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Posgrado en Ciencias Biológicas

**VARIACIÓN SUCESIONAL Y ESPACIAL DE  
CARACTERES Y GRUPOS FUNCIONALES DE  
PLANTAS LEÑOSAS EN UN BOSQUE TROPICAL  
SECO**

Tesis que presenta

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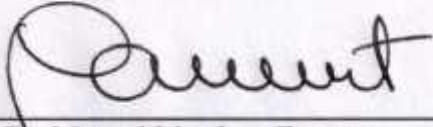


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## **LISTADO DE ABREVIATURAS**

Dis	Dispersal syndrome	LPb	Leaf pubescence
Ex	Plant exudates	LPulv	Leaf pulvation
FDiv	Functional Divergence	MPU	Minimal photosyntethic unit
FEve	Functional Eveness		
FRic	Functional Richness	OG	Old-growth forest specialist
FS	Flat-site specialist	SG	Second-growth forest specialist
G	Generalist		
HS	Hill specialist	SES	Standard Effect Sizes
LA	Leaf area	SLA	Specific leaf area
LC	Leaf compoundness	Sp	Plant spininess
LD	Leaf deciduousness	TGA	Trait Gradient Analysis
LDMC	Leaf dry matter content	WSG	Wood specific gravity
LP	Leaf petiole		

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## RESUMEN

Los caracteres funcionales de las especies constituyen una herramienta útil para explicar su distribución y para entender el efecto que tiene el ambiente en el ensamblaje de sus comunidades a diferentes escalas espaciales. La finalidad de este trabajo fue obtener, mediante el uso de los caracteres funcionales, una aproximación sobre cuáles características de las plantas leñosas son clave para su coexistencia y dominancia en un gradiente de sucesión y topografía en la Península de Yucatán. Esto se realizó en tres etapas: (1) Se analizó qué caracteres funcionales distinguen a los grupos de especies leñosas especialistas y generalistas en ambos gradientes. Las especies pioneras sólo se diferenciaron de las tardías y las generalistas por la presencia de pulvinos (característica asociada al control de la temperatura) y las pioneras de las tardías por el hábito deciduo de las primeras. Las especies generalistas fueron más similares a las especies tardías, con hojas o foliolos pequeños y perennes. Las generalistas dominaron en todas las edades sucesionales, lo que reflejaría la historia de disturbio de la zona o un gradiente ambiental muy pequeño. Las especies tardías co-dominaron con generalistas en edades sucesionales tardías únicamente en cerros. (2) A partir del análisis de la diversidad funcional se determinó que la fase de regeneración (brinzales) es susceptible a procesos de filtrado ambiental en todas las edades de la sucesión y en los cerros. Los adultos, por el contrario, fueron favorecidos por las condiciones de edades sucesionales jóvenes e intermedias, en donde mostraron una alta riqueza funcional; asimismo, mostraron filtrado ambiental sólo en la edad sucesional más tardía en cerros. También se encontró evidencia de competencia en etapas jóvenes de la sucesión en la fase regenerativa, y ninguna señal en adultos. (3) El análisis del gradiente de caracteres permitió establecer que la co-variación de caracteres de adultos (y por ende la diferenciación funcional de las especies) es mínima entre parcelas, lo que sugiere la ausencia de filtros ambientales que produzcan un recambio funcional entre diferentes edades de sucesión u otros gradientes del paisaje. Por el contrario, la diferenciación funcional ocurre al interior de las comunidades. La conclusión general es que en el bosque semideciduo estudiado los procesos de filtrado ambiental y competencia son determinantes en el ensamblaje de las comunidades de plantas leñosas más jóvenes, y su efecto se incrementa hacia las edades más avanzadas de la sucesión. En las plantas adultas existe un continuo de variación en estrategias ecológicas en las plantas leñosas, pero ésta obedece

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principalmente a factores locales (que es necesario investigar) y no a diferencias ambientales o de otro tipo a escala de paisaje.

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## SUMMARY

Functional traits of species, i.e. measurable features affecting their fitness in a given environment, provide insights into how species are distributed, and how the environment shapes plant community assembly at different spatial scales. Secondary succession is one of the most important scenarios in which these processes can be analyzed from a functional perspective. The objective of this study was to obtain, through the use of functional traits, a better understanding of which traits are key for plant coexistence and dominance over successional and topographical gradients in the Yucatan Peninsula. We achieved this through three different approaches: (1) We characterized functionally generalist and specialist plant species found along successional and topographic (flat sites vs hills) gradients. We found scarce differentiation between these groups. Early-successional species differed from late-successional and generalists in having pulvinate leaves (a trait related to temperature control) and from late-successional species because the former were deciduous. Generalists showed the greatest functional variation, but they were more similar to late successional species by sharing small perennial leaves or leaflets. Generalists were dominant in all successional stages, probably reflecting the long history of disturbance of the area. (2) Functional diversity analysis showed that the regenerative phase (saplings) was the only one that suffered an increasing reduction of trait range by environmental filtering during succession on flat sites and hills. In contrast, adults showed an increased range of traits, indicating favourable conditions and a more complete use of resources than expected by chance at early and intermediate successional ages. Besides, adults showed environmental filtering only in the oldest plots on hills. We also found evidence of competition for saplings at early successional age, and no evidence for adults. (3) Trait gradient analysis showed that trait covariation of adults (or species functional differentiation) occurred mainly within communities, indicating that the successional/topographical gradient do not result in a strong functional differentiation among species in this forest. The general conclusion is that environmental filtering and competition drives community assembly of saplings in this semideciduous forest, with an increasing effect towards late successional stands. For adult plants there is a functional continuum of variation that is driven by local factors (which deserve further investigation) and not by environmental differences at the landscape scale.



## INTRODUCCIÓN

La sucesión secundaria inicia con un cambio drástico en las condiciones biológicas y ambientales con respecto a las que existían antes del disturbio, y ocasiona cambios dinámicos en la composición de la vegetación a lo largo del tiempo; en consecuencia, la sucesión representa una oportunidad ideal para investigar el ensamblaje de las comunidades (Lasky *et al.*, 2014). Las plantas son entidades dinámicas que interactúan entre sí, procesan los recursos y se adecuan a su ambiente. Algunas de estas interacciones y procesos pueden analizarse mediante sus caracteres funcionales, es decir, aquellas características morfológicas, fisiológicas o de historia de vida con valor adaptativo (Violle *et al.*, 2007). Los caracteres funcionales son una herramienta que permite inferir muchas de las interacciones entre las especies (competencia, facilitación, herbivoría), determinan su capacidad para establecerse, crecer, sobrevivir y reproducirse bajo ciertas condiciones ambientales e influyen en los procesos ecosistémicos, como la producción primaria y los ciclos biogeoquímicos del carbono, agua y nutrientes, entre otros (Lavorel, 2013; Westoby y Wright, 2006).

Existen caracteres funcionales vegetales que co-varían negativamente entre muchas especies, y que reflejan la baja disponibilidad de recursos limitantes como el agua, la luz o los nutrientes, por lo que las plantas pueden maximizar únicamente ciertas funciones a costa de limitar otras (Reich, 2014). Debido a que estas disyuntivas influyen en su estrategia ecológica y distribución (Kneitel y Chase, 2004), los análisis de comunidades de plantas basados en caracteres funcionales tienen un poder explicativo mucho mayor que aquellos que analizan las especies y su diversidad (Keddy, 1992a; Reich *et al.*, 2003; Tilman *et al.*, 1997). Por esto, los estudios de la sucesión secundaria basados en caracteres funcionales se han convertido en una herramienta fundamental para su entendimiento (Buzzard *et al.*, 2015; Lohbeck *et al.*, 2015; Zhang *et al.*, 2015).

Los análisis funcionales permiten inferir porqué las especies que se establecen en fases iniciales de la sucesión lo hacen, y porqué son reemplazadas por otras en fases intermedias y tardías, en relación al cambio ambiental que ocurre simultáneamente como consecuencia del desarrollo de la vegetación (Lebrija-Trejos *et al.*, 2010a). Pero los estudios funcionales no se limitan al entendimiento de la dinámica de la comunidad; también permiten predecir el comportamiento en términos de resistencia y resiliencia de

los ecosistemas ante eventos locales de perturbación (asociados principalmente con las actividades humanas y ante cambios de escala global, McGill *et al.*, 2006) y los servicios ambientales que aportan (Lavorel, 2013; Lavorel y Grigulis, 2012). Por esto, su aplicación en bosques tropicales secos es muy adecuado por ser un ecosistema que ha sido poco estudiado en comparación con los bosques tropicales húmedos, y que está altamente amenazado debido al uso intensivo, transformación y degradación históricos de la que ha sido objeto (Portillo-Quintero y Sánchez-Azofeifa, 2010; Miles *et al.*, 2006).

Utilizando como herramienta una aproximación basada en caracteres funcionales en un bosque tropical semideciduo de Yucatán, en este trabajo se analizaron las estrategias ecológicas de especies especialistas y generalistas tanto en el gradiente ambiental asociado a la sucesión secundaria (bosque joven y viejo) como el asociado con la topografía (sitios planos o en cerros), y los posibles procesos de ensamblaje de estas comunidades.

