20

González-Zamora A, Arroyo-Rodríguez V, Chaves OM, Sánchez-López S, Stoner KE. (2011). Influence of climatic variables, forest type and condition on activity budget of Geoffroyi´s spider monkeys throughout Mesoamerica. American Journal of Primatology. 73:1189–1198.

González-Zamora A, Arroyo-Rodríguez V, Oyama K, Sork V, Chapman CA, Stoner KE. (2012). Sleeping sites and latrines of spider monkeys in continuous and fragmented rainforests: implications for seed dispersal and forest regeneration. PLoS ONE 7(10): e46852. doi:10.1371/journal.pone.0046852.

González-Zamora A, Arroyo-Rodríguez V, Escobar F, Rös M, Oyama K, Ibarra-Manríquez G, Stoner KE, Chapman CA. (submitted) Contagious deposition of seeds in spider monkeys' sleeping trees limits effective seed dispersal in fragmented landscapes

Herrera CM, Jordano P, Lopez-Soria L, Amat JA. (1994). Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. Ecological Monographs 64: 315–344.

Herrera JM, Garcia D. (2010). Effects of forest fragmentation on seed dispersal and seedling establishment in ornithochorous trees. Conservation Biology 24: 1089– 1098.

Heymann EW. (1995). Sleeping habits of tamarins, *Saguinus mystax and Saguinus fuscicollis* (Mammalia; Primates; Callitrichidae), in north-eastern Peru. Journal of Zoology 237: 211–226.

Howe H. (1989). Scatter- and clump-dispersal and seedling demography: hypothesis and implications. Oecologia 79: 417–426.

Howe HF, Smallwood J. (1982). Ecology of seed dispersal. Annual Review of Ecology and Systematics 13: 201–228.

Howe HF, Miriti MN. (2004). When seed dispersal matters. Bioscience 54: 651– 660.

Ibarra-Manríquez G, Cornejo Tenorio G. (2010). Diversidad de frutos de los árboles del bosque tropical pefennifolio de México. Acta Botánica Mexicana 90**:** 51–104.

Janzen DH. (1970). Herbivores and the number of tree species in tropical forests. American Naturalist 104: 501–528.

Jordano P. (1992). Fruits and frugivory. Seeds: The Ecology of Regeneration in Plant Communities. In: M. Fenner (ed) CAB International, Wallingford, pp 105–156

Jordano P, Schupp EW. (2000). Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. Ecological Monographs 70: 591–615.

Jost L. (2006). Entropy and diversity. Oikos 113: 363–375.

Jost L. (2007). Partitioning diversity into independent alpha and beta components. Ecology 88: 2427–2439.

Jost L. (2010). The relation between evenness and diversity. Diversity 2: 207–232.

Julliot C. (1997). Impact of seed dispersal by red howler monkeys *Alouatta seniculus* on the seedling population in the understorey of tropical rain forest. Journal of Ecology 85: 431–40.

Karubian J, Duraes R. (2009). Effects of seed disperser social behavior on patterns of seed movement and deposition. Oecologia Brasileira 13: 45–57.

Laurance WF, Delamonica P, Laurance SG, Vasconcelos HL, Lovejoy TE .(2000). Rainforest fragmentation kills big trees. Nature 404: 836.

Laurence WF, Nascimiento HHEM, Laurence SG, Anndrade AC, Fearnside PM, Ribeiro JEL, Capretz RL..(2006). Rain forest fragmentation and the proliferation of succesional tress. Ecology 87: 469–482.

Link A, Galvis N, Marquez Mateo, Guerrero Jane, Solano C. Stevenson P.R. (2012). Diet of the critically endangered brown spider monkey (*Ateles hybridus*) in an inter-andean lowland rainforest in Colombia. American Journal of Primatology 00:1–9.

McConkey KR, Prasad S, Corlett RT, Campos-Arceiz A, Brodie JF, Rogers H, Santamaria L. (2012). Seed dispersal in changing landscapes. Biological Conservation 146: 1–13.

McFarland Symington M. (1988). Food competition and foraging party size in the black spider monkey (*Ateles paniscus chamek*). Behaviour 105: 117–132.

Melo FPL, Rodriguez-Herrera B, Chazdon RL, Medellin RA, Ceballos GG. (2009). Small tent-roosting bats promote dispersal of large-seeded plants in a Neotropical Forest. Biotropica 41: 737–743.

Michalski F, Peres CA. (2005). Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. Biological Conservation 124: 383–396.

Milton K. (1980). The foraging strategy of howler monkeys: a study in primate economics. New York: Columbia University Press.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GA, Kent J. (2000) .Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

Nathan R, Muller-Landau HC. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology and Evolution 15: 278–285.

Nunes A. (1998). Diet and feeding ecology of *Ateles belzebuth* at Maracá ecological station, Roraima, Brasil. Folia Primatologica 69: 61–76.

Orians GH, Pearson NE. (1979). On the theory of central place foraging. In: Horn DJ, Mitchell RD, Stairs GR, eds. Analysis of ecological system. Ohio: Ohio University Press. Pp. 155–177.

