



UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
INSTITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD
ECOLOGÍA

**EL PAPEL DE PALMAS COMO FACTOR ESTRUCTURADOR DE LA
COMUNIDAD DE ÁRBOLES DE UNA SELVA HÚMEDA NEOTROPICAL**

TESIS

(POR ARTÍCULO CIENTÍFICO)

**COMPETITIVE EFFECTS OF A DOMINANT PALM ON SAPLING
PERFORMANCE IN A NEOTROPICAL RAINFOREST**

QUE PARA OPTAR POR EL GRADO DE:

MAESTRA EN CIENCIAS BIOLÓGICAS

PRESENTA:

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Directora General de Administración Escolar, UNAM
Presente

Me permito informar a usted que en la reunión ordinaria del Subcomité de Biología Experimental y Biomedicina, del Posgrado en Ciencias Biológicas, celebrada el día 01 de junio de 2020, se aprobó el siguiente jurado para la presentación del examen de grado de **MAESTRA EN CIENCIAS BIOLÓGICAS** en el campo de conocimiento de **Ecología**, de la estudiantee, **NORIEGA PIÑA KAREN**, con número de cuenta con **310188890**, por la modalidad de graduación de tesis por artículo Científico titulado: **"Competitive effects of a dominant palm on sapling performance in a Neotropical rainforest"**, que es producto del proyecto realizado en la maestría que lleva por título, **"El papel de palmas como factor estructurador de la comunidad de árboles de una selva húmeda neotropical"**, realizada bajo la dirección del **DR. MIGUEL MARTÍNEZ RAMOS**, quedando integrado de la siguiente manera:

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Sin otro particular, me es grato enviarle un cordial saludo.

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"POR MI RAZA HABLARÁ EL ESPÍRITU"
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“You and I are flesh and blood, but we are also stardust.”

- **Helena Curtis**

“When the last tree is cut down, the last fish eaten, and the last stream poisoned, you will realize that you cannot eat money.”

- **Proverbio Cree**

Para Pepe y Estefanía

ÍNDICE

ABSTRACT	2
INTRODUCCIÓN.....	3
Áreas protegidas y problemas antropogénicos asociados a ellas: el caso de la Estación de Biología Tropical “Los Tuxtlas.....	3
La competencia interespecífica en las selvas tropicales y su análisis con un enfoque de vecindarios	4
La importancia de la luz en los bosques tropicales húmedos.....	5
Medición de las interacciones de la palma <i>Astrocaryum mexicanum</i> con otras plantas.....	6
MANUSCRITO DEL ARTÍCULO ENVIADO A LA REVISTA BIOTROPICA.....	9
ABSTRACT	11
RESUMEN	12
1. INTRODUCTION.....	13
2. METHODS	17
2.1 Study site	17
2.2 Study species.....	17
2.3 Study system.....	18
2.4 Data analysis.....	19
3. RESULTS.....	22
3.1 Palm light interference	22
3.2 Light interference on sapling canopy displacement.....	23
3.3 Light interference on sapling growth	24
3.4 Neighborhood effects on sapling performance	25
3.5 Competitive effects and functional traits.....	25
4. DISCUSSION	25

TABLES	32
FIGURE LEGENDS.....	35
FIGURES	38
ACKNOWLEDGEMENTS	45
DISCLOSURE STATEMENTS.....	45
REFERENCES.....	46
SUPPLEMENTARY INFORMATION.....	55
DISCUSIÓN GENERAL.....	62
CONCLUSIÓN GENERAL.....	65
LITERATURA CITADA (secciones Introducción, Discusión general y Conclusiones) ...	66

RESUMEN

La eliminación de herbívoros debido a las actividades humanas puede producir una explosión demográfica de las especies de plantas presas que son altamente competitivas, lo que a su vez reduce la diversidad de la comunidad de plantas en general. Esto sucede en la selva húmeda de Los Tuxtlas, México, donde como resultado de la disminución en las poblaciones de herbívoros, las poblaciones crecientes de la palma *Astrocaryum mexicanum* están excluyendo a las especies arbóreas. Sin embargo, los mecanismos de exclusión aún se desconocen. Utilizamos un enfoque de vecindario para explorar los efectos de la competencia de la palma por interferencia o por explotación sobre la supervivencia y el crecimiento de los árboles jóvenes de seis especies de árboles comunes. Seleccionamos 16-32 brinzales focales (1.5-2.5 m de altura) por especie, como centros de áreas de vecindario circulares de radio creciente (2, 3 y 4 m). Medimos la altura y el DAP de los árboles jóvenes al comienzo del estudio y un año después. También se midió el desplazamiento de la copa de los brinzales, ocasionado por el sombreado de la palma, así como rasgos funcionales de los brinzales que pueden ser indicadores de la tolerancia de las especies a la sombra y a la competencia. En los vecindarios, se midió la altura y la cobertura de todos los individuos de *Astrocaryum mexicanum* y el diámetro de todos los árboles (DAP \geq 1 cm). La interferencia de la luz causada por la palma se estimó utilizando fotografías hemisféricas. Se usó un índice de aglomeración en el vecindario para evaluar los efectos dependientes de la densidad de palmas y de árboles sobre la supervivencia y el crecimiento de los brinzales focales. La mortalidad de los brinzales fue baja (7.2%). El crecimiento de los brinzales se vio afectado negativamente a mayor intercepción de luz por parte de la palma y/o por la aglomeración de estas, pero no por la aglomeración de los árboles. *Astrocaryum mexicanum* ejerció efectos competitivos por interferencia y/o por explotación, dependiendo de la tolerancia a la sombra de las especies de brinzales implicadas.

Palabras clave: Coexistencia de especies de plantas; competencia por explotación; competencia por interferencia; competencia en vecindarios; crecimiento de árboles; Los Tuxtlas, México; modelos basados en individuos; rasgos funcionales.

ABSTRACT

Severe eradication of herbivores due to human activities produces demographic outburst of highly competitive prey species, which in turn reduces the diversity of plant communities. This happens at Los Tuxtlas tropical rainforest, Mexico, where due to eradication of herbivores, growing populations of the palm *Astrocaryum mexicanum* are excluding tree species. However, exclusion mechanisms are still unknown. We used a neighborhood approach to explore the competitive effects exerted by the palm through interference or exploitation on survival and growth of saplings of six common tree species. We selected 16-32 focal saplings (1.5-2.5 m height) per species, as centers of circular neighborhood areas of increasing radius (2, 3 and 4 m). We measured height and DBH of saplings at the beginning of the study and one year later. Sapling crown displacement due to palm shading, and functional traits of saplings related to their tolerance to shade and competition were also measured. In the neighborhoods, height, and cover of all stemmed *Astrocaryum mexicanum* palms and diameter of all trees (DBH \geq 1cm) were measured. Palm light interference was estimated using hemispherical photographs. A neighborhood crowding index was used to assess density-dependent effects of palms and trees on focal saplings. Overall, sapling mortality was low (7.2%), which prevented us from evaluating the negative effects of palms on survival. Sapling growth was negatively affected by palm light interference and/or palm crowding, but not by tree crowding. *Astrocaryum mexicanum* exerted competitive interference and/or exploitation effects on saplings, depending on species shade-tolerance.

Keywords: Functional traits, individual based models, Los Tuxtlas, Mexico, neighborhood competition, tree growth, competition through exploitation, competition through interference.

INTRODUCCIÓN

Áreas protegidas y problemas antropogénicos asociados a ellas: el caso de la Estación de Biología Tropical “Los Tuxtlas

Las áreas naturales protegidas tienen un papel crucial en la conservación de la biodiversidad. Sin embargo, el valor de conservación de las reservas puede verse disminuido por las actividades humanas que se efectúan con frecuencia en los paisajes aledaños a ellas y que no están protegidos (Laurance *et al.*, 2012; Martínez-Ramos *et al.*, 2016).

En esos paisajes, la deforestación y la cacería furtiva comprometen la viabilidad de las poblaciones de plantas, animales y el funcionamiento de todo el ecosistema (Melo *et al.*, 2013; Dirzo *et al.*, 2014) y tales efectos pueden extenderse de manera activa o pasiva hacia las reservas. Por lo tanto, estudiar la dinámica de las comunidades bióticas en reservas, rodeadas por paisajes fuertemente modificados por actividades humanas, puede ayudar a entender los efectos de dichas actividades sobre la función de conservación de un área natural protegida.

La reserva de selva alta perennifolia (Miranda y Hernández-X, 1963) que protege la Estación de Biología Tropical “Los Tuxtlas” (EBTLT) ha sido afectada por un proceso de aislamiento por la deforestación y por la defaunación que ha ocurrido a lo largo de más de 40 años en las áreas que la rodean.

Uno de los efectos de tales perturbaciones es el extraordinario crecimiento poblacional de la palma *Astrocaryum mexicanum* Liebm., la especie dominante del sotobosque. La población de la palma ha aumentado de manera exponencial pasando de alrededor de 1,000 palmas adultas (> 1 cm de longitud del tallo) a más 4,000 por hectárea de 1975 a 2013.

Tal crecimiento poblacional puede ser consecuencia de: i) el aumento en la producción de frutos de la palma al incrementarse la luz en el sotobosque, al haber una mayor tasa de formación de claros en el dosel por efectos de borde; y/o ii) la pérdida de mamíferos medianos y grandes que depredaban las semillas, plántulas y palmas jóvenes y que controlaban a la población de *Astrocaryum mexicanum* (p. ej. venado de cola blanca, ciervo de collar, pecarí y tapir) (Martínez-Ramos *et al.*, 2016).

Este aumento poblacional se ha acompañado de una reducción en la abundancia y diversidad de especies de árboles, sobre todo a nivel del sotobosque (Piñero *et al.*, 1986; Martínez-Ramos *et al.*, 2016). Tal relación indica que la palma está desplazando a las especies arbóreas y que con el tiempo la diversidad arbórea de esta selva podría disminuir aún más. Se requiere un análisis de cómo está ocurriendo este efecto de desplazamiento para entender las consecuencias sobre el potencial de regeneración de especies arbóreas y su posible impacto sobre el valor de conservación de la reserva a largo plazo.

La competencia interespecífica en las selvas tropicales y su análisis con un enfoque de vecindarios

La competencia puede definirse como “una interacción entre individuos, provocada por la necesidad compartida de un recurso y que conduce a una reducción en la supervivencia, el crecimiento y/o reproducción de al menos algunos de los competidores involucrados” (Begon, Townsend y Harper, 2006).

Una manera de observar la competencia entre plantas en la naturaleza es estableciendo vecindarios de competencia, que son áreas en las cuales una planta puede ser afectada por factores locales como la abundancia de plantas vecinas. A su vez, un vecindario de competencia puede ser un área circular alrededor de un individuo y que circunscribe a todos los individuos que interactúan con él (Stoll & Weiner, 2000).

En general, podemos decir que las plantas crecen en ambientes heterogéneos en donde la presencia de vecindarios de competencia conespecíficos o heteroespecíficos puede afectar severamente su crecimiento, supervivencia, reproducción, así como sus interacciones bióticas y abióticas (Pacala & Silander, 1985; Moreira *et al.* 2017).

Se sabe que la competencia interespecífica en comunidades naturales de plantas es altamente dependiente de la disponibilidad de los nutrientes. Cuando existen altos niveles de nutrientes, la competencia es principalmente por la luz y cómo la luz es un recurso unidireccional, los atributos de un competidor exitoso por este recurso pueden resumirse como “atributos que permiten sobrepasar a sus vecinos”, es decir, que los individuos más altos siempre son favorecidos (Aerts, 1999; Levin *et al.* 2009).

Para el caso de las selvas tropicales, la formación de claros es algo frecuente debido a la caída de árboles o ramas. En éstos la luz solar es el principal recurso por el que compiten los organismos que se ven implicados en la regeneración, es decir, en el cierre del claro.

Cuando se forma un claro, los árboles pequeños expuestos completamente al sol crecen rápidamente y comienzan a sobrepasar a otros. Posteriormente, los individuos que pertenecen a especies características del dosel crecen y sobrepasan a los demás y los del sotobosque crecen muy lentamente (Farrion *et al.* 2016).

Se espera que la selección natural favorezca a las especies de árboles que tengan una relación alométrica de diámetro del tronco y altura que les permita acceder al nivel superior del dosel de la selva permitiéndoles expandir la copa y aumentar la probabilidad de interceptar la luz (Bongers & Sterck, 1998).

Se plantea que la palma *Astrocaryum mexicanum* pudo convertirse en la especie dominante en el sotobosque de la selva de Los Tuxtlas (ver especie y sitio de estudio más adelante), al ser una planta que produce gran cantidad de semillas y que tiene altas tasas de supervivencia juvenil, en el contexto de la defaunación y deforestación en la selva, esta última favoreciendo un aumento en la frecuencia de formación de claros (Martínez-Ramos *et al.* 2016).

La importancia de la luz en los bosques tropicales húmedos

En los bosques tropicales y subtropicales húmedos la radiación solar es el factor más limitante para el crecimiento de las plantas (Campanello *et al.* 2011). Además, la calidad y la cantidad de luz en los bosques cambian conforme esta pasa a través del dosel. La cantidad de radiación solar que llega al sotobosque (entre 0.6 y 5 m sobre el suelo) puede constituir tan sólo entre el 2 % y el 4 % del total que llega a la superficie del dosel (Clark *et al.*, 1996).

Adicionalmente, la altura de la vegetación es heterogénea aún en el mismo estrato, por tanto, el ambiente lumínico debajo del dosel es sumamente complejo (Percy, 1988). Bajo la densa cobertura del dosel, las semillas de algunas de las plantas de especies sucesionales tempranas con semillas fotoblásticas que no pueden germinar debido a una baja relación de luz roja/rojo lejana en el suelo, lo cual impide

que rompan su latencia (Bazzaz, 1996). Esto es relevante debido a que la abundancia de plántulas y juveniles repercute en la probabilidad de las especies de persistir a futuro en la comunidad de la selva (Martínez-Ramos, 1994).