## **CAPÍTULO 1.**

### **1.1 ANTECEDENTES**

#### **1.1.1 Los caracteres funcionales en plantas leñosas y sus asociaciones**

Los caracteres funcionales de las plantas (Cuadro 1.1) son aquellas características morfológicas, fisiológicas o fenológicas medibles a nivel de individuo, que impactan de forma indirecta la adecuación de la especie a través de sus efectos en la biomasa vegetativa, la reproducción o la supervivencia de la planta (Violle *et al.*, 2007). En múltiples especies se han descrito las correlaciones de los caracteres funcionales que determinan la estrategia ecológica de las plantas, siendo ésta la manera en que las especies mantienen sus poblaciones bajo una variedad de ambientes, con la presencia de competidores y bajo procesos de disturbio que determinan su coexistencia (Westoby, 1998). Estas correlaciones obedecen a dos tipos de fenómenos: 1) limitantes físicas, fisiológicas o de desarrollo que limitan la evolución independiente de los caracteres, y 2) procesos de selección natural que favorecieron ciertas combinaciones de caracteres sobre otras (Wright *et al.*, 2007). Las disyuntivas o interacciones funcionales negativas (trade-offs), en las que los patrones de asignación de recursos en una función ocurre a expensas del funcionamiento de otra (Kneitel y Chase, 2004; Semenova y van der Maarel, 2000), son de interés particular por su papel en la diferenciación de nicho, en la coexistencia de las especies y en el recambio de especies en gradientes ambientales (Wright *et al.*, 2007). Las disyuntivas pueden analizarse conforme a su papel en la historia de vida de las plantas: aquellas asociadas con la adquisición, procesamiento y conservación de recursos (eje económico) y aquellas asociadas con la reproducción.

Dentro del primer eje, se encuentran aquellas disyuntivas relacionadas con caracteres funcionales de hojas, tallos y raíces. Por ejemplo, las especies que fotosintetizan más por unidad de peso de N en hojas (es decir, que tienen alta eficiencia del uso fotosintético del nitrógeno o PNUE) tienden a tener altas tasas de crecimiento y a distribuirse en sitios perturbados o hábitats altamente productivos (Hikosaka, 2004). El PNUE se correlaciona de forma negativa con el peso foliar por unidad de área (LMA por sus siglas en inglés). Las especies con alto LMA y bajo PNUE se encuentran en hábitats poco productivos o extremos, y se caracterizan por tener hojas de longevidad larga pero con bajas

concentraciones de nitrógeno y bajas tasas fotosintéticas por unidad de peso ( $A_{mass}$ ), con láminas gruesas, venas protuberantes, alta densidad de los tejidos o alguna combinación de esas características. La disyuntiva entre PNUE y LMA se debe a que, para producir hojas más duras, la planta requiere asignar más biomasa y nitrógeno para formar paredes celulares gruesas, reduciendo la conductancia del mesófilo y la asignación de N al aparato fotosintético. Dado que las plantas no pueden maximizar tanto PNUE como LMA, hay una *disyuntiva entre fotosíntesis y persistencia* de las hojas (Hikosaka, 2004).

Cuadro 1.1 Caracteres funcionales de plantas comúnmente medidos.

Abreviatura en inglés	Descripción	Obtención y/o unidades
H	Altura	m
SA	Área de la albura	cm <sup>2</sup>
SLA	Área foliar específica	Área hoja en fresco / peso seco hoja (cm <sup>2</sup> g <sup>-1</sup> )
LA o LSz	Área o tamaño de la hoja	cm <sup>2</sup>
LDMC	Contenido seco foliar	100 x peso hoja desecada / peso hoja saturado (%)
<sup>wood</sup> PNUE	Densidad de madera Eficiencia del uso fotosintético del nitrógeno	Peso seco / volumen verde (g cm <sup>-3</sup> ) Incremento en biomasa por unidad de N tomado o perdido (Kg mol <sup>-1</sup> )
WSG	Gravedad específica de la madera	Densidad madera / Densidad agua (sin unidades)
LA/SA	Inverso del valor de Huber, Área total de hojas/Área de la albura	cm <sup>2</sup>
LL	Longevidad foliar	(meses)
PL	Longitud pecíolo	cm
N <sub>area</sub> o LNC <sub>a</sub>	Nitrógeno por unidad de área foliar	LNC <sub>m</sub> / SLA (mg cm <sup>-2</sup> )
N <sub>mass</sub> o LNC <sub>m</sub>	Nitrógeno por unidad de peso o Contenido de Nitrógeno foliar	%
Seed <sub>mass</sub>	Peso de la semilla	g
LMA	Peso foliar por unidad de área	1 / SLA; peso seco hoja / área hoja en fresco (g <sup>-1</sup> cm <sup>2</sup> )
<sup>min</sup> LNP	Potencial hídrico estacional mínimo Productividad de nitrógeno foliar	MPa Tasa de incremento en peso seco por unidad de N en hoja por unidad de tiempo (g g <sup>-1</sup> día <sup>-1</sup> )
Sz	Tamaño de la semilla	cm <sup>3</sup>
NAR o ULR	Tasa de asimilación neta	Incremento en biomasa por área de hoja (g m <sup>-2</sup> día <sup>-1</sup> )
RGR	Tasa de crecimiento relativo	NAR X LAR (g g <sup>-1</sup> día <sup>-1</sup> )

Abreviatura en inglés	Descripción	Obtención y/o unidades
$A_{\text{area}}$	Tasa fotosintética foliar por unidad de área foliar	$\mu\text{mol m}^{-2} \text{s}^{-1}$
$A_{\text{mass}}$	Tasa fotosintética foliar por unidad de peso foliar	$\mu\text{mol g}^{-1} \text{s}^{-1}$

De una forma similar, se ha descrito la disyuntiva entre la asignación de biomasa a fibras, rayos o paredes celulares de vasos y traqueidas (lo que confiere una resistencia mecánica mayor a la madera pero menor área de conducción de agua), o la de favorecer su almacenamiento y conducción (Chave *et al.*, 2009). Se ha encontrado que árboles de bosques tropicales con alta capacidad de almacenamiento de agua en la albura (es decir, en parénquima, espacios capilares y vasos y traqueidas) mantienen tasas máximas de transpiración por una fracción mayor del día que otros árboles con menor capacidad de almacenar agua (Goldstein *et al.*, 1998). También se ha demostrado que la capacitancia de la albura disminuye a medida que se incrementa la densidad de la madera (Meinzer *et al.*, 2003). A su vez, las fuertes relaciones entre el aporte de agua a las hojas y la capacidad fotosintética máxima ( $A_{\text{max}}$ ), sugieren que esta capacidad está limitada por el aporte del sistema vascular (Brodrribb y Feild, 2000; Santiago *et al.*, 2004), por lo que la densidad de la madera se asocia inversamente con las tasas de crecimiento, fotosíntesis y el área foliar específica (SLA por sus siglas en inglés, Cuadro 1.1) (Ishida *et al.*, 2008; Bucci *et al.*, 2004; Reich *et al.*, 1997). Con base en estas relaciones, se ha propuesto una *disyuntiva entre la eficiencia hidráulica del tallo y la seguridad* (Pineda-García *et al.*, 2013; Tyree y Sperry, 1989). Las especies muy eficientes en la conducción de agua, que pueden sostener altas tasas fotosintéticas y que en general son deciduas, son altamente susceptibles a la cavitación. (Pineda-García *et al.*, 2013; Méndez-Alonso *et al.*, 2012; Marksteijn *et al.*, 2011; Sobrado, 1997, 1993). Por el contrario, las especies perennifolias que tienen una capacidad más reducida de transporte de agua y de fotosíntesis, pueden funcionar con potenciales hídricos del suelo mucho más bajos antes de que ocurra la formación de émbolos que obstruyan el movimiento del agua en el xilema (Pineda-García *et al.*, 2013; Méndez-Alonso *et al.*, 2012; Marksteijn *et al.*, 2011; Sobrado, 1997, 1993).

Aparentemente, la combinación de dos mecanismos para evitar la sequía, el almacenamiento de agua en la albura (asociado con una baja densidad de madera) y el

hábito deciduo de las hojas, permiten desacoplar a las especies de potenciales muy negativos del suelo (Pineda-García *et al.*, 2013). El almacenamiento de agua en la albura, asociado principalmente con especies de fases tardías de la sucesión en el bosque tropical seco, están a su vez asociadas con raíces someras (Paz *et al.*, 2015). Por el contrario, las especies de fases tempranas de la sucesión, sometidas a condiciones más rigurosas de sequía, y que en general presentan baja capacidad de almacenar agua en la albura pero alta resistencia a la cavitación, muestran un sistema de raíces de mayor longitud y de mayor profundidad (Paz *et al.*, 2015). Tales relaciones sugieren una *disyuntiva entre la profundidad de las raíces y la capacidad de almacenamiento de agua en la albura* (Paz *et al.*, 2015).