Pereira HM, Leadley PW, Proença V, Alkemade R, Scharlemann JPW, Fernandez-Manjarrés JF, Araújo MB, Balvanera P, Biggs R, Cheung WWL, Chini L, Cooper HD, Gilman EL, Guénette S, Hurtt GC, Huntington HP, Mace GM, Oberdorff T, Revenga C, Rodrigues P, Scholes RJ, Sumaila UR, Walpole M. (2010). Scenarios for global biodiversity in the 21st century. Science 330, 1496–1501.

Pontes AR, Soares M. (2005). Sleeping sites of common marmosets (*Callithrix jacchus*) in defauned urban forest fragments: a strategy to maxime food intake. Journal of Zoology 26: 55–63.

Ramos-Fernández G, Wallace RB. (2008). Spider monkey conservation in the twenty-first century: recognizing risks and opportunities. In: J.C. Campbell (ed) Spider monkeys. The biology, behavior and ecology of the genus *Ateles*. Cambridge University Press, New York, pp. 351–372.

Ramos-Fernández G., Mateos J.L., Miramontes O., Larralde H., Cocho G, Ayala-Orozco B. (2004). Lévy walk patterns in the foraging movements of spider monkeys (Ateles geoffroyi). Behavioral Ecology and Sociobiology 55: 223–230.

Ramos-Fernández G, Smith Aguilar SE, Schaffner CM, Vick LG, Aureli F. (2013). Site fidelity in space use by spider monkeys (*Ateles geoffroyi*) in the Yucatan Peninsula, Mexico. PLoS ONE 8: e62813. doi:10.1371/journal.pone.0062813.

Reichard U. (1998). Sleeping sites, sleeping places, and presleep behavior of Gibbons (*Hylobates lar*). American Journal of Primatology 46: 35–62.

Rogers ME, Voysey BC, McDonald KE, Parnell RJ, Tutin CEG. (1998). Lowland gorillas and seed dispersal: the importance of nest sites. American Journal of Primatology 45: 45–68.

Russo SE, Augspurger CK .(2004). Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. Ecology Letters 7: 1058–1067.

Russo SE, Portnoy S, Augspurger CK. (2006). Incorporating animal behavior into seed dispersal models: Implications for seed shadows. Ecology 87: 3160–3174.

Sansevero JBB, Prieto PV, de Moraes LFD, Rodrigues PJP. (2011). Natural regeneration in plantations of native trees in lowland Brazilian Atlantic Forest: community structure, diversity, and dispersal syndromes. Restoration Ecology 19: 379–389.

Schupp EW. (1993). Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio 107: 15–29.

Schupp EW, Milleron T, Russo SE. (2002). Dissemination limitation and the origin and maintenance of species-rich tropical forests. D.J. Levey, W.R. Silva and M.M. Galetti (eds). New York. Pp. 19–33.

Schupp EW, Jordano P, Gómez JM. (2010). Seed dispersal effectiveness revisited: a conceptual review. New Phytologist 188: 333–353.

Shimooka Y. (2005). Sexual Differences in Ranging of *Ateles belzebuth belzebuth* at La Macarena, Colombia. International Journal of Primatology 26: 385–406.

Sigg H, Stolba A. (1981). Home range use and daily march in a hamadryas baboon troop. Folia Primatologica 36: 40–75.

da Silva Júnior WM, Meira-Neto JAA, da Silva Flávia MC, Rodrigues de Melo F, Santana Moreira L, Ferreira Barbosa E, Dias LG, da Silva Peres CA. (2009). Habitat quality of the woolly spider monkey. Folia Primatologica 80: 295–308.

Smith AC, Knogge C, Huck M, Löttker P, Buchanan-Smith HM, Heymann EW. (2007). Long term patterns of sleeping site use in wild saddleback (*Saguinus fuscicollis*) and mustached tamarins (*S. mystax*). American Journal of Physical Anthropology 134: 340–353.

Spehar NS, Link A, Di Fiore A. (2010). Male and Female Range Use in a Group of White-Bellied Spider Monkeys (*Ateles belzebuth*) in Yasuní National Park, Ecuador. American Journal of Primatology 72: 129–141.

Stevenson PR. (2000). Seed dispersal by woolly monkeys (*Lagothrix lagothricha*) at Tinigua National Park, Colombia: dispersal distance, germination rates, and dispersal quantity. American Journal of Primatology 50:275–289.

Teichroeb JA, Holmes JA, Sicotte P. (2012). Use of sleeping trees by ursine colobus monkeys (*Colobus vellerosus*) demonstrates the importance of nearby food. Primates (early view, doi:10.1007/s10329-012-0299-1).

Tuomisto H. (2010). A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. Ecography 33**:** 2–22

Valero A, Byrne RW. (2007). Spider monkey ranging patterns in Mexican subtropical forest: do travel routes refelct planning?. Animal Congnition 10: 305-315.

Wallace RB. (2006). Seasonal variations in black-faced black spider monkey (*Ateles chamek*) habitat use and ranging behaviour in a southern Amazonian tropical forest. American Journal of Primatology 68: 313–332.

Wallace RB. (2008). Factors influencing spider monkey habitat use and ranging patterns. In: Campbell CJ (ed) Spider monkeys. The biology, behavior and ecology of the genus *Ateles*. Cambridge University Press, New York. Pp. 138–154

Wang BC, Smith TB. (2002). Closing the seed dispersal loop. Trends in Ecology and Evolution 17: 379–385.