También, los requerimientos lumínicos de cada especie son particulares y están en función de su historia de vida, edad y vigor (Bazzaz, 1996). En el caso de las selvas altas perennifolias, existen las plantas pioneras que demandan altos niveles de luz y las especies tardías que son capaces de vivir bajo el dosel tolerando la baja disponibilidad de radiación solar a nivel del sotobosque. Algunas de las especies sucesionales tardías pueden crecer bajo condiciones de sombra, como es el caso de *Astrocaryum mexicanum*, de tal manera que presentan bajas tasas de crecimiento en comparación con las pioneras. Sin embargo, para alcanzar la madurez requieren de una mayor disponibilidad de luz,.

Como un ejemplo de la importancia de la luz en las plantas de la selva alta perennifolia, existe un estudio realizado en un invernadero en la EBTLT en donde se analizó el papel de las asociaciones micorrízicas, la luz y la adición de nutrientes en el crecimiento de plántulas de *Poulsenia armata*. En este estudio se encontró que las plántulas de esta especie tienen una alta tasa de mortalidad y que en el tratamiento de alta disponibilidad de luz se encontró una mayor tasa relativa de crecimiento con respecto a los tratamientos de adición de micorrizas y nutrientes (Sánchez-Gallén y Guadarrama, 2003).

Medición de las interacciones de la palma *Astrocaryum mexicanum* con otras plantas

En un estudio realizado por Dyer (1990), sobre la interacción de *Astrocaryum mexicanum* y la comunidad arbórea de Los Tuxtlas, se encontró que en tres de cinco parches de selva alta perennifolia con dosel cerrado y con pendiente escasa, estas palmas eran las principales responsables del ambiente lumínico del sotobosque. En ese mismo estudio, se analizó la distribución espacial de dos especies, *Pseudolmedia glabrata* y de *Poulsenia armata*, la cual su distribución se relacionó con la intercepción de luz provocada por *Astrocaryum mexicanum*. El resultado fue que los brinzales de la

primera especie tienden a no desarrollarse en sitios de alta interceptación lumínica, en cambio los de la segunda tienen una distribución aleatoria.

Por otro lado, un estudio reciente analizó el comportamiento poblacional de *Astrocaryum mexicanum* en la EBTLT en los años 1975-1981 y 2005-2013 en seis sitios de observación permanente (Ortiz-Rodríguez, 2015). Lo que encontró este autor fue que la producción de semillas y la tasa de crecimiento de los juveniles ha aumentado en los años 1975 a 2013 debido a una elevación en la tasa de formación de claros y como consecuencia de la disminución de las poblaciones de mamíferos herbívoros que controlaban a la población de la palma. Como resultado de lo anterior, la población de *Astrocaryum mexicanum* ha aumentado de manera considerable, de 1,243 a 4,058 individuos adultos por ha (Ortiz-Rodríguez, 2015).

En su estudio, Ortiz-Rodríguez (2015) encontró que al analizar la diversidad de especies arbóreas entre los años 1976 a 2013, ésta disminuyó en 34%. Al analizar el ensamble de especies arbóreas en el sotobosque de la selva (individuos menores de 10 m de altura) se encontró una tendencia negativa en la diversidad con relación a la cobertura de las copas de *Astrocaryum mexicanum*, sin embargo, esto no ocurrió con las especies del dosel. La palma se mantuvo como la especie más abundante, con un incremento poblacional de 3 % anual en los 37 años del estudio (Martínez-Ramos *et al.* 2016). Por el contrario, al disminuir la densidad de *Astrocaryum mexicanum*, se incrementa la densidad de las especies del sotobosque principalmente la de *Faramea occidentalis* (Piñero *et al.* 1977; Ortiz-Rodríguez, 2015).

Por lo todo lo anterior, el presente estudio explora los mecanismos ecológicos a través de los cuales la palma podría estar desplazando a algunas especies de árboles. Se examinará si *Astrocaryum mexicanum* excluye a otras especies por competencia debido a explotación o por interferencia lumínica. También se estudiará si la intensidad del desplazamiento depende de algunos rasgos funcionales de las especies arbóreas, o bien opera de manera equivalente para todas las especies analizadas.

En la tabla 1 se resumen algunas de las características de las especies arbóreas utilizadas en este estudio y en la figura 1 se muestran imágenes de las especies en campo.

Tabla 1. Características generales de las especies arbóreas seleccionadas para este estudio

Nombre científico	Estrato	Familia	Nombre común	Altura máxima (m)	DAP máximo (cm)	Densidad de la madera (g/cm ³)	Referencia
<i>Faramea occidentalis</i> (L.) A. Rich.	Sotobosque-Subdosel	Rubiaceae	Huesito	15	20	0.55-0.62	de la Peña-Domene <i>et al.</i> 2017
<i>Psychotria faxlucens</i> Lorence & Dwyer	Sotobosque	Rubiaceae	-	10	-	-	Bongers <i>et al.</i> 1988
<i>Pseudolmedia glabrata</i> (Liebm.) C.C. Berg	Subdosel	Moraceae	Ramón colorado, tomatillo	30	100	0.68-0.72	Fern, 2018; Pennington y Sarukhán, 1998 Ruiz-Guevara <i>et al.</i> 2016
<i>Poulsenia armata</i> (Miq.) Standl.	Dosel	Moraceae	Ababábite	25	90	0.32	Martínez-Ramos, 1985 Pennington y Sarukhán, 1998
<i>Brosimum alicastrum</i> Sw.	Dosel	Moraceae	Ojite, ojoche, ramón	45	150	0.44-0.56	Pennington y Sarukhán, 1998
<i>Trophis mexicana</i> (Liebm.) Bureau	Dosel	Moraceae	Ramoncillo, estrellita	20	25	-	González-Soriano <i>et al.</i> 1997; Tropicos.org, 2020



Figura 1. Especies de árboles usadas en este estudio

- A) *Farama occidentalis*, B) *Psychotria faxlucens*, C) *Pseudolmældia glabrata*,
D) *Poulsenia armata*, E) *Trophis mexicana*, F) *Brosimum alicastrum*

MANUSCRITO DEL ARTÍCULO ENVIADO A LA REVISTA BIOTROPICA

Competitive effects of a dominant palm on sapling performance in a Neotropical rainforest

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ABSTRACT

Severe eradication of herbivores due to human activities produces demographic outburst of highly competitive plant prey species, which in turn reduces plant species diversity. This happens at the protected reserve of “Los Tuxtlas” Tropical Biology Station, where growing population of the palm *Astrocaryum mexicanum* is excluding tree species. However, exclusion mechanisms are still unknown. We used a neighborhood approach to determine the effects of palm competition through interference or exploitation on survival and growth of saplings of six common tree species: *Faramea occidentalis*, *Psychotria faxlucens*, *Pseudolmellia glabrata*, *Poulsenia armata*, *Trophis mexicana* and *Brosimum alicastrum*.

We selected in the field 16-32 focal saplings (1.5-2.5 m height) per species, as centers of circular neighborhood areas of increasing radius (2, 3 and 4 m). We measured height and *DBH* of saplings at the beginning of the study and one year later. Sapling crown displacement due to palm shading, and functional traits of saplings (related to species shade and competition tolerance), were also measured. A neighborhood crowding index was used to assess density-dependent effects of palms and neighboring trees on focal tree saplings. The results show that overall sapling mortality was low (7.2%). Sapling growth was negatively affected by palm light interference and/or palm crowding, but not by neighboring tree crowding. Canopy displacement varied among species, but it has no effect on RGR. We conclude that the palm *Astrocaryum mexicanum* had mostly competitive interference effects but also exploitation effects on saplings, depending on species shade-tolerance.

Keywords: Competition through exploitation, competition through interference, functional traits, individual based models, Los Tuxtlas, Mexico, neighborhood competition, tree growth.

RESUMEN

La eliminación de herbívoros debido a actividades humanas produce una explosión demográfica de especies de plantas presas que son altamente competitivas, lo que a su vez reduce la diversidad de especies de plantas. Esto sucede en la reserva protegida de la Estación de Biología Tropical “Los Tuxtlas”, México, donde las poblaciones crecientes de la palma *Astrocaryum mexicanum* están excluyendo especies arbóreas. Sin embargo, los mecanismos de exclusión aún se desconocen. Utilizamos un enfoque de vecindario para explorar los efectos de la competencia con la palma, debidos a interferencia o a explotación, sobre la supervivencia y el crecimiento de los brinzales de seis especies de árboles comunes: *Faramea occidentalis*, *Psychotria faxlucens*, *Pseudolmestia glabrata*, *Poulsenia armata*, *Trophis mexicana* y *Brosimum alicastrum*. Seleccionamos en el campo de 16-32 brinzales focales (1.5-2.5 m de altura) por especie, como centros de áreas de vecindarios circulares de radio creciente (2, 3 y 4 m). Medimos la altura y el DAP de los brinzales al comienzo del estudio y un año después. También medimos el desplazamiento de la copa de los brinzales, ocasionado por el sombreado de la palma, así como rasgos funcionales de los brinzales que pueden ser indicadores de la tolerancia de las especies a la sombra y a la competencia. Los resultados muestran que la mortalidad fue baja (7.2%). El crecimiento de los brinzales se vio afectado negativamente por la intercepción de la luz por parte de la palma y/o por la aglomeración de palmas, pero no por el de los árboles. Concluimos que *Astrocaryum mexicanum* ejerció efectos competitivos por interferencia y/o por explotación, dependiendo de la tolerancia a la sombra de las especies.

Palabras clave: Coexistencia de especies de plantas; competencia por explotación; competencia por interferencia; competencia en vecindarios; crecimiento de árboles; Los Tuxtlas, México; modelos basados en individuos; rasgos funcionales.

1. INTRODUCTION

Increasingly, several tropical rainforest localities are under the threat of human disturbances (Joppa *et al.* 2008; Laurance *et al.* 2012), and those disturbed ecosystems provide opportunities to explore the role of mechanisms structuring biotic communities. Deforestation, fragmentation, isolation, and hunting reduce or eliminate vertebrate herbivores, and this may have profound effects on other trophic levels (Malhi *et al.* 2014; Dirzo *et al.* 2014). When this happens, some plant populations increase in numbers with consequences for the forest community structure, composition, and dynamics (Terborgh & Feeley, 2010, Estes *et al.* 2011, Martínez-Ramos *et al.* 2016).

The competition interactions also become modified when the trophic chain is altered. In the case of plants, it is known that they compete with their closest neighbors (Berger *et al.* 2008; Gillet, 2008). These neighbors can affect their growing, survive, reproduction and their biotic and abiotic interactions (Pacala & Silander, 1985; Moreira *et al.* 2017). In tropical rainforest, competition is mainly modulated by light when the amount of nutrients is high. The most successful competitor is the highest (Aerts, 1999; Levin *et al.* 2009).

Competition can occur through exploitation or interference (Begon *et al.* 2006; Amarasekare, 2002). Exploitative competition happens when the individuals have indirect negative effects on other individuals by acquiring a resource, and thus depriving others of access to it. For example, by taking nutrients from soil (e.g., Melgoza *et al.* 1990; Tardy *et al.* 2017). Interference competition is where individuals have direct negative effects on other individuals by preventing access to resources via aggressive behaviors such as overgrowth or undercutting. In this case, each consumer alters others' ability to exploit resources at any level of abundance (Vance 1984, Amarasekare, 2002, Levin *et al.* 2009, van Breugel *et al.* 2012; Fernandez *et al.* 2016). For

example, when a plant prevents neighboring smaller plants the acquisition of light resources, or when the space gained by a plant prevents the establishment of another plant due to limited light availability (e.g., van Breugel *et al.* 2012; Fernandez *et al.* 2016). Both type of competition can happen at the same time, but we can observe consequences mainly caused by one or another.

A way to explore competition in plant populations is assessing the effects of neighboring plants on the vital rates —survival, growth, and/or reproduction— of focal plants (Harper, 1977; Stoll & Weiner, 2000; Pacala & Silander, 1985). In this approach, fine-scale spatial interactions modulate the demography of component tree species; that is, it relates effects of distance-dependent or distance-independent measures of local abundance of competitors with the vital rate of a focal individual (Pacala *et al.* 1996; Canham & Uriarte, 2006). This neighborhood analysis approach has been used in temperate (e.g. Canham *et al.* 2004) and tropical forests (e.g., Uriarte *et al.*, 2004; Zambrano *et al.* 2019) to assess competition among tree species.

The competitive ability might vary for species differing in their ability to capture and use resources, which can be inferred from species functional traits (Kunstler *et al.* 2016). In tropical rainforest, tree species survivorship rate increases with wood density (*WD*) and decreases with specific leaf area (*SLA*), and the opposite is true for growth rate (Poorter *et al.* 2008). Species with low *WD* and high *SLA* have lower competitive tolerance than species with high *WD* and lower *SLA* (Kunstler *et al.* 2016).

However, in case of light competition, plasticity in the morphological growth patterns of plants may buffer the shading effects of other plants. For example, plants may avoid neighbors by growing towards areas with higher light availability and reduced interference competition; this phenomenon is called “canopy displacement effect” (Muth & Bazzaz, 2002, 2003). Then, trees in

clumped one side neighborhoods show stronger canopy displacement away from neighbors than trees from more symmetrical neighborhoods (Muth & Bazzaz, 2003).