Finalmente, en lo que respecta a la reproducción, múltiples estudios han propuesto una *disyuntiva entre el tamaño de las semillas y su número*, pues se ha encontrado que la producción de semillas se correlaciona de forma negativa con su peso (Westoby, 1998; Westoby *et al.*, 2002; Weiher *et al.*, 1999). Además, se ha descrito en diversos estudios que las plántulas de especies con semillas más grandes tienden a tener mayores reservas en relación a las partes autótrofas en funcionamiento de la plántula, por lo que pueden mantener la respiración por un tiempo más largo bajo déficit de carbono (Westoby *et al.*, 2002). La supervivencia de las plántulas también se relaciona positivamente con el tamaño de las semillas porque las plántulas provenientes de semillas grandes pueden competir mejor con otras plantas ya establecidas, pueden emerger después de estar enterradas en suelo u hojarasca y pueden resistir mejor la sequía (Westoby *et al.*, 2002; Leishman y Westoby, 1994; Moles y Westoby, 2004). Dado que las especies con semillas pequeñas tienen alta fecundidad, y las plántulas de las especies que provienen de semillas grandes mayor habilidad competitiva y/o tolerancia a diversas condiciones estresantes, se ha propuesto la *disyuntiva entre fecundidad y habilidad competitiva* (Tilman, 1994). Esta disyuntiva plantea que las especies competitivas tienen fecundidad baja, por lo que las semillas pueden llegar a un número reducido de parches; en cambio, las especies poco competitivas producen un número grande de semillas, lo que les permite colonizar un gran número de parches y sobrevivir en aquellos en los que no haya especies competitivas (Tilman, 1994). Sin embargo, la evidencia empírica y modelos matemáticos han demostrado que la coexistencia mediada por esta disyuntiva es inconsistente, pues para explicar la coexistencia de las especies se requiere de una fuerte

asimetría en habilidad competitiva (Muller-Landau, 2010; Coomes y Grubb, 2003). Debido a que al parecer la ventaja de las semillas grandes radica en su mayor tolerancia al estrés producido por la sequía o la sombra, recientemente se ha propuesto la *disyuntiva entre tolerancia y fecundidad* como mecanismo de explicación para la coexistencia de las especies con diferentes tamaños de semilla. De acuerdo con esta hipótesis, las especies más tolerantes (con semillas grandes) se establecerán en todos los sitios con condiciones estresantes, mientras que las no tolerantes (con semillas pequeñas) serían más exitosas en los sitios menos estresantes. Este mecanismo permitiría la coexistencia de un gran número de especies (Muller-Landau, 2010).

En el continuo de variación funcional de las plantas, las disyuntivas en hojas, tallos y raíces permiten identificar bajo diferentes condiciones y regímenes de disturbio un espectro económico rápido-lento de adquisición, uso y conservación de recursos (Reich, 2014). Esto quiere decir que la coordinación entre los caracteres y recursos resulta en especies con estrategia ecológica lenta o rápida, sin importar si el factor limitante principal es la luz, el agua, la temperatura, el nitrógeno o el fósforo (Reich, 2014). La estrategia rápida, también descrita como adquisitiva o productiva, comprende aquellas especies que adquieren y utilizan de forma acelerada recursos como el agua, los nutrientes o la luz mediante órganos de bajo costo. Por ejemplo, hojas con alto contenido de nitrógeno en aparato fotosintético pero bajo contenido de carbono, o un tronco con alta conductividad hidráulica pero con alta susceptibilidad a la cavitación y daño mecánico. Esta estrategia es favorecida bajo condiciones de alta disponibilidad de recursos. Por el contrario, cuando los recursos son limitantes, predomina la estrategia lenta, conservadora o tolerante al estrés, con especies que adquieren de forma lenta los recursos, pero que los retienen por largos períodos de tiempo. Por ejemplo, este tipo de especies tienen hojas con baja productividad pero larga longevidad o troncos con baja conductividad hidráulica pero con alta densidad de la madera, asociada a una alta resistencia a la cavitación y al daño mecánico (Reich, 2014). El reconocimiento de este continuo ayuda a comprender el recambio de especies que ocurre en gradientes ambientales en respuesta a la disponibilidad diferencial de los recursos más limitantes, el ensamblaje de sus comunidades y el funcionamiento de los ecosistemas (Reich, 2014).

### 1.1.2 El papel del filtrado ambiental y la competencia en el ensamblaje de las comunidades de plantas leñosas

El ensamblaje de las comunidades de plantas está determinado por limitantes a la dispersión (Hubbell, 1999), procesos neutrales (Hubbell, 2005), facilitación (Michalet y Pugnaire, 2016), competencia (Tilman, 1987) y filtrado ambiental (Weiher y Keddy, 1995). El concepto de filtro ambiental se refiere a las condiciones abióticas que previenen el establecimiento o la permanencia de una especie en un sitio determinado (Kraft *et al.*, 2015), y actúan de forma jerárquica, pues seleccionan de forma progresiva a las especies mejor adaptadas a las condiciones locales conforme a sus caracteres funcionales (De Bello *et al.*, 2013). Las variables ambientales que varían a gran escala, como la elevación, precipitación o la temperatura, actúan como el primer filtro y determinan la presencia-ausencia de las especies (Toledo *et al.*, 2012; Kraft *et al.*, 2008); de forma subsecuente otros factores ambientales con variación más local, como la radiación, topografía o pendiente eliminan especies con menor adecuación, hasta que quedan únicamente las más adaptadas (De Bello *et al.*, 2013). Finalmente, los filtros que varían en escalas cada vez más finas, como el microclima, actúan predominantemente sobre los caracteres que diferencian a las especies, y tienen efectos en su abundancia y dominancia (De Bello *et al.*, 2013). Desde esta perspectiva, el ambiente actúa como una fuerza selectiva, y las especies que coexisten en las comunidades comparten caracteres funcionales que reflejan su tolerancia al ambiente (Kraft *et al.*, 2015). Esto ha generado una línea de investigación en la que se asume la existencia del filtrado ambiental si se detecta la convergencia de caracteres en ejes funcionales clave en relación a un modelo nulo, basado en el muestreo aleatorio del conjunto de especies del área de estudio (Kraft *et al.*, 2008; Cornwell *et al.*, 2006).

El principio de exclusión competitiva, por otra parte, establece que dos especies ecológicamente idénticas no pueden coexistir indefinidamente (Macarthur y Levins, 1967). Con base en este principio, la teoría de nicho explica la coexistencia de un gran número de especies de plantas al establecer que la coexistencia en un espacio y tiempo determinados es posible porque las especies se diferencian en la forma en como usan y adquieren los recursos que utilizan, y esa diferenciación se refleja en sus caracteres funcionales (Schwilke y Ackerly, 2005). Así, mientras que los filtros ambientales producirían una mayor similitud funcional entre las especies, la exclusión competitiva por el contrario

incrementaría la diferenciación funcional entre las mismas (Villéger *et al.*, 2008). Sin embargo, otros mecanismos han sido propuestos para explicar la coexistencia de una alta diversidad de especies. El efecto de almacenamiento o storage effect en particular (Warner y Chesson, 1985) ha sido considerado cada vez más en los últimos años (Mayfield y Levine, 2010). La teoría del efecto de almacenamiento aplica en particular a las situaciones en las que las condiciones ambientales favorecen a diferentes especies en diferentes tipos de parches (conectados éstos por dispersión), y en donde ocurre la competencia por recursos; así, las altas tasas de crecimiento poblacional en los parches con condiciones favorables compensan por las bajas tasas de crecimiento en los que tienen condiciones desfavorables (Sears y Chesson, 2007). De forma similar, a lo largo del tiempo los bancos de semillas o los adultos de vida larga “almacenan” los efectos positivos de los años favorables, y amortiguan los efectos negativos de los años malos cuando las poblaciones comienzan a declinar (Sears y Chesson, 2007). Esto significa que el efecto de almacenamiento promoviendo la coexistencia es posible únicamente cuando hay diferencias ecológicas entre las especies (i. e. de nicho) y una covariación entre las respuestas de las plantas al ambiente y la competencia (Warner y Chesson, 1985).

Los análisis más actuales de la coexistencia de las especies han apuntado a que ésta es posible bajo dos tipos de diferencias entre las especies: de nicho y de jerarquía competitiva, y ambas se reflejan en las diferencias de caracteres funcionales entre las especies (Mayfield y Levine, 2010). Cuando dos especies A y B difieren en el nicho ecológico que ocupan, y las condiciones ambientales favorecen a la especie A, la competencia intraespecífica de A tiene más importancia que la interespecífica con B (Chesson, 2000). Esto permite que las diferencias de nicho faciliten la coexistencia al favorecer a las especies que llegan a tener bajas densidades (Chesson, 2000). Por el contrario, cuando las especies A y B no difieren en el nicho que ocupan, pero sí difieren en su habilidad competitiva, el resultado es la exclusión de la menos competitiva, independientemente de la abundancia de ambas (Chesson, 2000). La coexistencia ocurre por tanto entre especies con poca diferenciación de nicho y poca diferencia en habilidad competitiva, o entre especies con nichos muy diferentes y una gran diferencia de habilidad competitiva (Mayfield y Levine, 2010). Si la habilidad competitiva está asociada con caracteres funcionales particulares, la exclusión competitiva (y no sólo el filtrado ambiental) puede producir la convergencia de caracteres en relación a un modelo nulo

(Kraft *et al.*, 2015; Kunstler *et al.*, 2012; Mayfield y Levine, 2010). Por ello, se ha sugerido ampliar el concepto de filtrado ambiental, de modo que incluya la exclusión competitiva basada en diferencias de habilidad o jerarquía competitiva entre las especies (Mayfield y Levine, 2010).