Wenny DG. (2001). Advantages of seed dispersal: A re-evaluation of directed dispersal. Evolutionary Ecological Research 3: 51–74.

Wiederholt R, Post E. (2010). Tropical warming and the dynamics of endangered primates. Biological Letters 6: 257–260.

Table 1. Pearson correlation coefficients between the STF of spider monkeys and five community-level seed rain patterns produced by this primate in sleeping trees located in two continuous forest sites and three forest fragments in the Lacandona rainforest, Mexico.

Forest condition	Sites	Abu	D^0	D^1	D^2	*EF*
Continuous forest sites	CF1	0.66**	0.56	0.45	0.42	-0.34
	CF2	0.59**	0.69**	0.63**	0.56*	-0.42
Forest fragments	FF1	0.48	0.81***	0.73***	0.61**	-0.53*
	FF2	0.81***	0.84***	0.39	0.30	-0.36
	FF3	0.70**	0.89***	0.78***	0.60**	-0.62**

The seed rain attributes included the abundance of seeds (Abu), species richness (^0D), exponential of Shannon's entropy (^1D), inverse Simpson concentration (^2D), and evenness factor (*EF*). *$P < 0.1$; ** $P < 0.05$; ***$P < 0.01$.

Figure legends

Fig. 1 Sleeping tree fidelity of spider monkeys in continuous (CF) and fragmented (FF) forests in the Lacandona region, Mexico. Differences among sites (a) and between forest conditions (b).

Fig. 2 Correlations between sleeping tree fidelity of spider monkeys and five community-level attributes of seed assemblages in continuous (panels a-e) and fragmented (panels f-j) forests in the Lacandona region, Mexico.

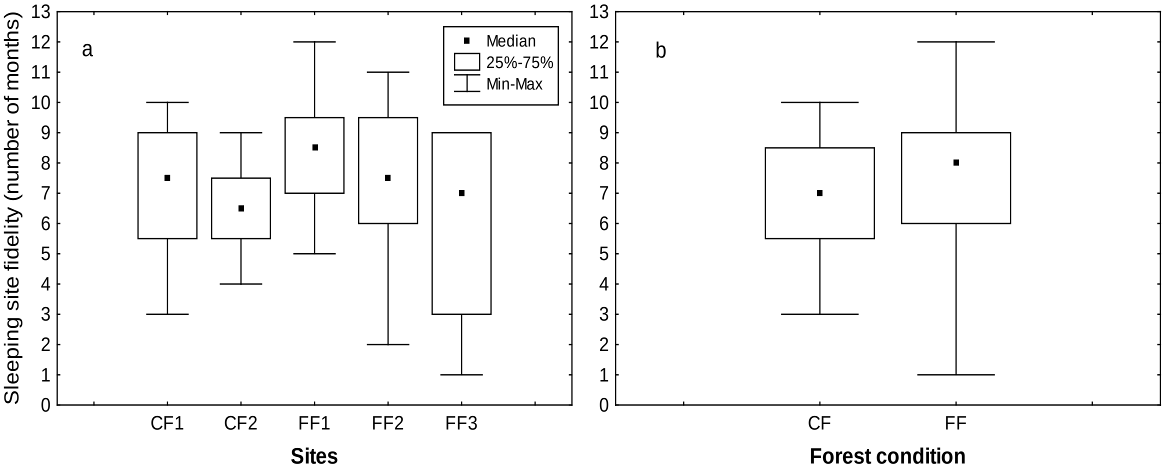
Sleeping site fidelity (number of months)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
a
■ Median
☐ 25%-75%
Min-Max
CF1
CF2
FF1
FF2
FF3
Sites
b
CF
FF
Forest condition