In the Mexican state of Veracruz, the protected reserve of “Los Tuxtlas” Tropical Biology Station (*LTTBS*) has been affected by strong deforestation in the surrounding landscapes (Dirzo & García, 1992; Mendoza *et al.* 2005 Martínez-Ramos *et al.* 2016). Also, hunting and forest habitat loss have threatened populations of medium-large herbivore mammals, otherwise predators of seeds and seedling of several tree species (Dirzo & Miranda, 1990). One of the plant species favored by the reduction of herbivores abundance is the understory, long-lived (*ca.* 130 years old) palm *Astrocaryum mexicanum*. The large seeds (5-cm long nuts) and seedlings of these palms are consumed by a large number of small and medium-large mammal species, including agouties, peccaries, white-tailed deer, brocket deer, and tapirs, which have been heavily depleted or locally extinct within the *LTTBS* (Dirzo & Miranda, 1990).

In addition, due to edge effects, on the reserve there has been an increased on the frequency of forest gap formation, light resources in the understory, and palm seed production by an order of 5 (Martínez-Ramos *et al.* 2016). More seeds and lower predation rates resulted in an exponential population growth of the palm, from 1,000 palms/ha (≥ 1 cm in height) in 1975 to more than 4,000 palms/ha in 2013 (Martínez-Ramos *et al.* 2016). Fifty years ago, *Astrocaryum mexicanum* appeared to be in a demographic equilibrium, regulated by negative density-dependent mechanisms operating mostly on mortality of seeds, seedlings, and juvenile palms (Martínez-Ramos *et al.*, 1988). The strong increase of the palm population was due to the disruption of such demographic regulation (Martínez-Ramos *et al.* 2016).

The population outbreak of *Astrocaryum mexicanum* on this area has been linked to a reduction in the density and richness of tree species, especially of species that grow in the forest understory (Piñero *et al.* 1986; Martínez-Ramos *et al.* 2016; Hernández-Ruedas *et al.* 2018). This indicates that the palm is displacing tree species, and in the long-term tree species diversity of the whole forest could decrease. This also suggest that competitive exclusion of the palm against tree species is occurring in the forest understory, but the way in which such a process could be taking place is, however, unknown.

In this paper, we determined the effects of palm competition through interference or exploitation on the survival and growth of saplings of six common tree species. This study used a neighborhood approach and was performed in the protected area of tropical rainforest “LTTBS”.

We hypothesized that (1) the negative influence of *Astrocaryum mexicanum* on the saplings of the most abundant tree species occurs to a greater extent due to competition for light resources or (2) the negative influence of *Astrocaryum mexicanum* on the tree saplings of the most abundant tree species occurs to a greater extent due to competition for soil resources. Also, we want to know if species responses depend on functional trades.

Finally, we believe that our study can help to understand the effects of human activities on the conservation function of natural protected areas surrounded by landscapes strongly modified by human activities.

2. METHODS

Competition through interference was assessed by quantifying whether the shading produced by taller nearest palms reduces vital rates —survival and/or growth rates— of saplings. Competition through exploitation was assessed exploring whether vital rates of the saplings decrease as density of all neighboring palms/trees increase, including those that do not shade the saplings. Also, we explored whether the response depends on functional traits of the focal species, or it operates in an equivalent manner for all species. For the study, we selected saplings of six species which are among the most abundant in the *LTTBS*, assuming that competitive interactions of *Astrocaryum mexicanum* could be most frequently with saplings of these species than with those of rarer species.

2.1 Study site

The *LTTBS* is in Veracruz, Mexico (18°34' N and 95°04' W; elevation range: 150 to 700 m asl). Mean annual precipitation is 4,639 mm with a dry period between March and May, and mean monthly temperature is 24.2 °C (González-Soriano *et al.* 1997). In the *LTTBS* (640 ha), the vegetation is tropical rainforest with a 25-35 m mean canopy height, with trees of *Nectandra ambigens* (Lauraceae) dominating in the upper canopy, trees of *Pseudolmedia glabrata* (Moraceae) the mid-canopy, and palms of *Astrocaryum mexicanum* (Arecaceae) dominating the understory (Bongers *et al.* 1988; González-Soriano *et al.* 1997).

2.2 Study species

The palm *Astrocaryum mexicanum* reaches a maximum height of 8 m, individuals have a single stem (4-7 cm in diameter) growing 4.8 cm per year in length. This palm has a single pivotal root approximately 60 cm long, and numerous adventitious roots. For more details about the description of *Astrocaryum mexicanum* see Piñero *et al.* 1977, 1984, 1986.

To test the hypothesized competitive effects of *Astrocaryum mexicanum*, we selected six common tree species at sapling's stage. Three were understory species: *Faramea occidentalis* (Rubiaceae), *Psychotria faxlucens* (Rubiaceae), and *Trophis mexicana* (Moraceae). The other three were canopy species: *Brosimum alicastrum*, *Poulsenia armata*, and *Pseudolmedia glabrata* (all Moraceae). An analysis of functional traits of saplings of these species (Supplementary material) showed that *Brosimum alicastrum*, *Faramea occidentalis*, *Pseudolmedia glabrata*, *Trophis mexicana* had similar values, having high leaf dry matter content (*LDMC*), high twig dry matter content (*TDMC*, equivalent to wood density), and a low number of leaves, low individual leaf area and low total leaf area (*TLA*). In contrast, *Poulsenia armata* and *Psychotria faxlucens* had lower *LDMC* and *TDMC*, but the first had the lowest *TLA* and the later the highest *SLA* among the six studied species (See Supplementary material for a description of how functional traits were measured. Table S1, Table S2, Fig. S1, and Fig. S2).

2.3 Study system

Focal sapling's measurements

We located, in an area of about 19 ha, 16-32 focal saplings per species, each 1.5-2.5 m in height (166 in total). For each sapling, we measured the diameter at breast height (*DBH*), height (from the ground to the tallest vertical point of the crown), the maximum (D_{\max}) and minimum diameter (D_{\min}) of the crown, and counted the number of leaves. To measure *DBH* we used a caliper (0.1 mm resolution), taking two perpendicular measurements. Sapling height was recorded with a measuring tape. Measurements were taken after one year for all the surviving individuals.

Light interference: hemispherical photographs

To quantify light interference produced by the nearest *Astrocaryum mexicanum* on focal saplings, we used hemispherical photographs from above the crown of each focal sapling and above the crown of the nearest palm shading the sapling. In all cases, the camera head was facing North. The height and crown cover of the nearest *Astrocaryum mexicanum* palm were recorded.

Crown displacement

We measured the distance between the stem base of a focal sapling and the vertical projection of the central point of the sapling's crown on the opposite direction to the palm (D_1), and the distance between the stem base of the sapling and the stem base of the nearest palm (D_2 ; Fig. S3).

Neighborhood approach measures

Around each of the 166 focal saplings, we established circular neighborhood areas in radius of 2, 3 and 4 m (those ratios were chosen based on the maximum cover of a single palm), where stemmed palms (≥ 1 cm stem height) of *Astrocaryum mexicanum*, and all neighboring trees with stems $DBH \geq 1$ cm were recorded. For each palm, we measured the stem height and the maximum and perpendicular to the maximum radii of the crown to estimate its crown cover (assuming an ellipsoid shape) and for each neighboring tree we measured their DBH . These records were taken at the beginning of the observation period (May 25 to June 2, 2018).

2.4 Data analysis

Sapling performance

We quantified annual survival and growth rates on tree saplings. Survival was obtained as the percentage of surviving saplings from the original number of saplings tagged one year before.

Growth was quantified as the relative growth rate (RGR) of each sapling, calculated as $RGR = [\ln$

$(\text{size}_{t+1}) - \ln(\text{size}_t) / [(t+1) - t]$, where size was the *DBH* or height of the sapling, $t = \text{year } 2018$, and $t+1 = \text{year } 2019$. We excluded saplings evidently damaged by falling canopy debris of these calculations and we deleted some *RGR* outliers following Grubb (1969), which most likely corresponded to measurement errors.

Crown cover was estimated as
$$\text{Crown cover} = \pi \left(\frac{D_{\max}}{2} \right) \left(\frac{D_{\min}}{2} \right)$$

Effects of light interference by palms on sapling responses

The photographs taken above saplings and about palms were analyzed with the software Gap Light Analyzer (*GLA*), version 2.0. to estimate the percent of canopy openness, and the mean values of transmitted total light radiation. Overexposed images were excluded.

We estimated the palm light interference (*interference*) by the nearest palm *Astrocaryum mexicanum* individual above focal saplings as $\text{Interference} = [(\text{light AP} - \text{light AS}) / \text{light AP}] \times 100$. Here, light AP is the light level (percent of canopy openness or total solar radiation that is the sum of the above direct and above diffuse radiation) recorded above the palm's crown, and light AS the light level above the sapling's crown.

To calculate canopy displacement, distances D_1 and D_2 were used to quantify the level of vertical canopy displacement experienced by a sapling in the presence of a neighboring taller palm. To assess the effect of light interference on sapling vertical growth morphology, we constructed a crown displacement index (*displacement*) as $\text{Displacement} = D_1 / D_2$, (Fig. S3).

We used linear models to analyze differences in *displacement* among species. We tested sapling total leaf area, the height and crown cover of the nearest palm, the difference between palm and sapling height (*DPS*), and the interactions among these factors on *displacement*. To test the sensitivity of *displacement* to changes in *interference*, we regressed *displacement* against *interference* for each species.

Effects of light interference by palms on sapling performance

To assess *interference* effects on sapling growth, we used linear models where *RGR* in *DBH* (RGR_{DBH}) or in height (RGR_H) were the response variables, *interference* an explanatory variable and species a categorical factor with six levels. We included total leaf area of saplings as covariables. The *interference* \times species interaction assessed interspecific differences in the effects of *interference*.

Neighborhood effects on sapling performance

To assess competition through interference and/or exploitation we used a neighborhood crowding index (*NCI*) (Uriarte *et al.* 2004).

We quantified $NCI = \sum \frac{S_i^2}{d_{ij}^2}$ here S_i is the size of the neighboring palm/tree i and d_{ij} is the distance between the stem base of the focal sapling tree (j) and the stem base of the neighbor palm/tree (i). We calculated *NCI* for neighborhoods of three different sizes (circular areas of 2, 3, and 4 m radius around focal saplings, each bigger area includes the smaller areas) and also we evaluated three different categories of neighborhoods (NCI_{All} , included all palms with a height \geq 1cm, NCI_L included palms with a height \geq 2.0 m., and NCI_T included all neighboring trees $DBH \geq$ 1cm, but not *Astrocaryum mexicanum* palms). These predictors helped us to infer the differential influence of palm and neighboring trees on sapling tree performance. NCI_L within 2-m radius included palms shading saplings and potentially competing for soil resources. NCI_L with radius of 3-m and 4-m included only palms with the potential to compete for soil resources. NCI_{All} included all palms with a height \geq 1cm, which added the possible competitive effects of small palms that were not shading focal saplings, and which could be competing just for soil resources. In these two neighborhood types that includes palms, we used palm crown cover as a measure of

S_i^2 , as cover is a good indicator of *Astrocaryum mexicanum* vigor (Piñero & Sarukán, 1982).

NCI_T assessed the possible competitive effect caused by neighboring trees and in this case, S_i was measured as the *DBH* of each neighboring tree.

For each neighborhood type and size, we used linear models to assess effects of crowding (NCI), species, and the interaction species \times crowding on RGR_{DBH} or RGR_{Height} . We introduced the interaction term to assess whether the effect of crowding changed among species. In these analyses, we included height and total leaf area of focal saplings as covariables. Finally, we conducted a regression analysis (RGR as a function of NCI) separately for each species when the first model failed to find a significant species \times crowding interaction effect. We discharged some RGR outliers, following Grubbs (1969), which corresponded to field measurement errors.

Palm competitive effects and sapling functional traits

For each species, the slopes of the relationship's *displacement vs. interference* and *RGR vs. NCI* were used as indicator of the strength of palm competition on sapling performance. The slope was multiplied by -1 to have an index of strength of competition, so that more positive values indicated stronger competition. Finally, to test whether the strength of competition was associated with species functional traits, the slopes were regressed against mean species values of each one of our six functional traits (Table S1).

3. RESULTS

3.1 Palm light interference

On average, across all species, the percentage of light reduction due to palm light interference (*interference*) was $44.8\% \pm 2.2\%$ (S.E.) considering percentage of canopy openness, and $46.9\% \pm$

2.3% considering transmitted total light radiation. We did not find significant differences in absolute light measurements, nor in *interference* among sapling tree species (Table 1).

Interference based on percentage of canopy openness was highly related with *interference* based on transmitted total light radiation ($R^2 = 0.84$, $P < 0.001$). Thus, in the following analysis only the *interference* based on canopy openness was used.

3.2 Light interference on sapling canopy displacement

Mean (\pm SE) crown displacement index across all saplings and species was 0.17 ± 0.01 ($n = 165$). Displacement varied among species ($F_{5,5} = 6.07$, $P < 0.001$), increased with the height of the nearest palm ($F_{1,1} = 38.02$, $P < 0.001$), decreased with the difference between palm and sapling height ($F_{1,1} = 6.42$, $P = 0.012$), and changed with the species \times palm height interaction ($F_{5,5} = 3.01$, $P = 0.012$).

Saplings of *Faramea occidentalis*, *Psychotria faxlucens*, and *Poulsenia armata* exhibited significantly lower displacement, and were less or not sensitive to changes in the height of the palm and in the difference between palm and sapling height, than saplings of *Brosimum alicastrum*, *Trophis mexicana* and *Pseudolmestia glabrata* (Fig. 1). In the first three species, but specially in *Faramea occidentalis*, crown displacement occurred only when the difference between palm and sapling height was very short, while in the other three species, especially in *Brosimum alicastrum*, displacement occurred in a wide range of the height of the nearest palm and the difference between palm and sapling height. In fact, for *Faramea occidentalis*, *Psychotria faxlucens*, and *Poulsenia armata* we did not find any relationship between displacement and interference, while in the other three species displacement increased with interference (Fig. 2).