Por otra parte, aunque recientemente han surgido estudios que tratan de explicar la coexistencia y el ensamblaje de algunas comunidades de plantas con base en la teoría reciente (Lasky *et al.*, 2014; Kunstler *et al.*, 2012), existe información muy limitada en cuanto a la variación de los procesos de ensamblaje en relación a los diferentes estadios ontogénicos de la plantas. Diversos estudios han mostrado que las fases más susceptibles a los filtros ambientales son la de las plántulas (Scholz *et al.*, 2011) y los briznales (Punchi-Manage *et al.*, 2013; Kanagaraj *et al.*, 2011), por lo que las condiciones ambientales experimentadas en ese periodo pueden influir fuertemente en la composición de las comunidades. Por ejemplo, la interacción de sombra y sequía tiene un efecto negativo mayor en plántulas y briznales que en árboles adultos (Niinemets, 2010). También se ha observado que en plantas de bosque tropical seco, la fase de briznal es altamente susceptible a reducciones de la precipitación, probablemente porque la capacitancia de las plantas de briznales es inferior (a veces menos de la mitad) que la de los adultos (Wolfe y Kursar, 2015). Esto es un indicio de que la competencia por el agua, recurso más limitante en los bosques secos, pudiera ser asimétrica entre adultos y briznales, lo que ocurriría si el potencial hídrico del tallo o ramas depende del tamaño de la planta (Schwinning y Weiner, 1998). Diferencias en capacitancia entre plantas adultas y jóvenes, como muestra el trabajo de Wolfe y Kursar (2015), podría significar diferencias en potencial hídrico asociado al tamaño, pues se ha descrito previamente una asociación directa entre capacitancia y potencial hídrico de las ramas en múltiples plantas de bosques tropicales y sabana (Scholz *et al.*, 2011). Sin embargo son necesarios estudios, especialmente en plantas de bosques tropicales secos.

Aunque la competencia por agua no ha sido medido de forma directa (Craine y Dybzinski, 2013)., se considera probable que ocurra mediante dos procesos distintos: a) considerando que no hay gradientes de concentración del agua en el suelo, las especies más competitivas serían aquéllas capaces de tomarla más rápidamente, y b) cuando hay un gradiente de mayor a menor concentración de agua entre el suelo lejano a la raíz y el

que está circundante a la misma, las especies más competitivas serían aquellas capaces de producir numerosas raíces de mayor longitud, logrando apropiarse del recurso antes de que llegue a estar en contacto con un competidor (preemption) (Craine y Dybzinski, 2013). En el caso de este último mecanismo, y asumiendo que la biomasa aérea se correlaciona de forma directa con la biomasa subterránea, es posible que las plantas de menor tamaño pudieran sufrir un mayor estrés hídrico. Además, este filtrado por competencia podría acentuarse con la sucesión, pues hay un importante incremento en la biomasa aérea y de raíces finas con el desarrollo de la vegetación a medida que transcurre la sucesión (Hernández-Stefanoni *et al.*, 2011; Vargas *et al.*, 2008). Sin embargo, los estudios de competencia por agua son muy escasos, y queda mucho por investigar en esta área (Craine y Dybzinski, 2013).

### 1.1.3 El bosque tropical seco

El bosque tropical seco (BTS) se caracteriza por un periodo de sequía de por lo menos 5 meses al año, una precipitación que varía entre los 400 y 1700 mm, y por una razón entre la precipitación y la evapotranspiración potencial menor a 1 (Pennington *et al.*, 2006; Gerhardt y Hytteborn, 1992; Murphy y Lugo, 1986). Durante la época seca, la precipitación es menor a 10 mm al mes, mientras que en la época de lluvia se rebasan los 100 mm (Maass y Burgos, 2011). La precipitación ocurre con una alta variabilidad interanual pero también intraestacional, pues dentro de una misma estación lluviosa ocurren múltiples eventos de pequeñas lluvias con menos de 20 mm de agua, y sólo unas cuantas tormentas con más de 50 mm que pueden contribuir con casi el 50% de la precipitación total anual (Maass y Burgos, 2011). Además, también se presentan períodos cortos de sequía dentro del periodo de lluvias, iguales o mayores a 10 días sin precipitación, que afectan el reclutamiento de las especies (Engelbrecht *et al.*, 2006).

Los procesos ecológicos también son fuertemente estacionales. La vegetación está dominada por al menos un 50% de especies deciduas en respuesta a la sequía (Portillo-Quintero y Sánchez-Azofeifa, 2010), y el crecimiento de todas las plantas y la producción de hojas ocurre durante la época de lluvias, mientras que la floración es más variable (Valdez-Hernández *et al.*, 2010; Borchert *et al.*, 2004). La disminución del índice de área foliar durante los meses de escasa precipitación permite la penetración de la luz al

sotobosque y la acumulación de materia orgánica en el suelo, que se descompone durante el periodo de lluvia (Pennington *et al.*, 2006). Los suelos de los BTS suelen ser ricos en nutrientos y la estacionalidad disminuye su pérdida por lixiviación, facilita el uso del fuego para control de malezas y disminuye las poblaciones de insectos, lo que les confiere un alto valor para la agricultura (Pennington *et al.*, 2006). En México, hasta el 2009 se había perdido más del 70 % de la cobertura potencial de estos bosques por efecto de diversos usos, lo que ha generado un mosaico de fragmentos con diferentes edades de sucesión (Portillo-Quintero y Sánchez-Azofeifa, 2010).

#### **1.1.4 Estrategias de vida de las plantas del bosque seco en relación a la sucesión secundaria y a la topografía**

La variación temporal y espacial de la disponibilidad de agua es uno de los principales factores que determinan la distribución y diversificación ecológica de las especies (Toledo *et al.*, 2012; Engelbrecht *et al.*, 2007). Tanto la sucesión secundaria como la topografía, que producen cambios locales en su disponibilidad, inciden por tanto en el recambio funcional de las especies (Lasky *et al.*, 2014; Méndez-Alonso *et al.*, 2013; Kraft y Ackerly, 2010; Lebrija-Trejos *et al.*, 2010a).

Existe un número muy reducido de estudios en los que se haya medido la variación promedio de condiciones y recursos entre diferentes edades de sucesión en los bosques tropicales secos (BTS) (Buzzard *et al.*, 2015; Pineda-García *et al.*, 2013; Lebrija-Trejos *et al.*, 2011). Esos estudios describen el ambiente en edades tempranas de la sucesión como seco, soleado y con altas temperaturas en el suelo y en el aire, condiciones que favorecen la pérdida de agua por transpiración en las plantas (Bhaskar y Ackerly, 2006). Un reducido número de especies pueden establecerse bajo estas condiciones (especialistas de bosque joven o pioneras), y generalmente poseen caracteres asociados con una estrategia conservadora de recursos, como raíces que penetran profundamente en el suelo (Paz *et al.*, 2015) u hojas grandes pero compuestas con foliolos muy pequeños, deciduas y en ocasiones con pulvinos, que les permiten evitar la carga de irradiancia y el control de la temperatura minimizando la transpiración (Lohbeck *et al.*, 2015; Lebrija-Trejos *et al.*, 2010a). Durante los primeros años de sucesión, las comunidades de leñosas están constituidas por plantas de estatura relativamente baja, área basal reducida, con bajas densidades de especies e individuos, con bajo índice de

área foliar y con una cobertura en parches (Alvarez-Añorve *et al.*, 2012; Williams-Linera *et al.*, 2011; Lebrija-Trejos *et al.*, 2010b; Madeira *et al.*, 2009; Kennard, 2002). En algunos bosques secos se ha descrito que el reclutamiento mediante rebrote también tiene su mayor importancia en edades sucesionales tempranas, sobre todo cuando el fuego empleado en la agricultura es de baja intensidad (Kennard *et al.*, 2002).

El microambiente se modifica con el desarrollo de la vegetación a medida que transcurre la sucesión, y el incremento en la densidad de plantas, su altura, biomasa e índice de área foliar permiten que haya un ambiente más húmedo y menos soleado, y un mayor contenido volumétrico de agua en el suelo (Buzzard *et al.*, 2015; Pineda-García *et al.*, 2013; Lebrija-Trejos *et al.*, 2011). En concierto con la disminución de la radiación, del albedo, de la demanda evaporativa del aire y con el incremento en la disponibilidad del agua en el suelo, las especies propias de fases tardías de la sucesión se caracterizan por una estrategia adquisitiva de recursos, con hojas predominantemente enteras y perennes, con baja densidad de madera y con semillas grandes dispersadas por animales (Lohbeck *et al.*, 2015; Lebrija-Trejos *et al.*, 2010a).

Aunque la disminución de la disponibilidad de luz con el desarrollo de la vegetación influye en el ensamblaje de las comunidades en los BTS (Buzzard *et al.*, 2015; Alvarez-Añorve *et al.*, 2012), este recurso tiene una importancia limitada en comparación con su papel en los bosques húmedos, pues el BTS tiene menos estratos y los árboles son de menor estatura y distribuidos de forma heterogénea, lo que permite el paso de luz al sotobosque aún en la época de lluvias (Murphy y Lugo, 1986).

La microtopografía es otro factor que contribuye con una distribución diferencial del agua e insolación en el paisaje, y por tanto con una mayor diversidad de nichos para las especies (Valencia *et al.*, 2004; Wright, 2002). Dado que las laderas y cimas de los cerros poseen una menor disponibilidad de agua que los valles o sitios planos (Markesteijn *et al.*, 2010; Gallardo-Cruz *et al.*, 2009; Daws *et al.*, 2002; Becker *et al.*, 1988), puede esperarse que las estrategias de vida asociadas a los cerros sean similares a las descritas para sitios sucesionales tempranos, es decir, especies con una estrategia conservadora de recursos que les permita tolerar las condiciones más adversas. También puede esperarse que las especies asociadas a los sitios planos, con mayor disponibilidad de agua, sean

más similares a las descritas para fases sucesionales tardías, con caracteres funcionales asociados a la adquisición de recursos. Efectivamente, estudios previos en bosques secos muestran que las especies que predominan en cerros tienden a tener madera de alta densidad, con baja capacidad para almacenar agua pero alta resistencia a la cavitación y hojas deciduas, mientras que en sitios planos predominan especies con densidad de la madera media o baja que pueden almacenar agua y con hojas perennes (Méndez-Alonso *et al.*, 2013; Borchert, 1994).