Fig. 1

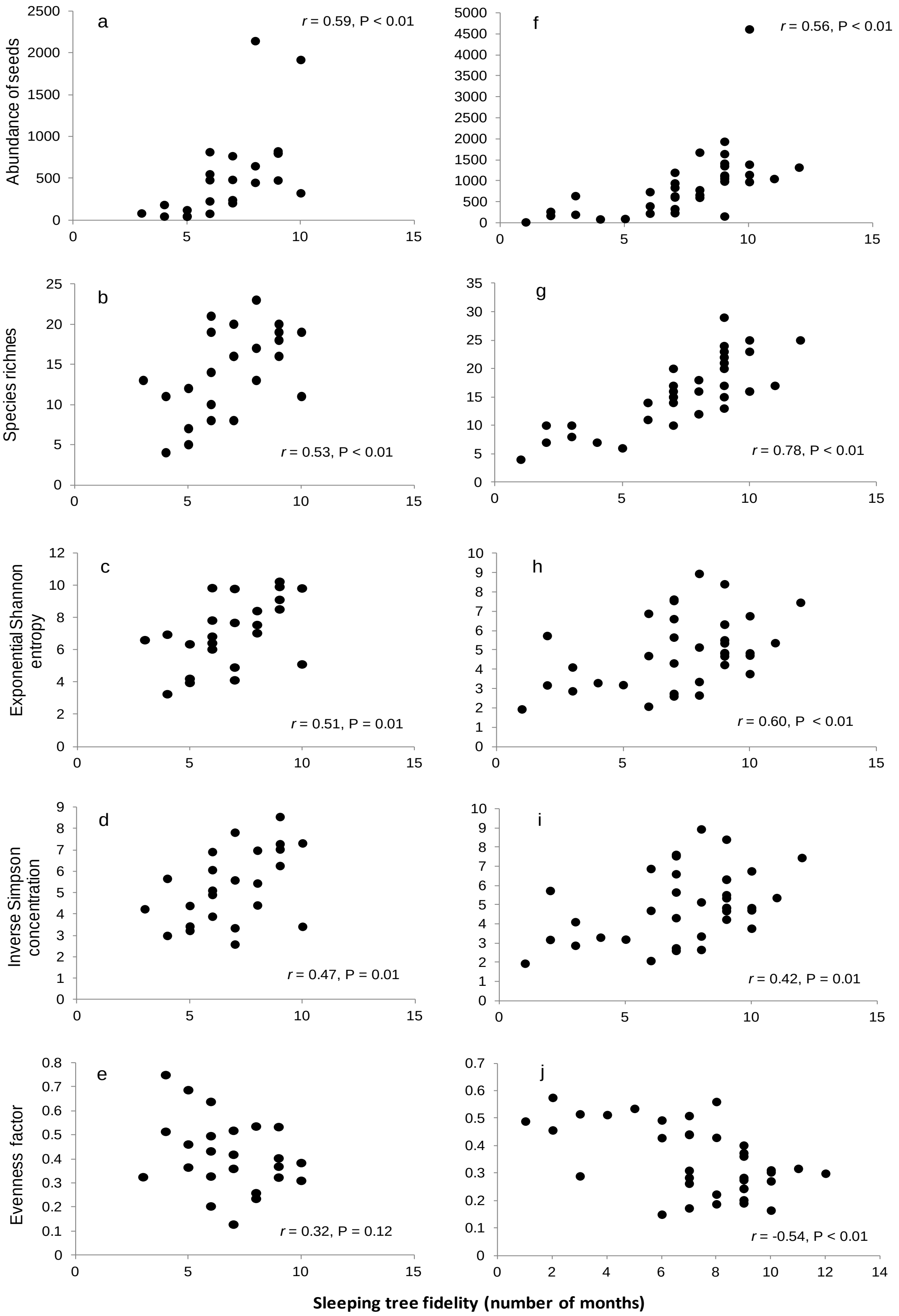
a
r = 0.59, P < 0.01
Abundance of seeds
2500
2000
1500
1000
500
0
f
r = 0.56, P < 0.01
5000
4500
4000
3500
3000
2500
2000
1500
1000
500
0
b
Species richnes
r = 0.53, P < 0.01
g
r = 0.78, P < 0.01
c
Exponential Shannon entropy
r = 0.51, P = 0.01
h
r = 0.60, P < 0.01
d
Inverse Simpson concentration
r = 0.47, P = 0.01
i
r = 0.42, P = 0.01
e
Evenness factor
r = 0.32, P = 0.12
j
r = -0.54, P < 0.01
0
5
10
15
Sleeping tree fidelity (number of months)

Fig. 2

6. CAPÍTULO VI: DISCUSIÓN GENERAL

En las últimas dos décadas, los estudios sobre dispersión de semillas espacialmente dispersa, han constatado la relevancia del servicio ecológico que los monos araña (género *Ateles*) prestan al dispersar miles de semillas de decenas de especies de plantas tropicales (van Roosmalen 1988; Champan 1989; Nunes 1998; Link & Di Fiore 2006; Dew 2008; Chaves *et al.* 2011). Sin embargo, aunque estos animales también dispersan una gran cantidad de semillas de forma agregada en letrinas ubicadas debajo de los árboles que utilizan para pernoctar (árboles dormidero), la información que existe acerca de este patrón de dispersión de semillas espacialmente agregada (*sensu* Howe & Smalllwood 1982, Howe 1989) es muy escasa.

La presente tesis aporta información novedosa y de gran valor para entender la dispersión de semillas en letrinas de *A. geoffroyi* en la selva Lacandona, México. De hecho, esta tesis representa el primer estudio sistemático que cuantifica la dispersión de semillas espacialmente agregada. Específicamente, este trabajo documenta la densidad y distribución espacial de los sitios dormideros, los árboles dormideros y las letrinas de los monos araña. Además, se documentan las especies arbóreas y las características estructurales de los árboles dormidero (i.e., tamaño y forma de la copa) que este primate usa para dormir. También se analiza la lluvia de semillas en las letrinas durante 13 meses, evaluando diferentes componentes de la diversidad (alfa, beta y gamma) a diferentes escalas espaciales. Finalmente, para entender los factores que determinan la lluvia de semillas, se analiza la asociación entre las características de la lluvia de semillas y la frecuencia de uso de los árboles dormidero; un aspecto fundamental que ha sido poco explorado en la literatura. El trabajo analiza un gran número de sitios dormideros (N = 60) en cinco sitios, tres fragmentos y dos sitios dentro del bosque continuo, permitiendo de esta manera evaluar si los patrones de uso de árboles dormidero y/o la dispersión de semillas en estos sitios se ven alterados en fragmentos. Así, el presente estudio tiene implicaciones ecológicas y de conservación de gran relevancia que se discuten a continuación.