Overall, seven saplings died across all species during the study year, accounting for a global mortality rate of $0.042 \text{ ind ind}^{-1} \text{ y}^{-1}$. The low sapling mortality prevented us from assessing the effects of *interference* on survival rate.

3.3 Light interference on sapling growth

Relative growth rate in *DBH* (RGR_{DBH}) differed among species ($F_{5,131} = 2.34$, $P = 0.05$). The understory sapling tree *Psychotria faxlucens* exhibited the highest RGR_{DBH} while the canopy sapling tree *Poulsenia armata* the lowest one (Fig. 3).

Overall, *interference* had a negative effect on RGR_{DBH} ($F_{1,1} = 3.73$, $P = 0.05$), while the effect of sapling total leaf area was positive ($F_{1,1} = 4.59$, $P = 0.03$). Also, there was a significant interaction between *interference* and total leaf area on RGR_{DBH} ($F_{1,1} = 4.9$, $P = 0.03$), and between species, *interference*, and sapling total leaf area ($F_{5,5} = 2.99$, $P = 0.01$). Only in *Pseudolmaldia glabrata* RGR_{DBH} did not change with *interference*. In this species RGR_{DBH} increased with sapling leaf area (Fig. 3). In the other species, RGR_{DBH} declined with increasing *interference* particularly faster in saplings with higher leaf area values, except for *Psychotria faxlucens*. *Interference* effect was more pronounced in, *Brosimum alicastrum*, *Famea occidentalis* and *Trophis mexicana* than in the other species.

Relative growth rate in terms of height (RGR_{Height}) did not differ significantly among species but it was significantly affected by the interaction between *interference* and species ($F_{5,5} = 2.72$, $P = 0.02$), the interaction between sapling total leaf area and species ($F_{5,5} = 2.70$, $P = 0.03$), and the interaction between *interference*, sapling leaf area and species ($F_{5,5} = 3.17$, $P = 0.01$). Only in *Poulsenia armata* RGR_{Height} decreased with *interference* (Fig. 4). In three species (*Pseudolmaldia glabrata*, *Brosimum alicastrum* and *F. occidentales*) RGR_{Height} increased with

sapling leaf area, particularly when *interference* was high. *Trophis mexicana* did not present changes in RGR_{Height} at any value of sapling total leaf area or *interference*.

3.4 Neighborhood effects on sapling performance

The effect of the interaction between species and sapling size or *NCI* on *RGR* (*DBH* or height) of focal saplings was not significant. Using regression analysis per species RGR_{DBH} of *Brosimum alicastrum* decreased with *NCI*, both considering all palms (≥ 1 cm height) or only the large ones (≥ 1 m height) (Table 2). Such effect was similar ($R^2 = 40\text{-}46\%$) in all neighborhood sizes (Fig. 5). RGR_{DBH} of *Psychotria faxlucens* also decreased with *NCI*, but in this case the explanatory power of *NCI* on the variation of *RGR* increased with neighborhood size, especially when all palms were considered (Fig. 5; Table 2). RGR_{Height} of *Poulsenia armata* decreased with *NCI* but this effect was marginal (Fig. 5; Table 3), restricted to the smaller neighborhood, and only when all palms were considered. Finally, no significant effects on *RGR* on *DBH* or height were detected due to *NCI* of neighboring trees for any sapling tree species just *Pseudolmestia glabrata* on the biggest neighborhood (Table 2, 3).

3.5 Competitive effects and functional traits

At the species level, the strength of competition due to *interference* on sapling crown displacement was negatively related only to leaf thickness (*LT*; Fig. 6a). The effect of palm crowding on RGR_{Height} declined significantly with the increase of twig dry matter content, especially in the smaller neighborhood including all palms (Fig. 6b), and with *SLA*, especially in the smallest neighborhood considering large palms only (Fig. 6c).

4. DISCUSSION

Overall, the results support our prediction that *Astrocaryum mexicanum* exerts competitive effects, both through interference and exploitation, on saplings of six common tree species. All

species exhibited reduction in sapling growth due to palm light interference (*interference*), palm crowding or both. The short-term nature of our study did not enable us to detect effects on sapling survivorship. As discussed below, the detected *interference* and palm crowding effects on sapling growth were species dependent, which can have implications for future forest structure and composition.

Light interference produced by palms

Along vertical light profiles in tropical rainforests, understory vegetation plays an important role in light attenuation at 2 m above the ground (Montgomery & Chazdon 2001; Montgomery, 2004). For the study site, we found that a single species, the understory palm *Astrocaryum mexicanum*, reduces light availability for tree saplings (around 2 m in height) as much as 50%. Similar results have been found in Costa Rica, Panama, Peru, and Brazil; where high abundance of palms reduce light availability; this is negatively correlated to tree saplings and seedlings density (Chazdon & Pearcy, 1986; Denslow *et al.* 1991, Montgomery, 2004).

The high density of *Astrocaryum mexicanum* at the study site constitutes a strong light filter for regenerating tree communities. It has been estimated that leaf area index of *Astrocaryum mexicanum* is about 2.5 (Martínez-Ramos *et al.* 2016), which means that the palm alone forms two and half layers of foliage covering the forest floor. Such thick cover can influence plant growth strategies, seedling, and sapling vital rates, and ultimately forest tree regeneration dynamics (Dyer, 1990; Montgomery, 2004; Martínez-Ramos *et al.* 2016). Also, we know that it is possible that competitive effects of *Astrocaryum mexicanum* on other species could be stronger on tree seedlings.

Palm light interference (*interference*) did not differ significantly among our six sapling tree species, which means that species were exposed to similar *interference* variation in our experimental system (Table 1). This means that if the trees species respond different to those levels of light it must be at least in some degree because of their identity (Kumordzi et al. 2015).

Crown displacement as strategy to avoid palm shadow

As expected, crown displacement was higher as the difference between sapling and palm height was smaller and weaker as the height of the nearest palm increased (Fig. 1).

This means that *interference* influences individual sapling responses and some of the species maybe using this strategy to avoid shadow as it has been seen in other studies (e.g. Muth & Bazzaz 2002, 2003; Lang *et al.* 2010).

Our results show that *displacement* is not a general strategy among the sapling tree species studied. Three species showed important levels of crown displacement — *Brosimum alicastrum*, *Pseudolmieldia glabrata*, *Trophis mexicana* — and were highly sensitive to changes in palm light interference (*interference*), while in *Faramea occidentalis*, *Poulsenia armata*, and *Psychotria faxlucens* crown displacement was significantly smaller and not related to palm light interference (Fig. 2). As discussed below, such differential interspecific responses to changes in palm light interference were related to different interspecific levels of shade and competition tolerance, as has been reported elsewhere (Longuetaud *et al.* 2013).

Palm competitive effects on sapling performance and its implications to tree diversity

In most species, growth in *DBH* or height was positively related to sapling total leaf area (Figs. 3, 4), a relationship exhibiting the importance of light capture for sapling growth in light limited environments (e.g. Sterck *et al.* 2003). Palm light interference, however, obliterated this leaf area

effect in three of our six studied species, for growth in *DBH* (Fig. 3 and Fig. 4). At the species level, saplings grew on average 10 times faster in diameter (mean $RGR_{DBH} \pm SE = 0.063 \pm 0.009$ cm cm⁻¹ y⁻¹, n =6) than in height ($RGR_{Height} = 0.027 \pm 0.005$), which suggests that saplings suffered strong limitations to vertical growth due to palm light interference. However, understory species grow horizontally (i.e., crown expansion) more than vertically, this allow them to increase light interception, while canopy species invest more energy in vertical growth to higher levels of light in the forest profile (King, 1991). Our understory species *Faramea occidentalis* ($RGR_{DBH}/RGR_{Height} = 3.3$), *Psychotria faxlucens* (4.1), *Trophis mexicana* and the canopy species *Poulsenia armata* (0.5) fit with this expectation, but not the canopy species *Brosimum alicastrum* (2.7) which exhibited very low RGR_{Height} and suffered a strong palm light interference effects on RGR_{DBH} (Fig. 3).

Effects of palm crowding on sapling growth were also important but not for all species. In three species —*Trophis mexicana*, *Faramea occidentalis*, *Pseudolmieldia glabrata*—we did not detect any palm crowding effect, and in two species —*Brosimum alicastrum* and *Psychotria faxlucens*— RGR_{DBH} decreased with crowding, especially as more palms were included in neighborhoods of increasing size. Relative growth rate in height (RGR_{Height}) of *Poulsenia armata* also decreased with palm crowding, but this occurred in the smallest-size neighborhood (Fig. 5). Since the RGR_{Height} of the *Psychotria faxlucens* was not affected by palm light interference (Fig. 3), we infer that crowding effect on this species resulted from exploitation competition rather than from interference competition. In contrast, RGR_{Height} in saplings of *Pseudolmieldia glabrata* and *Trophis mexicana* were affected by palm light interference but not by palm crowding, therefore we infer these species suffered more from interference competition than from exploitation competition. Finally, we infer that growth of saplings of *Brosimum alicastrum* and

Poulsenia armata were affected by both competition types, as growth in *DBH* or height decreased with palm light interference and palm crowding.

The fact that our studied species responded differentially to palm interference and crowding supports the idea that interspecific variation in response to competition contributes to species coexistence in tropical rainforests (Uriarte *et al.* 2004). Also, our results are similar to other studies showing that above and/or below ground competition affect development of tropical rainforest trees at early life-cycle stages (Lewis & Tanner, 2000; Magalhães *et al.* 2014). What is novel in our study is that we document the importance of single understory palm species, *Astrocaryum mexicanum*, as a strong competitor for saplings of common tree species, and perhaps as a major determining factor of the local forest structure, composition and dynamics (Martínez-Ramos *et al.* 2016). This idea is strongly supported by the fact that we did not detect any competitive effects due to neighborhood tree crowding (Table 2). In contrast, other studies performed in Barro Colorado Island, Panama, showed that sapling performance was affected by crowding by tree neighbors (e.g., Hubbell *et al.* 1999; Peters, 2003; Uriarte *et al.* 2004). It is likely that the high density of *Astrocaryum mexicanum* at “Los Tuxtlas” Tropical Biology Station (*LTTBS*), which represented 25-48% of all stems (palms and trees $DBH \geq 1$ cm) in the studied neighborhoods (Table S3), obliterated potential tree crowding effects.

Palm competitive effects lack of fit with classic understanding of sapling functional traits

It has been documented that species with conservative functional traits (e.g., high leaf thickness, *LT*; high wood density, *WS*; high leaf dry matter content, *LDMC*; and low specific leaf area, *SLA*), which are important for maintaining and making a good use of light resources in shaded environments (Wilson *et al.* 1999), have a higher ability to tolerate competition compared to species with acquisitive traits (Wright *et al.* 2010; Kunstler *et al.* 2016). In agreement with this

expectation, species with higher leaf thickness suffered lower crown displacement in response to the strength of palm light interference (Fig. 6a). Also, species with higher twig dry matter content (*TDMC*) suffered weaker effects from the strength of palm crowding on sapling RGR_{Height} , especially in the smallest neighborhoods, where competition effects of palm light interference and palm crowding combine (Fig. 6b).

Contrary to our expectations, strength of competition on sapling RGR_{Height} in response to palm crowding was stronger in species with lower *SLA* (Fig. 6c). It has been documented that species with low *SLA* are in the extreme of shade-tolerance (Dwyer *et al.* 2014), and tolerance to competition (Kunstler *et al.*, 2016), which is associated with slow plant growth rates (Poorter *et al.* 2009). Among our six studied mature forest species, the species that suffered more from strength of palm competition—*Poulsenia armata*—exhibited both an acquisitive trait (smaller *TDMC*) and a conservative trait (lower *SLA*), while the species that suffered less —*Trophis mexicana*—exhibited the opposite traits; which suggest that maybe our understanding of the role of functional traits may be inaccurate. From a practical point of view, the use of these traits could help identify which species are potentially more vulnerable to palm competition. From an ecological and functional perspective, we hypothesize that, under a high competition neighborhood, sapling tree species with a higher *TDMC* (a surrogate of wood density) have the ability to compete better for soil resources (e.g. mineral nutrients or water in the dry season) than saplings with lower *TDMC*. Other studies have found that wood density in tropical tree species is higher in ecosystems in which soils are limited in mineral nutrients compared to those with nutrient-rich soils (e.g., Mori *et al.* 2019). Also, when competition for light is high, a higher *SLA* could enable saplings to capture more light for growth. One advantage of high *SLA* values is enhanced light capture economics (Poorter *et al.* 2009). In fact, under the effect of palm light

interference, for most species we found a positive effect of sapling total leaf area on relative growth rate, both in *DBH* and height (Figs. 3 and 4). Finally, the fact that the strongest relationships between strength of palm competition and *TDMC*, and *SLA* occurred in the smallest neighborhoods, where the effects of palm interference and palm crowing are combined, suggests the importance of conserving soil resources and capturing light for sapling growth.

Conclusion

The palm *Astrocaryum mexicanum* competitively affected the growth of saplings of common tree species at the “Los Tuxtlas” Tropical Biology Station. Such effect differed in intensity and origin (light interference and/or exploitation of soil resources) among sapling tree species. Long-term studies in natural conditions, should show to what extent these effects cause a differential exclusion of tree species, and an overall reduction of forest tree diversity due to the *Astrocaryum mexicanum* population outburst.

TABLES

TABLE 1. Mean (\pm standard error) values of light levels recorded above crowns of saplings (S) of six tree species, and above crowns of nearest *Astrocaryum mexicanum* neighboring palms (P) shading saplings, at the “Los Tuxtlas” Tropical Biology Station (*LTTBS*).