### **1.1.5 El bosque tropical de la Península de Yucatán y el papel del disturbio**

Debido al gradiente de precipitación que se incrementa desde el noroeste hacia el sureste de la Península, en el estado de Yucatán se presentan varios tipos de bosques como el bajo caducifolio, el mediano subcaducifolio o el bajo inundable (Flores *et al.* 2010). Estudios previos en los bosques medianos subcaducifolios de la Península han mostrado que existe una similitud relativamente alta entre comunidades de plantas leñosas de edades sucesionales distintas (Dupuy *et al.*, 2012a; Schultz, 2003; Rico-Gray y García-Franco, 1992). Algunos autores han propuesto que esa similitud se debe a que la vegetación se encuentra en un estado de sucesión detenida, producto del uso recurrente de la vegetación por más de 2000 años, desde los mayas pre-colombinos hasta los habitantes actuales (Schultz, 2003; González-Iturbe *et al.*, 2002; Mizrahi *et al.*, 1997; Rico-Gray y García-Franco, 1992). El disturbio crónico del bosque es consecuencia principalmente de la agricultura de roza-tumba y quema, pero también de la eliminación de especies consideradas como indeseables; de la extracción, selección y propagación de otras con usos maderables, medicinales, alimenticios o de construcción; de la cacería, y más recientemente de la agricultura, la ganadería y el crecimiento urbano (Dupuy *et al.*, 2015; Zamora Crescencio *et al.*, 2009; Rico-Gray y García-Franco, 1992). Además, no se puede dejar de considerar el disturbio que ocurre de forma natural en la península por el impacto de los huracanes, aunque aparentemente éste tiene un impacto mucho menor (Bonilla-Moheno, 2012; Whigham *et al.*, 1991). En particular, el bosque tropical subcaducifolio que constituye el área de estudio se ubica en la región Puuc, cerca de la Sierrita de Ticul, por lo que se presentan zonas planas donde se realiza preferentemente la agricultura, y pequeños lomeríos. La zona también tiene una larga historia de uso: la más antigua se remonta al año 600 a. C. con un asentamiento maya de varios kilómetros; más recientemente, a la comunidad de San Sebastián (mediados del siglo XVI)

(<http://www.kaxilkiuic.org.mx>) y actualmente a pueblos cercanos como Yaxhachen, Xkobenhaltún o Xul, que aprovechan los recursos del área con actividades como cacería, agricultura, producción de miel, construcción y usos medicinales (obs. pers.).

## 1.2 JUSTIFICACIÓN

A pesar del manejo reciente e histórico y a la perturbación recurrente en los bosques de la península de Yucatán, se han publicado relativamente pocos estudios que expliquen los cambios en la estructura de la comunidad vegetal durante la sucesión secundaria, en relación a características ambientales, geográficas y de configuración del paisaje (Dupuy *et al.*, 2012; Hernández-Stefanoni *et al.*, 2011; Schultz, 2003; González-Iturbe *et al.*, 2002; Turner II *et al.* 2001; Rico\_Grey y García-Franco, 1992). En particular, el bosque mediano subcaducifolio es el ecosistema terrestre más importante el Estado de Yucatán, con una extensión aproximada de 1,264,568.9 ha (Secretaría de Desarrollo Urbano y Medio Ambiente, 2007). Sin embargo, no se ha efectuado ningún análisis de la ecología funcional de este ecosistema, a pesar de que es sabido que los caracteres funcionales ofrecen un método altamente promisorio para entender cómo cambian las propiedades de la vegetación en relación a gradientes físicos y geográficos (Westoby y Wright, 2006). Es más, sólo recientemente se han iniciado en México los estudios de bosques tropicales secos desde un punto de vista funcional, que caracterizan funcionalmente las especies pioneras y tardías, o que analizan la variación de los caracteres funcionales de las comunidades en relación con el tiempo de sucesión y sus condiciones microambientales (Paz *et al.*, 2015; Pineda-García *et al.*, 2015, 2013, 2011; Lohbeck *et al.*, 2013; Méndez-Alonso *et al.*, 2013; Lebrija-Trejos *et al.*, 2010a).

En este trabajo se hizo un análisis funcional de las comunidades de plantas leñosas en un bosque tropical subcaducifolio de Yucatán, con la finalidad de obtener información sobre cómo responden las plantas leñosas ante un gradiente sucesional y topográfico, información fundamental para hacer un manejo y uso racional de las especies (Grime, 2006). Este estudio podrá ser base para generar nuevas líneas de investigación con aplicaciones futuras, por ejemplo para la selección de especies en programas de restauración ecológica, de reforestación o en la evaluación de servicios ecosistémicos (Chazdon *et al.*, 2010; Franks *et al.*, 2009; Brown 2004).

### **1.3 PREGUNTAS DE INVESTIGACIÓN**

- ¿Qué características funcionales distiguen a los grupos de plantas leñosas especialistas -de etapas tempranas o tardías de la sucesión y de sitios planos y cerros- de las especies generalistas? ¿las especies generalistas dominan a lo largo de la sucesión y en diferentes posiciones topográficas en este bosque sometido a largos procesos de disturbio?
- ¿Cómo varían los procesos de ensamblaje de las comunidades (filtrado ambiental vs competencia) durante la sucesión secundaria y en relación a la posición topográfica? ¿Varía la importancia relativa de estos procesos entre los brizales y las plantas adultas leñosas?
- ¿El filtrado ambiental local (i. e. dentro de las comunidades) y el asociado al gradiente sucesional (i. e. entre comunidades) han favorecido asociaciones particulares de caracteres en las plantas leñosas?
- ¿En qué medida la variación de los caracteres funcionales entre comunidades ocurre en respuesta a los gradientes ambientales asociados a la edad sucesional y a las características del suelo?

### **1.4 OBJETIVO GENERAL**

Cuantificar para las especies más dominantes de plantas leñosas de un bosque tropical subcaducifolio de la Península de Yucatán algunos caracteres funcionales clave para su coexistencia, para inferir los procesos de ensamblaje de esas comunidades y la variación de estrategias ecológicas en respuesta a los gradientes asociados con la sucesión secundaria y la topografía.

### **1.5 OBJETIVOS ESPECÍFICOS**

- Identificar los caracteres funcionales que distinguen a las especies que se establecen en todo el gradiente sucesional y los de aquellas especies que se especializan en porciones particulares del mismo.

- Analizar cómo varían en importancia los procesos de filtrado ambiental y competencia en las comunidades de brizales y adultos de especies leñosas durante la sucesión secundaria.
- Analizar cómo co-varían los caracteres funcionales dentro y entre las comunidades de plantas leñosas, y qué variables ambientales asociadas con la sucesión secundaria, el suelo o la topografía explican esa variación.

## 1.6 HIPÓTESIS

a) Se encontrarán dos grupos generales de especies: aquellas especialistas, es decir que se ven favorecidas (en términos de abundancia) en porciones restringidas del gradiente sucesional (pioneras o tardías) o posición topográfica (sitios planos vs cerros), y las generalistas o especies capaces de establecerse y llegar a ser dominantes en todo el gradiente ambiental.

b) Como las condiciones de menor disponibilidad de agua ocurren al inicio de la sucesión o en cerros, las especialistas de esos sitios presentarán caracteres funcionales de hojas y tallos que les permitan evitar o resistir la sequía (por ejemplo hojas compuestas y deciduas, pulvinos, alta densidad de la madera), mientras que las especialistas de bosques viejos o de sitios planos presentarán caracteres asociados con ambientes más mesicós (como hojas enteras y perennes, baja densidad de la madera).

c) Considerando la capacidad de las especies generalistas de establecerse pronto en la sucesión y persistir hasta edades tardías, se espera que las generalistas muestren una posición funcional intermedia entre las especialistas de bosque joven/ cerros y las especialistas de bosque maduro/sitios planos, aunque siendo más similares a las primeras.

d) El aprovechamiento de la vegetación en diversos ecosistemas y sus usos ha favorecido la proliferación de especies capaces de establecerse en amplios rangos de variación ambiental (generalistas), y desfavorecido a aquellas especies con requerimientos más estrechos para completar su ciclo de vida (especialistas) (Dar y Reshi, 2014; Devictor *et al.*, 2008; Vellend *et al.*, 2007; McKinney, 2006; Smart *et al.*, 2006; Rooney *et al.*, 2004; McKinney y Lockwood, 1999). Dada la larga historia de manejo de este bosque, se espera que las generalistas sean el elemento dominante en todas las edades sucesionales y posiciones topográficas.

e) El filtrado ambiental (observado como baja riqueza funcional) determinará de forma principal el ensamblaje de las comunidades en fases tempranas de la sucesión y en cerros, como resultado de un microambiente menos favorable en estas condiciones, tal como se ha descrito en otros bosques secos.

f) El efecto de filtrado ambiental será más fuerte en los brizales que en los adultos, dado que la fase regenerativa es mucho más susceptible a condiciones desfavorables.

g) Los procesos de competencia (observados como una alta divergencia y alta equitatividad funcional) serán más importantes en edades sucesionales intermedias y tardías, debido a que la competencia por recursos limitantes como el agua puede incrementarse con el mayor desarrollo de raíces finas de individuos de mayor tamaño.

h) Los procesos competitivos limitarán más a los brizales, pues es posible que enfrenten una competencia asimétrica por el agua con los adultos.

i) Debido a que las comunidades (i. e. parcelas) de diferente edad sucesional poseen distintas condiciones ambientales y de competencia como consecuencia del desarrollo de la vegetación, se encontrarán a nivel de paisaje (entre parcelas) asociaciones de caracteres funcionales que reflejen el recambio de especies de una estrategia conservadora en parcelas jóvenes a una estrategia adquisitiva de recursos en parcelas de edad más avanzada.

j) Por el contrario, debido a que se espera que las condiciones ambientales dentro de las comunidades sean más homogéneas que entre las parcelas de diferente edad sucesional, las asociaciones de caracteres serán más débiles o estarán ausentes dentro de las comunidades.

k) Finalmente, se espera que el suelo explique una proporción similar de la covariación de los caracteres funcionales que la edad de sucesión, pues las propiedades del suelo varían en respuesta a los cambios de la vegetación que ocurren con la sucesión secundaria.