En particular, esta tesis demuestra que la densidad de sitios dormidero y letrinas en la selva Lacandona es similar en bosque continuo y fragmentado. Sin embargo, la distribución espacial de los sitios dormideros y letrinas es más agregada en los fragmentos, ya que la distancia entre sitios dormideros es prácticamente el doble en los sitios del bosque continuo que en los fragmentos. Este hallazgo puede estar relacionado con la menor disponibilidad de espacio y alimento en fragmentos (Chaves *et al.* 2011, 2012), así como con una menor disponibilidad de árboles grandes (Material Suplementario del Capítulo IV), que son más comúnmente usados como árboles dormidero (Capítulo III). Sea cual sea la causa directa de este patrón (discutidas en detalle en el Capítulo III), las consecuencias para la dispersión de semillas son claras. Al reducirse la distancia entre letrinas, la eficacia de los monos araña como dispersores de semillas también se reduce, ya que limita las distancias de dispersión (Schupp 1993) y, puede incrementar la concentración de semillas (mayor densidad) en áreas del bosque cercanos entre sí. Este segundo patrón puede resultar en una mayor incidencia de factores de mortalidad densodependientes (depredadores, hongos y patógenos; Janzen 1970; Connell 1971), reduciendo potencialmente la probabilidad de supervivencia de las semillas en letrinas de fragmentos. Sin embargo, esta hipótesis necesita ser probada en estudios futuros ya que en este trabajo no se evaluó la supervivencia de semillas, ni el establecimiento de plántulas en letrinas. Esta información es fundamental para tener un mejor entendimiento del papel de las letrinas en la regeneración del bosque, ya que existen evidencias de que la gran densidad de semillas en estos sitios puede saturar a los depredadores, por lo que muchas semillas pueden escapar de la depredación, germinar y reclutar como plántulas de manera agregada dentro del bosque (Russo & Augspurger 2004). De hecho, estos autores demuestran que la deposición agregada de *Virola calophylla* por *A. belzebuth* en el bosque tropical húmedo de la estación biológica Cocha Cashu, en el Parque Nacional Manu, Perú, resulta en comunidades de plántulas espacialmente agregadas, un patrón que se mantiene en la comunidad de árboles adultos de *V. calophylla*. Se requieren por tanto estudios que evalúen el reclutamiento y sobrevivencia de plántulas en letrinas, ya que apesar de la alta agregación de semillas, los depredadores especialistas o generalistas pueden verse saturados por la gran cantidad de semillas que llegan a las letrinas, lo que podría permitir una alta sobrevivencia de semillas y/o plántulas.

De manera muy interesante, la mayoría de las letrinas están localizadas debajo de pocas especies de árboles, principalmente (66%) en árboles de *Dialium guianense* y *Brosimun alicastrum* (Capítulo III). Así, el uso continuo de estos árboles facilitaría el establecimiento de plántulas de las especies preferidas en la dieta (e.g., *Spondias radlkoferi*, *Dialium guianense*, *Brosimun alicastrum*), lo que podría fomentar dentro del bosque la formación agregada de futuros "jardines de vegetación" (*sensu* Milton 1980) y de asociaciones de vegetación particulares en las periferias de los árboles dormidero de estas especies. Tradicionalmente, los botánicos han clasificado los bosques tropicales del sureste de México en función de asociaciones vegetales específicas (e.g., *Terminalia-Dialium, Brosimum-Dialium*: Sarukhán 1968; Rzedowski 2006). Este estudio soporta la idea de que la dispersión de semillas por monos araña puede contribuir positivamente a crear este tipo de asociaciones, dado que este primate activamente selecciona árboles de *Terminalia*, *Dialium* y *Brosimum* para dormir, depositando grandes cantidades de semillas de especies importantes en la dieta como *Dialium* y *Brosimum*, además de otras especies (Capítulo III). Dado el uso preferente de los monos araña por árboles de *D. guianense* y *B. alicastrum* para dormir, se requieren estudios que analicen los factores (e.g., protección química, humedad) que favorecen la germinación de semillas y el crecimiento de plántulas en letrinas bajo la copa de estas especies arbóreas reconocidas como facilitadoras (Vázquez-Yanes *et al*. 1999; Boege & Dirzo 2004). Ambas especies arbóreas son importantes en la selva Lacandona, de modo que para tener un mejor entendimiento del papel de estas especies arbóreas y las letrinas en la regeneración y en la formación de asociaciones vegetales, es determinante evaluar diversidad de plántulas y juveniles presentes en las periferias de letrinas ubicadas bajo la copa de estas y otras especies arbóreas; un tema para el que no existen evidencias empíricas.