Light records are given as percentage of canopy openness (PCO) and mean daily direct (DLR), diffuse (DFR), and total light radiation (TLR). For PCO and TLR the percentage of light intercepted by palms are indicated as *Interference* = (S/P) \times 100. In all cases, for each light metric, there were no significant differences among species according to Kruskal-Wallis tests (percentage values) or ANOVA (light radiation values).

Species	PCO-P (%)	PCO-S (%)	Interference-PCO (%)	DLR-P (Mols/m ² /d)	DLR-S (Mols/m ² /d)	DFR-P (Mols/m ² /d)	DFR-S (Mols/m ² /d)	TLR-P (Mols/m ² /d)	TLR-S (Mols/m ² /d)	Interference-TLR (%)
<i>Brosimum alicastrum</i>	5.50 \pm 0.70	2.90 \pm 0.50	55.90 \pm 9.00	1.53 \pm 0.24	0.95 \pm 0.20	1.64 \pm 0.25	0.92 \pm 0.17	3.17 \pm 0.46	1.87 \pm 0.36	51.40 \pm 8.90
<i>Faramea occidentalis</i>	6.90 \pm 1.00	3.40 \pm 0.40	43.40 \pm 5.20	2.46 \pm 0.41	1.39 \pm 0.20	2.24 \pm 0.33	1.18 \pm 0.15	4.96 \pm 0.97	2.56 \pm 0.34	46.30 \pm 5.40
<i>Poulsenia armata</i>	5.80 \pm 1.30	2.80 \pm 0.50	49.80 \pm 4.10	1.81 \pm 0.51	0.87 \pm 0.18	1.83 \pm 0.42	0.92 \pm 0.17	3.64 \pm 0.92	1.79 \pm 0.34	54.00 \pm 4.30
<i>Psychotria faxlucens</i>	4.10 \pm 0.70	2.20 \pm 0.40	40.90 \pm 4.60	1.33 \pm 0.33	0.69 \pm 0.13	1.35 \pm 0.24	0.70 \pm 0.12	2.56 \pm 0.55	1.41 \pm 0.23	41.80 \pm 5.6
<i>Pseudolmedia glabrata</i>	4.60 \pm 0.60	2.40 \pm 0.30	44.50 \pm 23.90	1.48 \pm 0.22	0.82 \pm 0.13	1.43 \pm 0.18	0.77 \pm 0.20	2.86 \pm 0.38	1.63 \pm 0.23	48.00 \pm 5.40
<i>Trophis mexicana</i>	4.90 \pm 0.80	2.90 \pm 0.30	40.40 \pm 23.70	1.62 \pm 0.41	0.87 \pm 0.13	1.48 \pm 0.27	0.88 \pm 0.10	3.11 \pm 0.67	1.75 \pm 0.23	40.2 \pm 6.7

TABLE 2. Neighborhood effects of *Astrocaryum mexicanum* palms and trees on the relative growth rate in stem diameter (RGR_{DBH}) of focal saplings of six tree species in the “Los Tuxtlas” Tropical Biology Station (*LTTBS*). The percentage of variance explained (R^2) and corresponding P -values that resulted from regressions between RGR and the neighborhood crowding index are shown for each species (sample size in parentheses next to species name). Letters indicating each type of neighborhood are: ALL = all *Astrocaryum mexicanum* palms higher than 1 cm, L = only *Astrocaryum mexicanum* palms ≥ 1 m, T = only trees with $DBH \geq 1$ cm. Neighborhood areas: 1 = 2 m radius, 2 = 3 m radius, 3 = 4 m radius. Bold numbers denote statistical significance at the $P < 0.05$ level, underlined numbers denote statistical significance at the $P < 0.10$.

Species	Type of neighborhood									
		ALL-1	ALL-2	ALL-3	L-1	L-2	L-3	T-1	T-2	T-3
<i>Brosimum alicastrum</i> (15)	R^2	0.400	0.420	0.410	0.440	0.460	0.430	0.190	0.051	0.063
	P	0.020	0.020	0.020	0.01	0.01	0.020	0.160	0.460	0.410
<i>Faramea occidentalis</i> (26)	R^2	0.049	0.038	0.041	0.018	0.008	0.014	0.058	0.067	0.038
	P	0.280	0.340	0.320	0.510	0.670	0.560	0.230	0.200	0.340
<i>Poulsenia armata</i> (28)	R^2	0.015	0.017	0.021	0.021	0.014	0.010	0.004	0.004	0.004
	P	0.570	0.530	0.490	0.490	0.570	0.640	0.760	0.760	0.750
<i>Psychotria faxlucens</i> (26)	R^2	<u>0.140</u>	<u>0.180</u>	0.23	0.120	<u>0.140</u>	0.190	<u>0.150</u>	<u>0.140</u>	0.130
	P	<u>0.070</u>	<u>0.050</u>	0.020	0.110	<u>0.070</u>	0.040	<u>0.070</u>	<u>0.080</u>	0.100
<i>Pseudolmedia glabrata</i> (31)	R^2	0.006	0.011	0.004	0.019	0.010	0.014	0.013	0.017	0.014
	P	0.680	0.860	0.750	0.470	0.600	0.540	0.570	0.510	0.550
<i>Trophis mexicana</i> (30)	R^2	0.001	0.002	0.004	0.003	0.006	0.009	0.002	0.022	0.020
	P	0.860	0.820	0.740	0.800	0.690	0.630	0.840	0.460	0.490

TABLE 3. Neighborhood effects of *Astrocaryum mexicanum* palms and trees on the relative growth rate in height (RGR_H) of focal saplings of six tree species in the “Los Tuxtlas” Tropical Biology Station (*LTTBS*). The percentage of variance explained (R^2) and corresponding P -values that resulted from regressions between RGR and the neighborhood crowding index are shown for each species (sample size in parentheses next to species name). Letters indicating each type of neighborhood are: ALL = all *Astrocaryum mexicanum* palms higher than 1 cm, L = only *Astrocaryum mexicanum* palms ≥ 1 m, T = only trees with DBH ≥ 1 cm. Neighborhood areas: 1 = 2 m radius, 2 = 3 m radius, 3 = 4 m radius. Underlined numbers denote statistical significance at the $P < 0.10$.

Species	Type of neighborhood									
	ALL-1	ALL-2	ALL-3	L-1	L-2	L-3	T-1	T-2	T-3	
<i>Brosimum alicastrum</i> (15)	R^2	0.005	<0.001	0.004	0.010	<0.001	0.006	<0.001	0.004	0.004
	P	0.800	0.910	0.820	0.720	0.830	0.780	0.930	0.830	0.820
<i>Faramea occidentalis</i> (26)	R^2	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.016	0.002	0.013
	P	0.980	0.980	0.950	0.920	0.980	0.970	0.540	0.810	0.580
<i>Poulsenia armata</i> (28)	R^2	<u>0.120</u>	<u>0.110</u>	0.100	0.043	0.046	0.038	0.110	0.110	0.100
	P	<u>0.080</u>	<u>0.090</u>	0.110	0.310	0.290	0.340	0.100	0.100	0.110
<i>Psychotria faxlucens</i> (26)	R^2	0.034	0.013	0.015	0.013	<0.001	<0.001	<0.001	0.001	<0.001
	P	0.400	0.600	0.580	0.610	0.950	0.930	0.890	0.870	0.940
<i>Pseudolmedia glabrata</i> (31)	R^2	0.039	0.032	0.042	0.066	0.051	0.066	0.093	0.097	<u>0.100</u>
	P	0.290	0.330	0.270	0.160	0.220	0.160	0.110	0.100	<u>0.090</u>
<i>Trophis mexicana</i> (30)	R^2	0.036	0.041	0.061	0.045	0.048	0.074	0.051	0.046	0.043
	P	0.340	0.310	0.210	0.290	0.270	0.170	0.280	0.290	0.310

FIGURE LEGENDS

Figure 1. Influence of height of the nearest *Astrocaryum mexicanum* palm and distance between sapling and palm crowns on crown displacement index (*displacement*) for saplings of six tree species. The 3-D surfaces resulted from the best generalized linear models fitted to empirical data. The adjusted model was: $Y = a + b * palm\ height + c * DPS$, where a is the intercept, b is a species-specific coefficient of palm height effect, and c a species-specific coefficient of the effect of difference in height of the sapling and the palm (DPS). Below each species' name the mean and one standard error (SE) of crown displacement index (*displacement*) are indicated. Mean values not sharing the same letter are significantly different ($P < 0.05$).

Figure 2. The effect of palm light interception (*interference*) on canopy displacement index (CDI) for focal saplings of six tree species. Species: Bral = *Brosimum alicastrum*, Faoc = *Faramea occidentalis*, Poar = *Poulsenia armata*, Psfa = *Psychotria faxlucens*, Psgl = *Pseudolmedia glabrata*, Trme = *Trophis mexicana*. Inside each graph statistics of the best-fitted regression model are shown, including the proportion of variance explained by the model (R^2) and the significance level (P).

Figure 3. Effect of palm light interference and sapling total leaf area (TLA) on relative growth rate in DBH (RGR_{DBH}) of focal saplings of six tree species (Sp) at Los Tuxtlas, Mexico. The 3D surfaces resulted from the best generalized linear models fitted to empirical data. The adjusted model was: $RGR_{DBH} = a + bSp + c * PLI + d * AFOL + e * Sp * PLI + f Sp * PLI * AFL$, where a is the intercept and b, c, d, e and f are coefficients of single or interactive effects of Sp, PLI and/or AFL . Below the species name the mean and SE of the crown displacement index are indicated. All independent variables, except Sp , were significant ($P < 0.05$). The proportion of total variance explained (R^2) by the whole model was 0.30 ($R^2_{adj} = 0.18, n = 120, P = 0.0025; AIC = -288.5$).

Figure 4. Effect of palm light interference and sapling total leaf area on relative growth rate in height (RGR_{Height}) of focal saplings of six tree species (Sp) at Los Tuxtlas, Mexico. The 3D surfaces resulted from the best generalized linear models fitted to empirical data. The adjusted model was: $RGR_{DBH} = a + b*Sp*PLI + c*SP*AF + d*Sp*PLI*AF$, where a is the intercept and b , c , and d are coefficients of single or interactive effects of Sp , PLI and AF . Below the species name the mean and SE of the crown displacement index are indicated. The effects of all independent variables, except Sp , were significant ($P < 0.05$). The proportion of total variance explained (R^2) by the whole model was 0.28 ($R^2_{adj} = 0.16$, $n = 103$, $P = 0.0025$; $AIC = -312.6$).

Figure 5. *Astrocaryum mexicanum* neighborhood effects on growth of focal saplings of six tree species at Los Tuxtlas, Mexico. For each species, results of regressions of relative growth rate in DBH (RGR_{DBH}) or height (RGR_{Height}) against neighborhood crowding index (*crowding*) are shown for two different neighborhood types (NCI_{All} and NCI_L) and three neighborhood sizes (circular areas of 2, 3 and 4 m radius). Neighborhood type NCI_{All} included all *Astrocaryum mexicanum* stemmed palms (≥ 1 cm height), while type NCI_L included big palms ≥ 100 cm height (≥ 2 m total height). Inside each panel, the adjusted model regression, the proportion of total variance explained (R^2), and the significance level are shown. Only significant regressions are included.

Figure 6. Relationships between strength of palm competition and functional traits of different sapling tree species studied. Only the best-fitted regression models (continuous line) are shown, including the proportion of variance explained (R^2) and the significance level (P). Strength of competition is measured as -1 multiplied by the slope of the regression between palm light interference (*interference*) or neighborhood crowding index (*crowding*) and sapling crown displacement (*displacement*) or RGR (DBH or height), so that strength of competition increases

as Y-values become more positive. *Crowding-ALL1* indicates the neighborhood circular area with a radius of 2 m, which included all palms with a stem ≥ 1 cm in height; *Crowding-L1* indicates the neighborhood of the same area but including only large palms with a stem ≥ 1 m in height. Species: BRAL = *Brosimum alicastrum*, FAOC = *Faramea occidentalis*, POAR = *Poulsenia armata*, PSFA = *Psychotria faxlucens*, PSGL = *Pseudolmedia glabrata*.