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## CAPÍTULO 2.

### WHAT MAKES A WOODY PLANT A GENERALIST OR A SPECIALIST? A FUNCTIONAL TRAIT ANALYSIS IN A SECONDARY TROPICAL DRY FOREST

*Artículo en preparación.*

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Heading: Plant generalists and specialists in a dry forest

#### 2.1 ABSTRACT

1. Tropical dry forests are being strongly impacted by human activities, and the human-induced environmental changes may result in the spread of common, generalist species, capable of surviving in a wide range of environmental conditions.
2. Our objective is to assess if generalist and specialist plant species within a successional gradient and among different topographical positions display different constellations of functional traits, and if generalists are the predominant component of a tropical dry forest landscape with a long history of human disturbance.
3. Using a multinomial model based on relative abundances of woody species in 273 plots, from the sixty five most abundant species 10 were classified as old growth forest specialists (old specialists), 6 species as young secondary forest specialists (young specialists), 27 species as generalists and 22 species as too rare to classify with confidence. Those same species were clasified according to topography, and we found 12 flat area specialists, 9 hill specialists, 23 generalists and 21 Too rare.

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4. Most of the young forest specialists were also flat sites specialists, and most of the old forest specialists were also hill specialists. PERMANOVA analysis using 13 functional traits for the 65 most abundant species revealed significant differences among groups. Leaf shedding was the main mechanism allowing young and flat specialists to avoid hydraulic failure, while old and hill specialists use different mechanisms to cope with drought.
  5. Generalist species were more similar to old and hill specialists, and tended to be more abundant than young and old specialists across the successional gradient, and as abundant as flat and hill specialists on topographical positions.
  6. A more thorough functional analysis is needed to determine which traits confer generalists competitive advantages over old specialists in flat areas, since both groups are functionally similar. Reproductive traits or resprouting may offer new insights.

**Key-words.** Hill, homogenization, pioneer, slash and burn agriculture, slope, succession, tolerant, Yucatan.

## 2.2 INTRODUCTION

As the current natural environments are increasingly threatened by human activities, it becomes more important to define the characteristics that differentiate a generalist from a specialist species (Chazdon *et al.*, 2011), under the rationale that the former one will be more plastic in its response to disturbance and will less likely become locally extinct. Forest conversion to agriculture, livestock pastures, urban areas, etc., has caused the loss of more than 70% of tropical forest cover in the last 15 years (Keenan *et al.*, 2015). Human-induced environmental change impose new filters on species, resulting in the spread of common, generalist species, capable of surviving in a wide range of environmental conditions, and a decline of specialist species, which leads to an increased similarity among communities (i.e. biotic homogenization), along with diminished diversity (Smart *et al.*, 2006; McKinney and Lockwood, 1999). Tropical dry forests are among the most threatened ecosystems in the world, because they are easily cleared and woody regeneration is effortlessly eliminated with fire; besides, the severe dry season suppresses pest and weed populations, facilitates the use of fire and slows soil degradation –characteristics that are highly valuable for agriculture and other land uses (Donfack *et al.*, 1995; Janzen, 1988).

The few functional and microenvironmental studies conducted on tropical dry forests show that elevated temperature and water vapour pressure deficit that result from higher radiation loads

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during the dry season can be the main drivers of functional differentiation in recently abandoned lands after agriculture (Lebrija-Trejos *et al.*, 2010). In the dry environments of these early stages of succession, dominating species are those with functional traits associated with irradiance load avoidance through leaf or leaflet movement, hydraulic failure avoidance through leaf shedding, high cavitation resistance and deeper root foraging capacity (Paz *et al.*, 2015; Méndez-Alonso *et al.*, 2013; Pineda-García *et al.*, 2011; Lebrija-Trejos *et al.*, 2010a), i.e. young secondary forest specialists, such as many legume species (Lebrija-Trejos *et al.*, 2010; Romero-Duque *et al.*, 2007; Gillespie *et al.*, 2000). At latter successional stages, when vegetation starts to recover, the increase in density of individuals and foliage modifies the microenvironment making it more shaded and humid, and such autogenic changes favor species capable of withstanding lower light availability, i. e. old growth forest specialists (Lebrija-Trejos *et al.*, 2010).

Topography is another important variable producing changes in vegetation structure and composition. Differences in soil water availability (lowest on hill-tops, intermediate on slopes and highest in valleys) have been previously reported (Pineda-García *et al.*, 2013; Lebrija-Trejos *et al.*, 2011; Markesteijn *et al.*, 2010; Gallardo-Cruz *et al.*, 2009; Becker *et al.*, 1988). For example, deciduous trees with high wood density and water-storing trees with low wood density are predominantly distributed in upland dry forests, while evergreen with high and low wood densities trees are confined to more humid lowland sites (Méndez-Alonso *et al.*, 2013; Borchert, 1994).

Few functional studies on tropical forest succession or in topographical gradients have focused on the functional differentiation between young secondary and old-growth forest specialists (Letcher *et al.*, 2015; Lasky *et al.*, 2014; Alvarez-Añorve *et al.*, 2012; Lebrija-Trejos *et al.*, 2010) or between upland and lowland specialists (Méndez-Alonso *et al.*, 2013; Borchert, 1994), but do not address the functional traits that may facilitate the establishment and survival of generalist species along the complete successional gradient.

Previous studies in forests of the Yucatan Peninsula, which have been managed for millennia, have found that patterns of plant species composition and structure are mainly determined by successional age and topography (López-Martínez *et al.*, 2013; Dupuy *et al.*, 2012a, 2012b; White and Hood, 2004). Therefore, the aim of this study is to assess if secondary succession and the mild topography present in our study area differentiate species into generalists and specialists, and to answer the following questions: Do generalist and specialist species display

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different constellations of traits? Are generalists dominant (more abundant) over the whole successional age gradient?

We expect that: 1) successional age and topography will differentiate species into generalist and specialists –either or both in young successional forest stands vs older stands and/or in hills vs flat areas. 2) specialists in young forest stands and in hills will show leaf and stem traits associated with drought resistance or avoidance (e.g. high wood specific gravity, deciduousness, compound leaves and pulvination), while the old growth forest and flat area specialists will show traits associated with more mesic environments, such as low wood specific gravity, evergreens and simple leaves. 3) Considering the capacity of generalists to establish early in succession but also to persist through latter successional ages, we expect that generalists would show an intermediate functional position between young seconday/hill-specialists and old growth/flat area specialist species but would be more similar to the former. 4) Finally, given the millenial history of management of our studied forest, we expect that generalist species will be more abundant than specialist species across all successional ages and topographical positions.

## 2.3 MATERIALS AND METHODS

### 2.3.1 Study site

The study area covers a 352 km<sup>2</sup> landscape of semi-deciduous tropical forest in the central part of the Yucatan Peninsula, Mexico (20° 01'07" to 20° 09' 36" N latitude, and 89° 35'59" to 89° 23'31" W longitude), and includes the Biocultural Reserve Xaxil Kiuic. The region is characterized by a sub humid warm climate -AW1 according to the modified Köppen system (García, 1981)- with summer rains and a sharp dry season from November to April; mean annual temperature is 26°C and mean annual precipitation ranges between 900 and 1100 mm. The landscape consists of flat areas with relatively deep (40–100 cm) clayey Luvisols and Cambisols and small limestone hills (elevations between 60 and 190 m asl) with shallow (5–20 cm) rocky Lithosols and Rendzines (Flores and Espejel 1994; Bautista-Zúñiga *et al.* 2003). Soil depth is greater in flat areas than on slopes (Bautista-Zúñiga *et al.*, 2003), while soil fertility shows the opposite pattern (Dupuy *et al.*, 2012a). The predominant land use has been traditional slash and burn agriculture, practiced by the Mayan people for over 2000 years (Rico-Gray and García-Franco, 1991). Consequently the vegetation is a shifting mosaic of small agricultural fields and forests of different successional ages.