Otro hallazgo importante de la tesis es que los monos usan árboles más grandes (en diámetro) en el bosque continuo que en los fragmentos (Capítulo III). Dada las diferencias en estructura de la vegetación entre ambas condiciones de bosque (Chaves *et al.* 2011, 2012; Capítulo IV), el diámetro de estos árboles en el bosque continuo fue dos veces mayor que aquellos usados en fragmentos. Los monos araña usan preferentemente árboles grandes para dormir (Chapman 1989; da Silva Júnior *et al.* 2009; Capítulo III), sin embargo, su densidad a menudo es menor en fragmentos (Arroyo Rodríguez & Mandujano 2006; Chaves *et al.* 2012) debido a la tala y al incremento de la mortalidad de árboles (Laurance *et al.* 2000, 2006). Consistente con esta idea, la densidad de árboles grandes (DAP > 60 cm) en fragmentos es significativamente menor que dentro de los sitios del bosque continuo (Capítulo IV). Por lo tanto, la combinación de la reducción del ámbito hogareño en fragmentos (Chaves *et al.* 2012) y la falta de árboles grandes, me llevó a hipotetizar que estos primates podrían usar los árboles dormidero disponibles de forma más frecuente en los fragmentos (i.e., mayor fidelidad) que en los sitios del bosque continuo. Los resultados apoyaron parcialmente esta hipótesis, ya que la gran variación en la frecuencia de uso entre árboles dormidero no permitió encontrar diferencias significativas entre condiciones de bosque (Capítulo V). Sin embargo, la fidelidad tendió a ser mayor en fragmentos, donde 13.8% de los sitios dormidero fueron usadas durante más de 10 meses, mientras que en el bosque continuo todas los árboles dormidero fueron utilizados por menos de 10 meses (Capítulo V). Abajo se discuten las implicaciones de este patrón de uso de árboles dormideros.

Con relación a la lluvia de semillas (Capítulo IV), se encontró que en fragmentos está dominada por pocas especies, particularmente por la palma *Sabal mexicana* y el árbol *D. guianense* (34% de todas las semillas registradas durante un ciclo anual en fragmentos). Este patrón de dominancia resultó en una comunidad de semillas menos equitativa en fragmentos. Este hallazgo soporta la hipótesis de que la escasez de frutos en fragmentos ‘obliga’ a los monos a usar los recursos disponibles de manera más intensa que en los sitios del bosque continuo (Chapman 1987), ya que estas especies son muy comunes en la región y fructifican durante largos periodos de tiempo (ver Capítulo IV). Como consecuencia, este patrón sugiere que la eficacia de la dispersión de semillas por monos araña es menor en fragmentos, ya que limita la disponibilidad de frutos para otros animales (e.g., monos aulladores, aves grandes y murciélagos frugivoros), reduciendo el gremio de potenciales dispersores de semillas. Además, la acumulación de miles de semillas de estas especies en fragmentos limita significativamente las distancias de dispersión (Schupp *et al.* 2002). Finalmente, esta dominancia de pocas especies de semillas en fragmentos limita el recambio de especies (diversidad beta) entre letrinas, en particular cuando consideramos a las especies abundantes y dominantes. De hecho, la menor heterogeneidad de la dieta de los monos araña en cada fragmento redujo el recambio de especies (menor diversidad beta) entre letrinas, lo que contribuye a desencadenar un proceso de homogenización biótica en fragmentos. Este proceso puede involucrar cambios futuros en la estructura y composición de las especies en las etapas iniciales de reclutamiento (Tabarelli *et al.* 2012). Además, la menor diversidad beta entre letrinas de los fragmentos limita la diversidad total (gamma) que las letrinas de los fragmentos pueden acumular.

El recambio de especies (diversidad beta) entre fragmentos fue mayor que entre los sitios dentro del bosque continuo por que en conjunto la mayoría de las semillas correspondieron a nueve especies que fueron las más dispersadas, mientras que en bosque continuo únicamente fueron cinco (Capítulo IV). Además, el alto recambio de especies en fragmentos puede estar relacionado con la diferencia en la composición y estructura de la vegetación entre fragmentos (Arroyo-Rodríguez *et al.* 2009, 2013); ya que como consecuencia del aislamiento entre fragmentos, el intercambio de especies puede verse limitado (Hubbell 2001). Además, las diferencias en los regímenes de disturbio (e.g., efecto de borde, tala), también pueden influenciar la composición de la comunidad de plantas en fragmentos (Laurance *et al.* 2002; Brown & Gurevitch 2004; Tabarelli *et al.* 2008; Arroyo-Rodríguez *et al.* 2013). Por lo tanto, dado que la diversidad beta de la lluvia de semillas depende de la composición de plantas dentro de cada sitio, se requieren estudios que evalúen a mediano y largo plazo la influencia de los patrones fenológicos sobre la estructura y composición de la vegetación en fragmentos con diferentes tamaño y grado de aislamiento, así como sus potenciales efectos en la lluvia de semillas y sobre los patrones espaciales de diversidad de semillas.

Con relación a la asociación entre la fidelidad y la lluvia de semillas, la tendencia señalada arriba de una mayor frecuencia de uso de árboles dormidero en fragmentos puede ayudar a explicar la acumulación de un mayor número de semillas en estos sitios (Capítulo V). Esto porque la presente tesis demuestra que el aumento en la frecuencia de uso resulta en un aumento significativo del número de semillas y de especies. La menor equitatividad en fragmentos también puede ser explicada por un mayor uso de los árboles dormidero, ya que los resultados demuestran que la frecuencia de uso está negativamente asociada con la equitatividad. Todas estas asociaciones pueden ser explicadas por las diferencias espaciales y temporales en la disponibilidad de frutos (Chapman *et al.* 1989; Capítulo V). En particular, la presencia de una comunidad de semillas más diversa en letrinas bajo árboles dormidero usados con mayor frecuencia soporta la idea de que estos árboles facilitan el acceso a los recursos (i.e., hipótesis del acceso a los recursos: Anderson 1998), ya que funcionan como puntos de inicio y retorno para diferentes subgrupos, lo cual permite a los monos araña un uso del espacio más eficiente. Por lo tanto, dado que los árboles dormidero localizados cerca de las “core areas” tienden a ser más frecuentemente usados que aquellos localizados fuera y que son usados ocasionalmente para los desplazamientos de exploración y la defensa del territorio (McFarland Symington 1988; Wallace 2006, 2008; Spehar *et al.* 2010; Asensio *et al.* 2011; 2012), la fidelidad aumenta y, en consecuencia, también incrementa la diversidad y la abundancia de semillas. Se requieren estudios que evalúen si la asociación positiva entre la fidelidad y atributos de la comunidad se mantiene en el tiempo y como la variación en la fidelidad pueden determinar la estructura espacial de los patrones de diversidad.