FIGURES

Figure 1

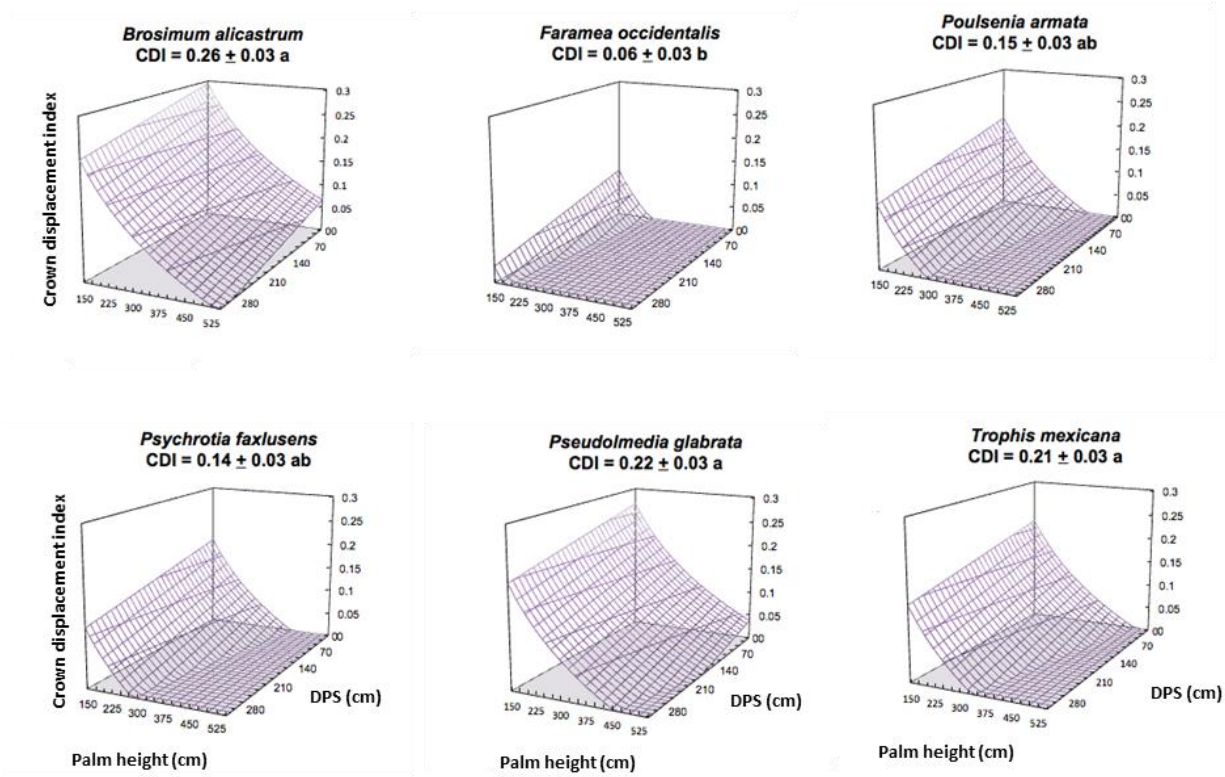


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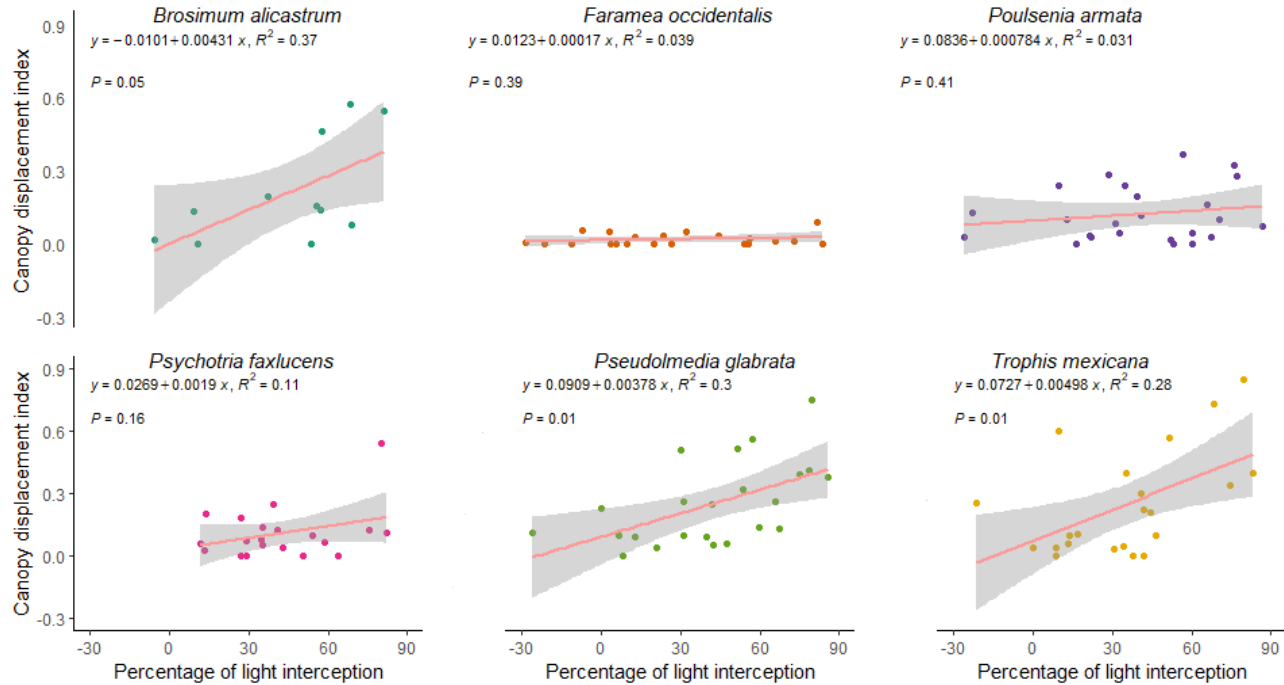


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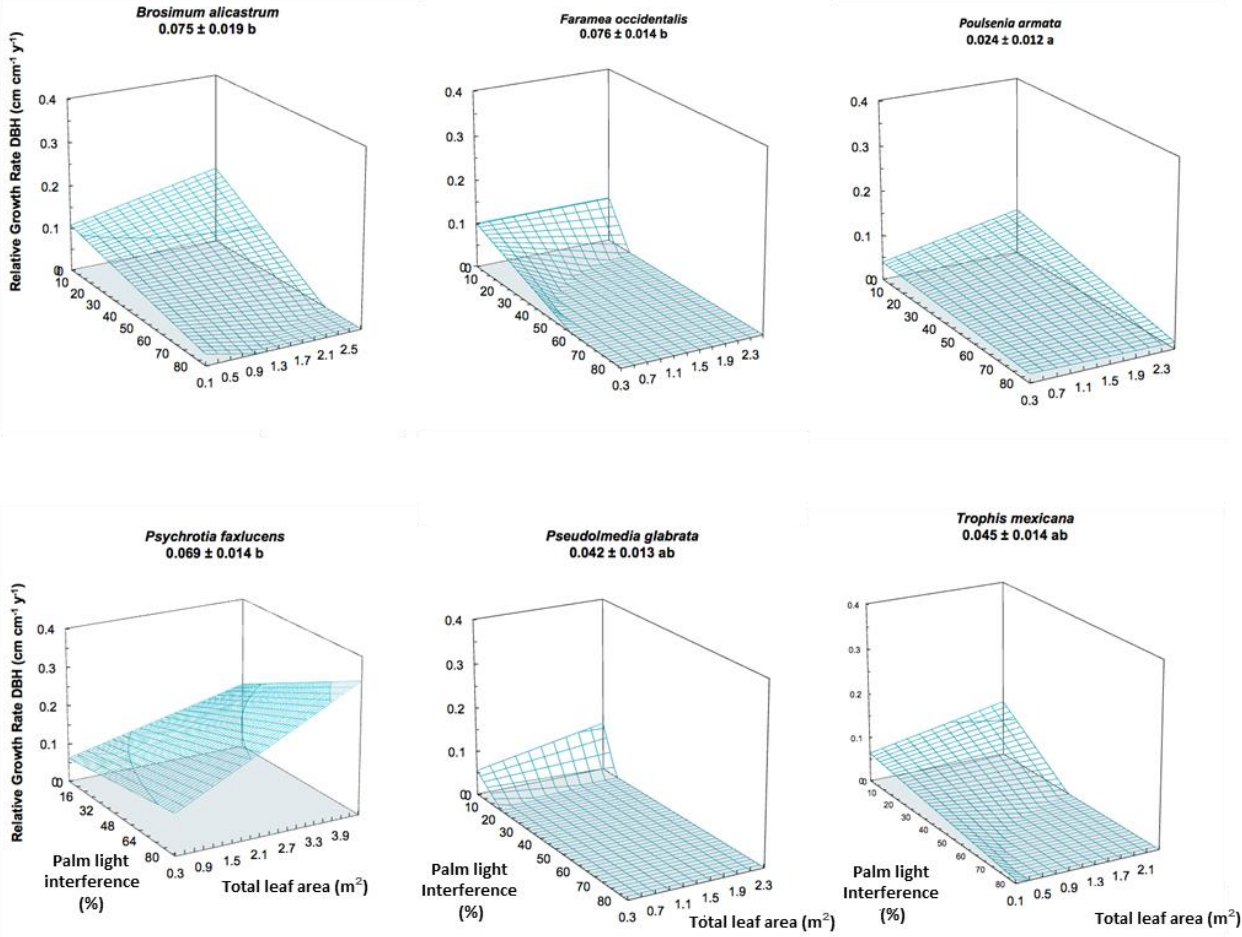


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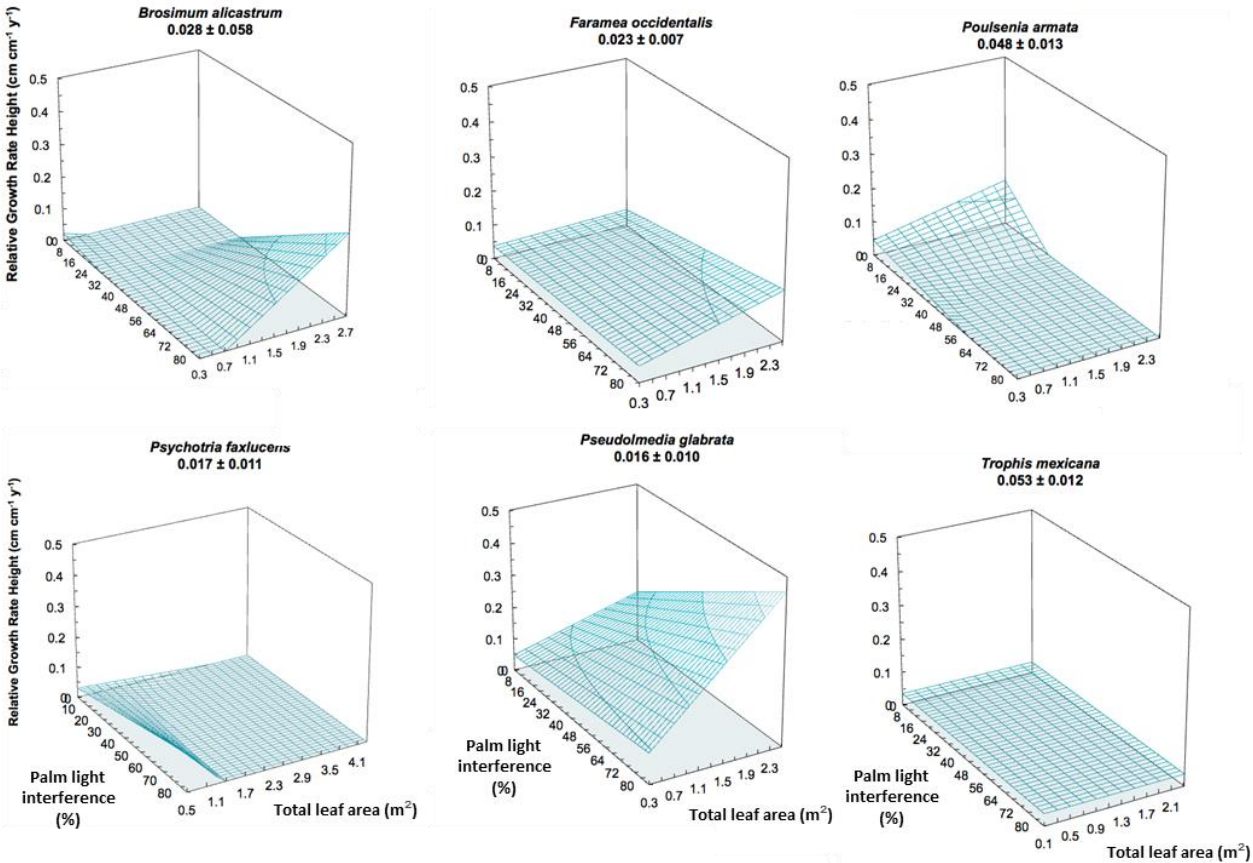
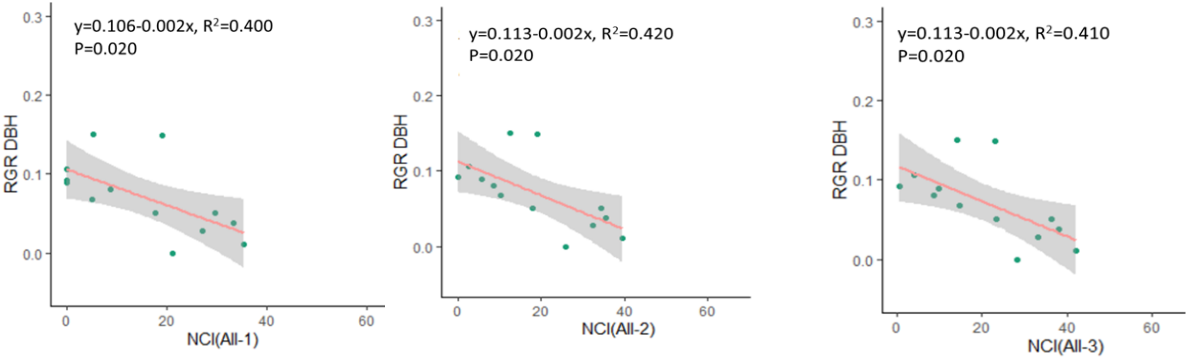
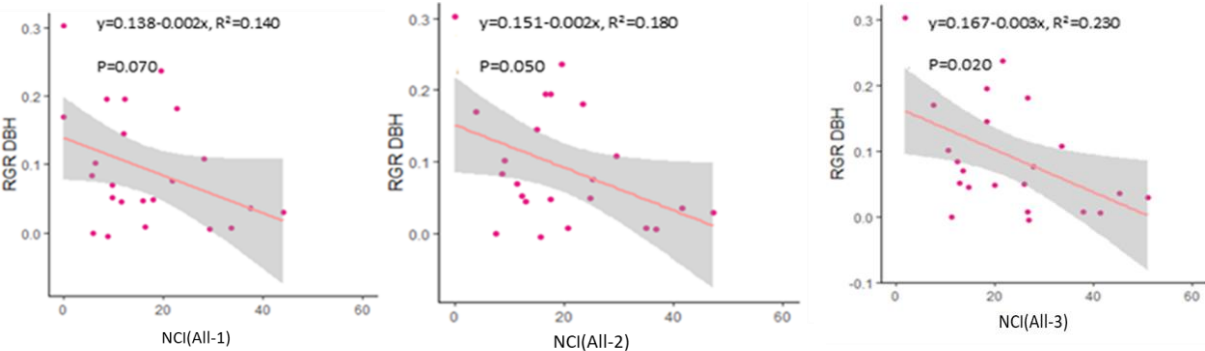