### 2.3.2 Sampling design

A Spot 5 satellite image acquired on January 2005 was used for a supervised classification in the following vegetation classes 1) 3 to 8 years of secondary succession, 2) 9 to 15 years, 3) > 15 years on flat areas, and 4) > 15 years on hills. Vegetation classes 1 and 2 occurred mostly in flat areas, since these are generally preferred by local farmers (Hernández-Stefanoni and Dupuy, 2008). In the summers of 2008 and 2009, twenty three 1 Km<sup>2</sup> landscape units were selected that encompassed the range of landscape conditions of disturbance and fragmentation. At each unit 12 sampling plots (3 in each vegetation class) were established (276 plots in total): Stand age of each plot was determined from interviews with local residents who lived in the area for 40 years and owned or worked the land. Mayan farmers have a keen empirical knowledge of forest succession, and their own detailed system of classifying and distinguishing several successional stages based on their knowledge of the local disturbance regime, and the presence and size of certain species, which makes their determination of forest stand age reliable (González-Cruz *et al.*, 2014; Hernández-Stefanoni *et al.*, 2006). Each plot consisted of a circular 200 m<sup>2</sup> area where all woody plants with a diameter at breast height (DBH, measured at 1.3 m height) > 5 cm were measured (for a detailed description of sampling design see (Hernández-Stefanoni *et al.*, 2011).

### 2.3.3 Species selection

We calculated the relative importance value (RIV) of all species in the four vegetation classes described earlier. The RIV of each species in each class was the sum of its relative abundance, frequency and basal area. For each vegetation class and separately for trees, lianas and shrubs, we selected those species that constituted at least 90% of the cumulative RIV, and obtained a total of 72 species covering all vegetation classes. However, we only include in the analyses 65 species for which we were able to collect material from at least 5 individuals, which represent  $90\% \pm 10\%$  (mean  $\pm$  standard deviation) of the total richness per plot; 45 species are trees, 11 species are shrubs, and 9 species are lianas.

### 2.3.4 Functional traits

Samples were collected from at least 5 individuals per species (14 individuals per species on average, total 934) during the rainy months of 2011 (from August to November) and 2012 (from September to November). We obtained 3 to 5 young, healthy and completely expanded leaves from sun-exposed branches from each individual. Fresh weight was determined to 0.001 g using

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a digital scale (Mettler Toledo PB4002-S/FACT, OH, USA) and samples were digitized using a flatbed scanner, oven-dried at ~60°C for three days, and weighed again. We measured petiole length (PL) and leaf or leaflet area (as an average of ten leaflets) with the software ImageJ 1.47b (Rasband, 2014). We separately quantified total leaf area (LA), which represents the leaf and petiole area for species with simple leaves and the sum of the area of all the leaflets and petiole for species with compound leaves, from the minimum photosynthetic unit (MPU) that represents the leaf area for the former and the average leaflet area for the latter. Specific leaf area (SLA) and leaf dry matter content (LDMC) were calculated using standard methods (Cornelissen *et al.*, 2003).

We obtained wood specific gravity (WSG) from 4 individuals per species with the largest DBH, which on average was 3.2 cm for lianas, 4.1 cm for shrubs and 16.4 cm for trees. Lianas were sampled with a knife by taking a 4 to 5 cm long and 1 cm wide slice from the trunk, tapering longitudinally towards the pith. We peeled off only bark that could be retrieved by hand. We proceeded in the same way with shrubs when there was a clearly defined trunk at least 4 cm wide. Otherwise we cut one branch at the first ramification and took a 4 to 5 cm long section. For trees, we took a sample from cortex to pit at breast height using a 5 mm diameter core borer, and samples were cut every centimetre. Green volume was measured using the water displacement method. Samples were oven dried at 100°C and weighed on an analytical scale (Ohaus Adventurer AP 2140, NJ, USA). Dry weight of each sample was divided over its green volume to obtain wood specific gravity. A weighted average per sampled tree was calculated weighting each core section by the cross-sectional area of the corresponding trunk (Muller-Landau, 2004).

From field specimens and bibliography, we determined some binary traits: leaf compoundness (LC; 0 = simple, 1 = compound); leaf pulvination (LPulv; 0 = absent, 1 = present); leaf pubescence (LPb; 0 = absent, 1 = present), dispersal syndrome (Dis; 0 = abiotic, 1 = biotic); plant exudates (Ex; 0 = absent, 1 = present), and plant spininess (Sp; 0 = absent, 1 = present). From parataxonomist Filogonio May Pat and bibliography we also determined leaf deciduousness (LD; 0 = evergreen, 1 = deciduous).

### 2.3.5 Statistical analyses

We classified woody plant species in our forest using a multinomial model based on estimated species relative abundances in early and late successional habitats (Chazdon *et al.*, 2011). Since the multinomial model classify species only between two habitats, we performed two

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analyses to identify specialist and generalist species, one considering the successional gradient, and another considering the topographical gradient.

In the first analysis, we compared plots of vegetation classes 1 and 2 (plots from 3 to 15 years of secondary succession) as representative of young forests, versus plots of vegetation classes 3 and 4 (plots older than 15 years of succession on flat areas and hills) as representative of older vegetation. The criteria to define the vegetation classes was based on their spectral signal, which allowed us to separate them under a supervised classification of SPOT 5 satellite imagery (see Hernández-Stefanoni and Dupuy, 2008). Although forests older than 15 years (and less than 80 years old) do not necessarily represent mature vegetation, the long history of human occupancy and millennial use of the vegetation in the Yucatan make it difficult to find older, mature-forest fragments. Besides, a previous study in the same area with 168 plots showed significant differences in species composition among the same vegetation classes (Dupuy *et al.*, 2012a) that we corroborated with a PERMANOVA analysis with our 273 plots (root squared transformation on abundance matrix of species, and Bray Curtis similarity; pseudo F = 15.908, p < 0.0001).

The model distinguished four groups of species: generalists, young secondary forest specialist (hereafter referred to as young specialists), old growth forest specialists (hereafter old specialists) and too rare to classify with confidence (hereafter too rare). When a species is shared among old-growth and young secondary forests, the multinomial model uses a threshold to determine if a species is classified as old specialists or young specialists. We used a conservative threshold of  $k = 2/3$ . This means that a species was considered as old specialist if its relative abundance in old-growth forests was twice its relative abundance in young secondary forests, while a species was considered as young specialists if its relative abundance in young secondary forest was twice its relative abundance in old growth forests. A one-sided statistical test was then performed to determine the minimum number of individuals of a species in old-growth ( $X_i$ ) or in young secondary forest ( $Y_i$ ) necessary to obtain a significant result at particular values of  $k$  and  $p$ . Those minimum values ( $X_{\min}$  and  $Y_{\min}$ ) are used as thresholds to differentiate generalists from young specialists and old specialists, and all these categories from Too rare. We used 40 as a minimum value to perform the classification, with  $p = 0.05/40 = 0.00125$  (Chazdon *et al.*, 2011).

We performed a second analysis where we compared plots on flat areas (vegetation classes 1 to 3, plots of all successional ages on flat sites) vs plots on hills (vegetation class 4, plots older than 15 years on hills). Although the ideal approach would include young plots on hills as well,

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agriculture is established mainly on flat areas, and we could not find enough replicates in this condition. We decided not to limit the analysis to plots older than 15 years on flat areas vs hills (vegetation classes 3 and 4) because removing younger plots reduced the observed proportion on flat areas for many species, and the multinomial model is very susceptible to total abundance. The model distinguished four groups of species: generalists, hill specialists, flat areas specialists (hereafter flat specialists) and too rare. Since the multinomial model is based on relative abundances of species, we used the total number of species registered ( $n = 137$  species, 273 plots) for both analyses. For all other analyses, we included only the 65 species (that represent more than 90% of total richness per plot) for which we determined functional trait information. The multinomial model was performed with vegan package (Oksanen *et al.*, 2016) in R software (R Development Core Team, 2015).

To determine if there were functional differences between generalists and specialists, we performed a PERMANOVA based on a matrix of dissimilarity obtained with euclidean distances of the 13 standardized functional traits in PRIMER v. 6.1.18 and PERMANOVA+ v. 1.08. In order to visualize which traits were associated with generalists and specialists, we performed a Principal Component Analysis (PCA) on the 13 traits. To test whether the proportion of attributes of binary traits differed among groups, we applied chi-square analyses and Tukey-type multiple comparison tests (Zar, 1999). In the case of continuous traits, we preformed a separate ANOVA for each trait and Tukey's *post hoc* analyses in InfoStat software (Di Rienzo *et al.*, 2013).

Finally, to determine if there were significant differences in relative abundance of generalists and specialists per plot in relation to successional age and topographic position, we performed the non-parametric Kruskal-Wallis test and paired comparisons among means of the ranks in InfoStat software (Di Rienzo *et al.* 2013) among the four vegetation classes: 1) 3 to 8 years of secondary succession on flat areas ( $n = 48$  plots), 2) 9 to 15 years on flat areas (78), 3) > 15 years on flat areas (84), and 4) > 15 years on hills (63).

## 2.4 RESULTS

In the successional gradient, the multinomial model classified 10 species as old specialists, 6 species as young specialists, 27 species as generalists and 22 species as too rare. According to topography, we found 12 flat specialists, 9 hill specialists, 23 generalists and 21 too rare (Table 2.1).

**Table 2.1** Species classification according to successional gradient and topographical position as specialists (YS = young forest specialist; OS = old forest specialist; FS = flat site specialist; HS = hill specialist), generalists (G) and too rare to classify (Too rare).