En este paisaje fragmentado de la selva Lacandona, la combinación de factores como la distribución espacial agregada y menor distancia entre sitios dormideros en fragmentos, la alta fidelidad y la mayor dispersión de semillas de pocas especies en letrinas (*S. mexicana*, y *D. guianense*), sugiere que la eficacia de dispersión de los monos araña está siendo limitada. La dominancia de pocas especies sobre los patrones espaciales de diversidad de semillas puede tener consecuencias importantes en los patrones iniciales de reclutamiento, en la regeneración y, en última instancia, en el mantenimiento de la diversidad en este paisaje fragmentado. Para conocer de forma más precisa el impacto real de las letrinas en la regeneración, se requieren estudios a mediano y largo plazo que evalúen el efecto de los nutrientes en letrinas (e.g., N, P, y diversos minerales) en la sobrevivencia y crecimiento de plántulas y juveniles que pueden favorecer la creación de mosaicos de vegetación bajo la copa de árboles dormidero.

La falta de animales dispersores de semillas en paisajes fragmentados es una de las mayores amenazas para la biodiversidad (Link & Di Fiore 2006; Galetti & Dirzo 2013), de modo que para contribuir al mantenimiento de la diversidad en paisajes fragmentados se requieren estrategias de conservación dirigidas a procurar la regeneración, restauración y enriquecimiento de la vegetación en fragmentos (Tabarelli *et al.* 2008; Melo *et al.* 2013). Para esto, considerando el potencial de dispersión de los monos araña y su capacidad de desplazamiento, es necesario implementar acciones efectivas de restauración a través de la creación de corredores entre fragmentos (Arroyo-Rodríguez & Mandujano 2006), los cuales pueden favorecer la conectividad estructural del paisaje y permitir el desplazamiento de monos entre fragmentos y en consecuencia, el intercambio de semillas (Chaves *et al.* 2011). Dada la extremada presión que sufren las poblaciones de monos araña en esta región por la pérdida de hábitat (Chaves *et al.*

2011), la extinción local de este importante agente dispersor en paisajes fragmentados puede significar el inicio de consecuencias en cascada para los futuros patrones espaciales de diversidad de semillas (Peres & Palacios 2007), así como para la distribución, composición, estructura y diversidad de las comunidades vegetales.

7. REFERENCIAS

Anderson JR .(1998). Sleep, sleeping sites, and sleep-related activities: Awakening to their significance. *American Journal of Primatology* 46: 63–75.

Arroyo-Rodríguez V, Mandujano S .(2006). Forest fragmentation modifies habitat quality for *Alouatta palliata*. *International Journal of Primatology* 27: 1079–1096.

Arroyo-Rodríguez V, Pineda E, Escobar F, Benítez-Malvido J .(2009). Value of small patches in the conservation of plant-species diversity in highly fragmented rainforest. *Conservation Biology* 23: 729–739.

Arroyo-Rodríguez V, Rös M, Escobar F, Melo FPL, Santos BA, Tabarelli M, Chazdon R .(2013). Plant β-diversity in fragmented rainforests: testing floristic homogenization and differentiation hypotheses. *Journal of Ecology* 101: 1449–1458.

Asensio N, Schaffner CM, Aureli F .(2011). Variability in core areas of spider monkeys (*Ateles geoffroyi*) in a tropical dry forest in Costa Rica. *Primates* 53: 147–156.

Asensio N, Lusseau D, Schaffner CM, Aureli F (2012). Spider monkeys use high-quality core areas in a tropical dry forest. *Journal of Zoology* 287: 250–258.

Boege K, Dirzo R .(2004). Intraspecific variation in growth, defense and herbivory in *Dialium guianense* (Caesalpiniaceae) mediated by edaphic heterogeneity. *Plant Ecology* 175: 59–69.

Brown KA, Gurevitch J .(2004) Long-term impacts of logging on forest diversity in Madagascar. *Procedings of Natural Academie Sci USA* 101: 6045–6049.

Chapman CA .(1987). Flexibility in diets of three species of Costa Rican primates. *Folia Primatologica* 49: 90–105.

Chapman CA .(1989). Primate seed dispersal: the fate of dispersed seeds. *Biotropica* 21: 148–154.

Chaves OM, Stoner KE, Arroyo-Rodríguez V, Estrada A .(2011). Effectiveness of spider monkeys (*Ateles geoffroyi vellerosus*) as seed dispersers in continuous and fragmented rain forests in southern Mexico. *International Journal of Primatology* 32: 177–192.