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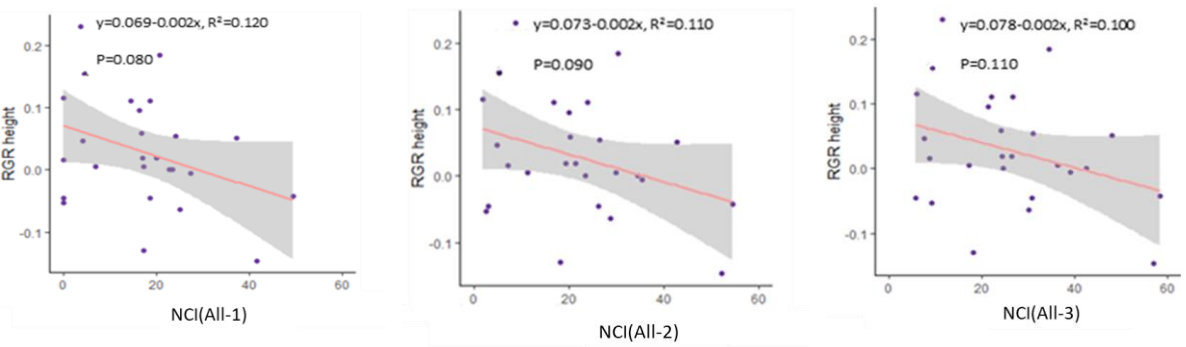
Brosimum alicastrum



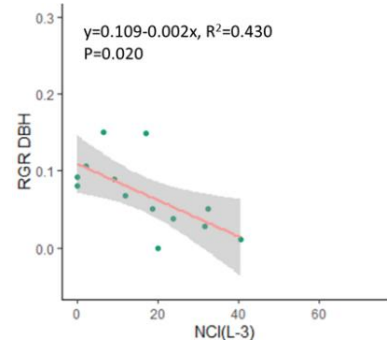
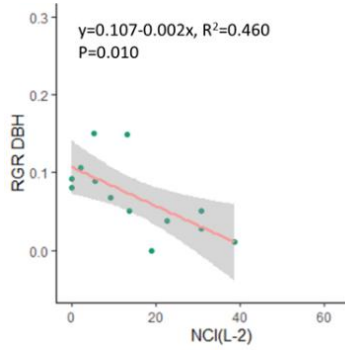
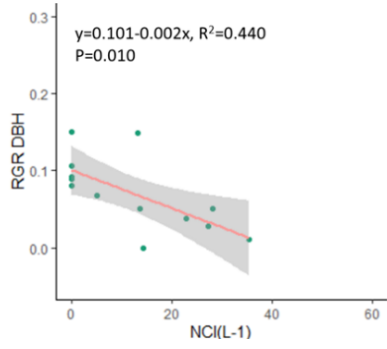
Psychotria faxlucens



Poulsenia armata



Brosimum alicastrum



Psychotria faxlucens

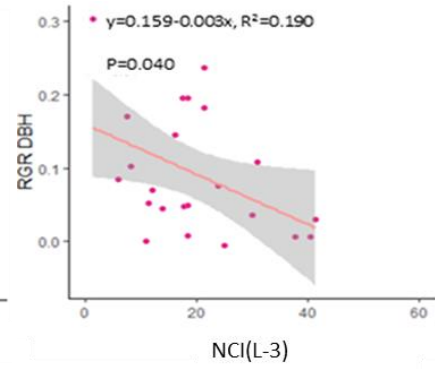
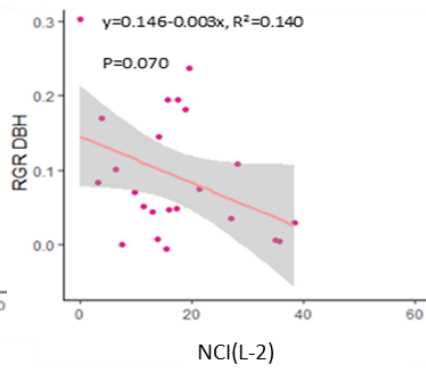
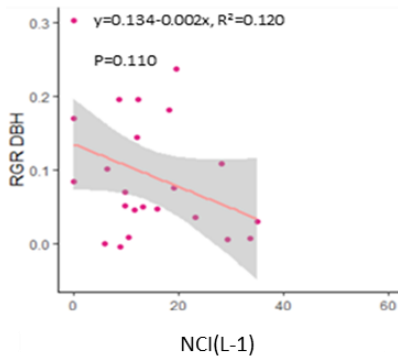
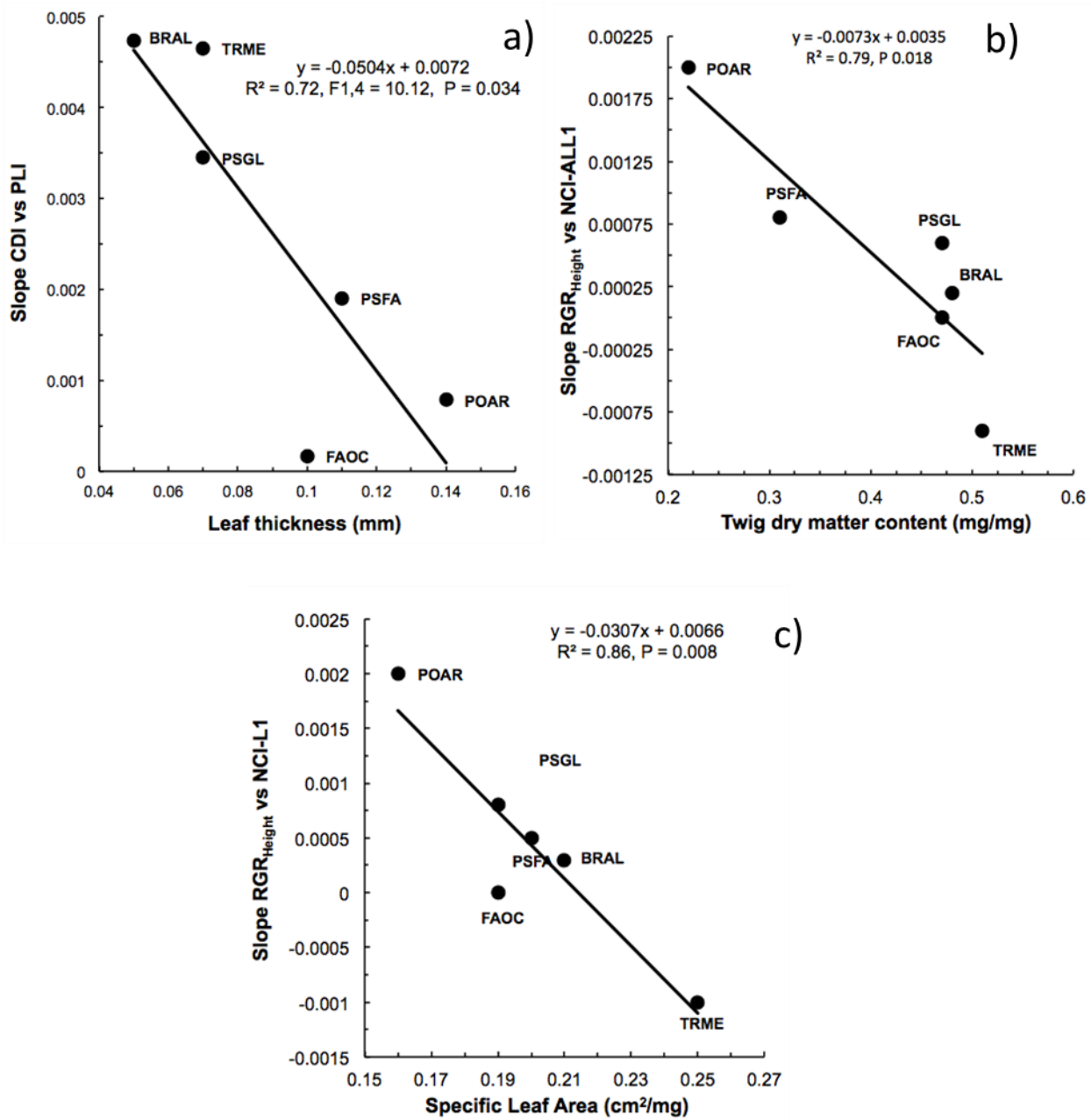


Figure 6



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Author Contribution Statement

Karen Noriega-Piña and Miguel Martínez-Ramos were involved in conceptualization, development of methodology, investigation, project administration, data curation, formal analysis, visualization, and writing. Daniel Piñero and Teresa Valverde were involved in research supervision and discussion. Miguel Martínez-Ramos was responsible for funding acquisition.

DISCLOSURE STATEMENTS

Conflict of Interest

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

Ethical Guidelines

Not applicable.

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SUPPLEMENTARY INFORMATION

Characterization of functional profile of saplings of six studied tree species

At the beginning of our experimental study we randomly collected 3-5 branches and leaves from three to eight different saplings per species from individuals other than our experimental ones to quantify leaf dry matter content (*LDMC*), leaf thickness (*LT*), leaf area (*LA*), specific leaf area (*SLA*) and twig dry matter content (*TDMC*). We followed protocols described by Pérez-Harguindeguy et al. (2013) to quantify these functional attributes. Also, for all focal saplings used in the neighborhood analysis (n = 164), we counted the total number of leaves; then, we multiplied leaf number by mean leaf area to obtain total leaf area per sapling (*TLA*). Tables S1 and S2 show mean (\pm SE) values for each functional trait, and Fig. S1 shows the differences in the functional profile (in the form of a radar chart) among species. An *NMDS* analysis differentiated *Poulsenia armata* and *Psychotria faxlucens* from the rest of study species (Fig. S2).

TABLE S1 Mean and standard error of morpho-functional traits of focal sapling tree species used to assess possible competitive effects of the palm *Astrocaryum mexicanum* at Los Tuxtlas Tropical Biology Field Station, Veracruz, Mexico.

Species	Height (cm)	Number of leaves	Total leaf area (m ²)	Crown cover (m ²)	Canopy displacement
<i>Brosimum alicastrum</i>	186.1 ± 7.7	86.5 ± 20.4	0.81 ± 0.17	1.11 ± 0.25	0.26 ± 0.05
<i>Faramea occidentalis</i>	201.0 ± 4.8	175.6 ± 20.2	0.92 ± 0.11	1.14 ± 0.10	0.05 ± 0.02
<i>Poulsenia armata</i>	206.1 ± 5.8	22.9 ± 2.4	0.72 ± 0.10	0.79 ± 0.06	0.14 ± 0.03
<i>Psychotria faxlucens</i>	201.7 ± 5.7	312.8 ± 28.8	1.64 ± 0.18	1.38 ± 0.12	0.14 ± 0.03
<i>Pseudolmedia glabrata</i>	193.8 ± 4.9	118.9 ± 12.5	0.61 ± 0.09	1.01 ± 0.10	0.26 ± 0.04
<i>Trophis mexicana</i>	198.2 ± 5.5	166.2 ± 23.0	0.64 ± 0.11	0.90 ± 0.11	0.22 ± 0.04

TABLE S2 Mean and standard error values for morpho-functional traits of non-focal saplings of the six dominant tree species used to assess possible competitive interactions with the palm *Astrocaryum mexicanum* at Los Tuxtlas Tropical Biology Field Station, Veracruz, Mexico. Traits measured are: Leaf dry matter content (*LDMC*), leaf thickness (*LT*), leaf area (*LA*), specific leaf area (*SLA*) and twig dry matter content (*TDMC*).