Chaves OM, Stoner KE, Arroyo-Rodriguez V .(2012). Differences in diet between spider monkey groups living in forest fragments and continuous forest in Lacandona, Mexico. *Biotropica* 44: 105–113.

Connell JH .(1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: den Boer PJ, Gradwell GR (eds). Dynamics of populations. Center for Agricultural Publication and Documentation, Wageningen. The Netherlands. Pp. 298–312.

da Silva Júnior WM, Meira-Neto JAA, da Silva Flávia MC, Rodrigues de Melo F, Santana Moreira L, Ferreira Barbosa E, Dias LG, da Silva Peres CA. (2009). Habitat quality of the woolly spider Monkey. *Folia Primatologica* 80: 295–308.

Dew JL .(2008). Spider monkeys as seed dispersers. In: Campbell CJ (ed). Spider monkeys. The biology, behavior and ecology of the genus *Ateles*. Cambridge University Press, New York. Pp. 155–182.

Howe HF, Smallwood J .(1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201–28.

Howe HF .(1989). Scatter and clump-dispersal and seedling demography: hypothesis and implications. *Oecologia* 79: 417–426.

Hubbell SP .(2001). The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Janzen DH .(1970). Herbivores and the number of tree species in tropical forests. *The American Naturalist* 104: 501–528.

Laurance WF, Delamonica P, Laurance SG, Vasconcelos HL, Lovejoy TE .(2000). Rainforest fragmentation kills big trees. *Nature* 404: 836.

Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC et al. (2002) Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology* 16: 605–618.

Laurence WF, Nascimiento HHEM, Laurence SG, Anndrade AC, Fearnside PM, Ribeiro JEL, Capretz RL .(2006). Rain forest fragmentation and the proliferation of successional tress. *Ecology* 87: 469–482.

Link A, Di Fiore A .(2006). Seed dispersal by spider monkeys and its importance in the maintenance of Neotropical rain-forest diversity. *Journal of Tropical Ecology* 22: 235–246.

Melo FPL, Arroyo-Rodríguez A, Fahrig L, Martínez-Ramos M, Tabarelli M . (2013). On the hope for biodiversity-friendly. *Trends in Ecology and Evolution* 28: 462–468.

McFarland Symington M .(1988). Demography, ranging patterns, and activity budgets of black spider monkeys (*Ateles paniscus chamek*) in the Manu National Park, Peru. *American Journal of Primatology* 15: 45–67.

Nunes A .(1998). Diet and feeding ecology of *Ateles belzebuth* at Maracá ecological station, Roraima, Brasil. *Folia Primatologica* 69: 61–76.

Peres CA, Palacios E .(2007). Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: implications for animal-mediated seed dispersal. *Biotropica* 39: 304–315.

Russo SE, Augspurger CK .(2004). Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. *Ecology Letters* 7: 1058–1067.

Rzedowski J .(2006). Vegetación de México. 1ra. Edición digital. Mexico city: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad.

Sarukhán J .(1968). Análisis sinecológico de las selvas de *Terminalia amazonia* en la planicie costera del Golfo de México. Tesis de maestría. Chapingo: Colegio de Posgraduados.

Schupp EW, Milleron T, Russo SE .(2002). Dissemination limitation and the origin and maintenance of species-rich tropical forests. In: Levey DJ, Silva WR, Galetti M (eds). Seed dispersal and frugivory: ecology, evolution and conservation. CABI Publishing, New York. Pp. 19–33.

Spehar NS, Link A, Di Fiore A .(2010). Male and female range use in a group of white-bellied spider monkeys (*Ateles belzebuth*) in Yasuní National Park, Ecuador. *American Journal of Primatology* 72: 129–141.

Tabarelli M, Lopes AV, Peres CA .(2008). Edge-effects drive tropical forest fragments towards an early-successional system. *Biotropica* 40: 657–661.

Tabarelli M, Peres CA, Melo FPL .(2012). The ‘few winners and many losers’ paradigm revisited: Emerging prospects for tropical forest biodiversity. *Biological Conservation* 155: 136–140.

van Roosmalen MGM, Klein LL .(1988). The spider monkeys, genus *Ateles*. In: Mittermeier RA, Rylands AB, Coimbra-Filho AF, da Fonseca GAB (eds). Ecology and behavior of Neotropical primates. World Wildlife Fund. Washington, DC. Pp. 455–537.

Vásquez-Yanes C, Batis-Muñoz AI, Alcocer-Silva MI, Díaz MG, Dirzo CS .(1999). Árboles y arbustos potencialmente valiosos para la restauración ecológica y la reforestación. Reporte técnico del proyecto J084. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad e Instituto de Ecología, Universidad Nacional Autónoma de México. Pp. 311.

Wallace RB .(2006). Seasonal variations in black-faced black spider monkey (*Ateles chamek*) habitat use and ranging behaviour in a southern Amazonian tropical forest. *American Journal of Primatolology* 68: 313–332.

Wallace RB .(2008). Factors influencing spider monkey habitat use and ranging patterns. In: Campbell CJ (ed). The biology, behavior and ecology of the genus *Ateles*. Cambridge University Press, New York. Pp. 155–182.