Species	LDMC (mg/g)	LT (mm)	LA (cm ²)	SLA (cm ² /mg)	TDMC (mg/mg)
<i>Brosimum alicastrum</i>	419.9 ± 11.8	0.05 ± 0.01	74.1 ± 9.90	0.21 ± 0.01	0.48 ± 0.01
<i>Faramea occidentalis</i>	352.7 ± 21.5	0.10 ± 0.01	48.2 ± 4.3	0.19 ± 0.01	0.47 ± 0.01
<i>Poulsenia armata</i>	305.3 ± 13.4	0.14 ± 0.01	293.2 ± 30.7	0.16 ± 0.01	0.22 ± 0.01
<i>Psychotria faxlucens</i>	205.0 ± 38.1	0.11 ± 0.01	38.4 ± 2.9	0.20 ± 0.02	0.31 ± 0.02
<i>Pseudolmedia glabrata</i>	435.0 ± 47.6	0.07 ± 0.01	39.3 ± 2.2	0.19 ± 0.01	0.47 ± 0.02
<i>Trophis mexicana</i>	375.2 ± 6.0	0.07 ± 0.01	38.2 ± 4.9	0.25 ± 0.01	0.51 ± 0.01

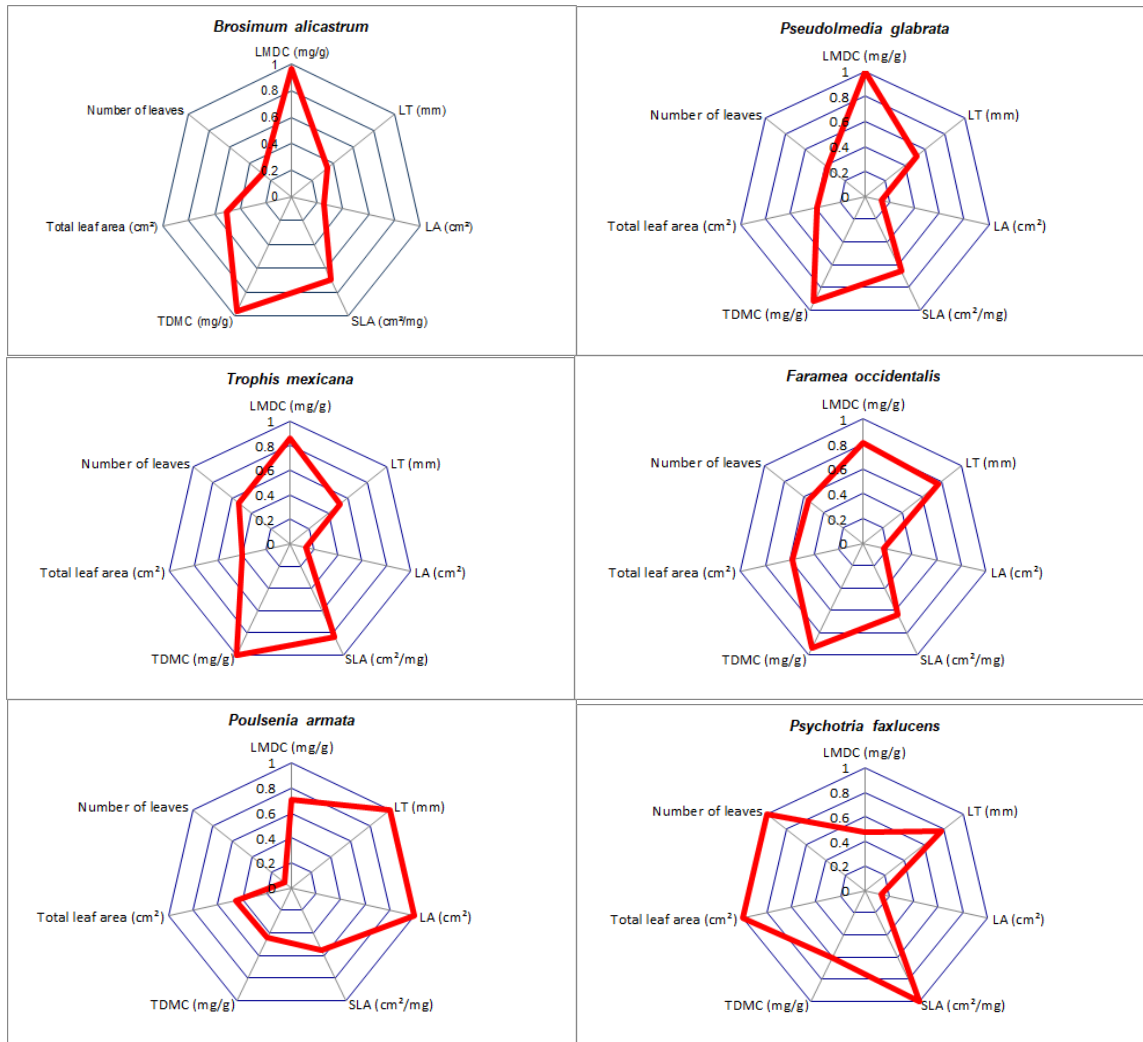


Figure S1. Radar charts describing functional profiles of saplings of the six studied tree species. Axes of each chart represent relative scales, with the species having the maximum trait value considered as 1 and the rest as proportions of this maximum. The red line in each chart joins the different relative trait values, showing the functional profile of each species.

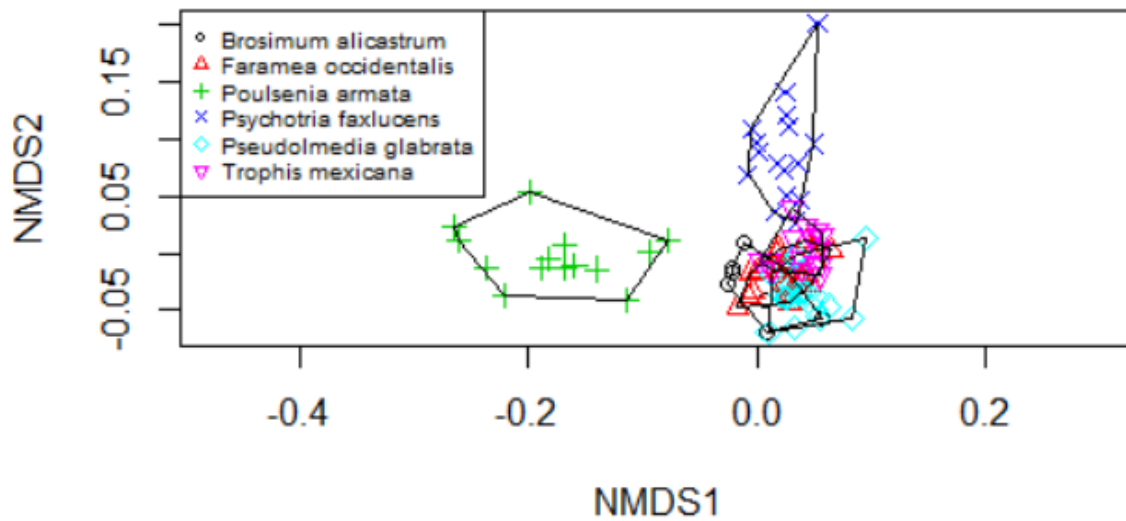


Figure S2. Results of non-metric multidimensional scaling (*NMDS*) of the six studied sapling tree species at Los Tuxtlas, Mexico. Ordination considered five functional traits (leaf dry matter content, leaf thickness, leaf area, specific leaf area, and twig dry matter content). Polygons enclose saplings (symbols) of different species. Clearly, *Poulsenia armata* and *Psychotria faxluocens* differ from the rest of the species. Stress value is 0.061.



Figure S3. Drawing showing distance measurements used to calculate sapling Canopy Displacement Index (*CDI*). D_1 = distance between the base of the stem of a focal sapling and the vertical projection of the tip of the sapling crown; D_2 = distance between the stem base of the sapling and the stem base of the nearest *Astrocaryum mexicanum* palm. *CDI* was calculated as D_1/D_2 .

TABLE S3. Mean number of *Astrocaryum mexicanum* palms and trees with DBH \geq 1 cm in neighborhoods (N) of increasing size (circular areas of 2, 3 and 4 m radius), having as focal sapling old-growth forest tree species at Los Tuxtlas, Mexico. At the bottom, the percentages of *Astrocaryum mexicanum* palms from the total number of plants recorded are shown.

Group	Species	N1	N2	N3
Palms	Bral	1.25	3.00	4.81
	Faoc	1.40	2.90	5.57
	Poar	0.87	2.47	5.47
	Psfa	0.93	1.90	4.10
	Psgl	1.60	3.07	5.87
	Trme	1.27	2.77	4.87
Trees	Bral	2.69	5.13	8.44
	Faoc	1.47	3.33	6.03
	Poar	1.67	3.30	6.40
	Psfa	2.80	5.77	11.20
	Psgl	1.80	3.93	7.77
	Trme	2.80	5.57	9.97
All (palms and trees)	Bral	3.94	8.13	13.25
	Faoc	2.87	6.23	11.60
	Poar	2.53	5.77	11.87
	Psfa	3.73	7.67	15.30
	Psgl	3.40	7.00	13.63
	Trme	4.07	8.33	14.83
%Palms	Bral	31.75	36.92	36.32
	Faoc	48.84	46.52	47.99
	Poar	34.21	42.77	46.07
	Psfa	25.00	24.78	26.80
	Psgl	47.06	43.81	43.03
	Trme	31.15	33.20	32.81

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DISCUSIÓN GENERAL

Encontramos que *Astrocaryum mexicanum* es capaz de reducirle hasta el 55% del porcentaje de apertura del dosel a las especies focales, afectando la radiación que reciben.

También encontramos que lo anterior aunado a la cercanía de la palma está positivamente relacionada con una respuesta física de los brinzales, como es el desplazamiento de sus copas.

Hallamos evidencias a favor y en contra de nuestras hipótesis principales para las distintas especies (Tabla 2). Para cinco de nuestras seis especies de estudio existe al menos alguna evidencia que apoya la existencia de competencia entre estas y la palma. Es importante destacar que cuando probamos los efectos del índice de vecindario calculado con los árboles vecinos no encontramos una relación negativa significativa entre este y la tasa de crecimiento de las especies focales, salvo para *Psychotria faxlucens*, lo que sugiere que los efectos de vecindario encontrados están dados por *A. mexicanum*.

Para los atributos funcionales sólo encontramos que el desplazamiento de las copas y la interferencia lumínica están positivamente relacionadas con el grosor de la hoja, lo que concuerda con lo que se sabe de las especies con atributos conservativos (Wright et al.,2010; Kunstler, 2016).

Las relaciones de la tasa de crecimiento en altura y el NCI_{ALL1} y el contenido de materia seca son positivas lo que también concuerda respecto a que las especies con atributos conservativos son más tolerantes a la competencia.

Sin embargo, para el caso de la de la tasa de crecimiento en altura y el NCI_{ALL1} y su relación con el área foliar específica se encontró una relación positiva lo cual resulta contradictorio con lo que se esperaba.

Adicionalmente, algunas de nuestras especies de estudio presentaron atributos funcionales tanto adquisitivos como conservativos, en el caso de la especie más afectada por la relación anterior – *Poulsenia armata* – un bajo contenido de materia seca en el tallo y baja área foliar específica y para la especie menos afectada – *Trophis mexicana*– niveles altos en los mismos atributos. Estos patrones si se comprueban para otras especies podrían servir para hacer predicciones sobre las especies vulnerables ante la competencia con la palma.

Tabla 2. Evidencias encontradas para establecer que existen relaciones de competencia entre nuestros árboles focales y *Astrocaryum mexicanum*

Evidencias que apoyan la competencia de los brinzales de distintas especies con <i>Astrocaryum mexicanum</i>	Evidencias a favor de la competencia por recursos lumínicos	Evidencias a favor de la competencia por recursos del suelo	Evidencias que no apoyan algún tipo de competencia u apoyan la competencia con otras especies
Que el NCI (AI_i, L) de las palmas esté correlacionado negativamente con las tasas de crecimiento de los brinzales de las especies <i>Brosimum alicastrum</i> , <i>Psychotria faxlucens</i> y <i>Poulsenia armata</i> (Figura 5, sobretiro del artículo) y NO ocurra lo mismo con el NCI de los árboles vecinos para ninguna de las seis especies	Que el NCI_L calculado sólo con las palmas altas que potencialmente pueden disminuir la luz que reciben los brinzales esté negativamente correlacionado con la tasa de crecimiento de <i>Brosimum alicastrum</i> y que el coeficiente de determinación sea alto y significativo en NCL₁ , el vecindario que contiene a los individuos más cercanos al focal (Figura 5, sobretiro del artículo)	Que el NCI_L calculado para los vecindarios que incluyen a los vecinos más lejanos al focal (vecindarios 2,3), estén negativamente correlacionados con la tasa de crecimiento de <i>Psychotria faxlucens</i> y que esta correlación sea significativa, no siendo así en los vecindarios de menor tamaño (Figura 5, sobretiro del artículo)	Que los NCI_{AI} / NCI_L / NCI_T , de los distintos tamaños de vecindarios no estén correlacionados con la tasa de crecimiento de <i>Pseudomelia glabrata</i> , <i>Trophis mexicana</i> y <i>Faramea occidentalis</i>
	Que exista una menor tasa de crecimiento en los individuos que estaban sometidos a mayores niveles de interferencia lumínica a causa de las palmas más cercanas y el área foliar total para <i>Faramea occidentalis</i> , <i>Brosimum alicastrum</i> y <i>Trophis mexicana</i> (Figura 3, sobretiro del artículo)	Que el NCI_{AI} calculado con todas las palmas vecinas, incluyendo las que no podrían interferirle la luz al focal esté negativamente correlacionado con la tasa de crecimiento de <i>Brosimum alicastrum</i> , en los tres vecindarios y <i>Poulsenia armata</i> en los vecindarios 1 y 2 (Figura 5, sobretiro del artículo)	Que no exista una relación entre la tasa de crecimiento y el porcentaje de interferencia lumínica a causa de las palmas más cercanas y el área foliar total para <i>Poulsenia armata</i> , <i>Psychotria faxlucens</i> y <i>Pseudomelia glabrata</i>
		Que el NCI_{AI} calculado con todas las palmas vecinas, incluyendo las que no podrían interferirle la luz al focal (vecindarios 2,3) esté negativamente correlacionado con la tasa de crecimiento de <i>Psychotria faxlucens</i> y que esta correlación sea significativa y más fuerte en el vecindario más lejano (Figura 5, sobretiro del artículo)	NCI_T este marginalmente relacionado de manera negativa con la tasa de crecimiento de <i>Psychotria faxlucens</i> en los tres vecindarios

CONCLUSIÓN GENERAL

Astrocaryum mexicanum afectó competitivamente el crecimiento de los brinzales de algunas de las especies arbóreas comunes en la Estación de Biología Tropical de Los Tuxtlas. Tal efecto difirió en intensidad y origen (interferencia de la luz y/o explotación de los recursos del suelo) entre las especies estudiadas. Los estudios a largo plazo en el campo deben mostrar hasta qué punto estos efectos causan una exclusión diferencial de especies arbóreas y una reducción general de la diversidad de árboles debido al estallido de la población de *A. mexicanum*.

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