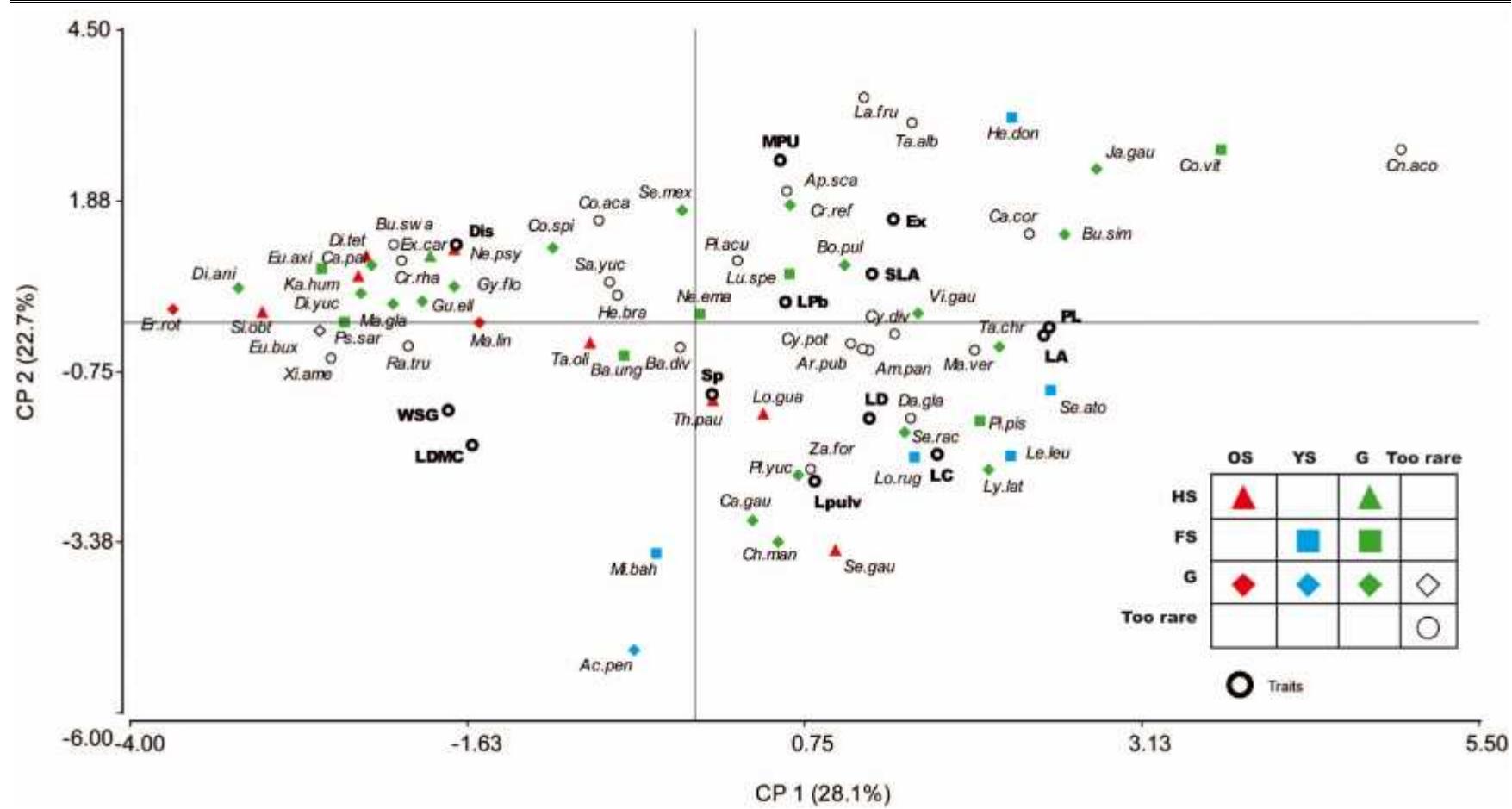
Species	Family	Life form	Succession	Topography
<i>Bauhinia unguifolia</i>	Fabaceae	Tree	G	FS
<i>Bourreria pulchra</i>	Boraginaceae	Tree	G	G
<i>Bursera simaruba</i>	Burseraceae	Tree	G	G
<i>Caesalpinia gaumeri</i>	Fabaceae	Tree	G	G
<i>Calyptrotheces pallens</i>	Myrtaceae	Tree	G	G
<i>Chloroleucon mangense</i>	Fabaceae	Tree	G	G
<i>Coccoloba spicata</i>	Polygonaceae	Tree	G	G
<i>Cochlospermum vitifolium</i>	Bixaceae	Tree	G	FS
<i>Croton reflexifolius</i>	Euphorbiaceae	Tree	G	G
<i>Diospyros anisandra</i>	Ebenaceae	Tree	G	G
<i>Diospyros yucatanensis ssp yucatanensis</i>	Ebenaceae	Tree	G	G
<i>Eugenia axillaris</i>	Myrtaceae	Tree	G	FS
<i>Exostema caribaeum</i>	Rubiaceae	Tree	G	HS
<i>Guettarda elliptica</i>	Rubiaceae	Tree	G	G
<i>Gymnopodium floribundum</i>	Polygonaceae	Tree	G	G
<i>Jatropha gaumeri</i>	Euphorbiaceae	Tree	G	G
<i>Luehea speciosa</i>	Malvaceae	Tree	G	FS
<i>Lysiloma latisiliquum</i>	Fabaceae	Tree	G	G
<i>Malpighia glabra</i>	Malpighiaceae	Tree	G	G
<i>Neomillspaughia emarginata</i>	Polygonaceae	Tree	G	FS
<i>Piscidia piscipula</i>	Fabaceae	Tree	G	FS
<i>Platymiscium yucatanum</i>	Fabaceae	Tree	G	G
<i>Psidium sartorianum</i>	Myrtaceae	Tree	G	FS
<i>Semialarium mexicanum</i>	Celastraceae	Tree	G	G
<i>Senna racemosa</i>	Fabaceae	Tree	G	G
<i>Tabebuia chrysantha</i>	Bignoniaceae	Tree	G	G
<i>Vitex gaumeri</i>	Lamiaceae	Tree	G	G
<i>Diospyros tetrasperma</i>	Ebenaceae	Tree	OG	HS

Species	Family	Life form	Succession	Topography
<i>Erythroxylum rotundifolium</i>	Erythroxylaceae	Tree	OG	G
<i>Karwinskia humboldtiana</i>	Rhamnaceae	Tree	OG	HS
<i>Lonchocarpus guatemalensis</i>	Fabaceae	Tree	OG	HS
<i>Machaonia lindeniana</i>	Rubiaceae	Tree	OG	G
<i>Neea psychotrioides</i>	Nyctaginaceae	Tree	OG	HS
<i>Senegalia gaumeri</i>	Fabaceae	Tree	OG	HS
<i>Sideroxylon obtusifolium</i>	Sapotaceae	Tree	OG	HS
<i>Talisia oliviformis</i>	Sapindaceae	Tree	OG	HS
<i>Thouinia paucidentata</i>	Sapindaceae	Tree	OG	HS
<i>Acacia pennatula</i>	Fabaceae	Tree	YS	G
<i>Heliocarpus donnell-smithii</i>	Malvaceae	Tree	YS	FS
<i>Leucaena leucocephala</i>	Fabaceae	Tree	YS	FS
<i>Lonchocarpus rugosus</i>	Fabaceae	Tree	YS	FS
<i>Mimosa bahamensis</i>	Fabaceae	Tree	YS	FS
<i>Senna atomaria</i>	Fabaceae	Tree	YS	FS
<i>Amphilophium paniculatum var molle</i>	Bignoniaceae	Liana	Too rare	Too rare
<i>Aphelandra scabra</i>	Acanthaceae	Shrub	Too rare	Too rare
<i>Arrabidaea pubescens</i>	Bignoniaceae	Liana	Too rare	Too rare
<i>Bauhinia divaricata</i>	Fabaceae	Shrub	Too rare	Too rare
<i>Bunchosia swartziana</i>	Malpighiaceae	Shrub	Too rare	Too rare
<i>Cardiospermum corindum</i>	Sapindaceae	Liana	Too rare	Too rare
<i>Cnidoscolus aconitifolius</i>	Euphorbiaceae	Shrub	Too rare	Too rare
<i>Coccoloba acapulcensis</i>	Polygonaceae	Tree	Too rare	Too rare
<i>Crossopetalum rhacoma</i>	Celastraceae	Shrub	Too rare	Too rare
<i>Cydista diversifolia</i>	Bignoniaceae	Liana	Too rare	Too rare
<i>Cydista potosina</i>	Bignoniaceae	Liana	Too rare	Too rare
<i>Dalbergia glabra</i>	Fabaceae	Liana	Too rare	Too rare
<i>Eugenia buxifolia</i>	Myrtaceae	Tree	Too rare	G
<i>Heteropterys brachiata</i>	Malpighiaceae	Liana	Too rare	Too rare
<i>Lasianthaea fruticosa</i>	Asteraceae	Shrub	Too rare	Too rare
<i>Mansoa verrucifera</i>	Bignoniaceae	Liana	Too rare	Too rare

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Species	Family	Life form	Succession	Topography
<i>Pisonia aculeata</i>	Nyctaginaceae	Liana	Too rare	Too rare
<i>Randia truncata</i>	Rubiaceae	Shrub	Too rare	Too rare
<i>Samyda yucatanensis</i>	Salicaceae	Shrub	Too rare	Too rare
<i>Tabernaemontana alba</i>	Apocynaceae	Shrub	Too rare	Too rare
<i>Ximenia americana</i>	Olacaceae	Shrub	Too rare	Too rare
<i>Zapoteca formosa</i>	Fabaceae	Shrub	Too rare	Too rare

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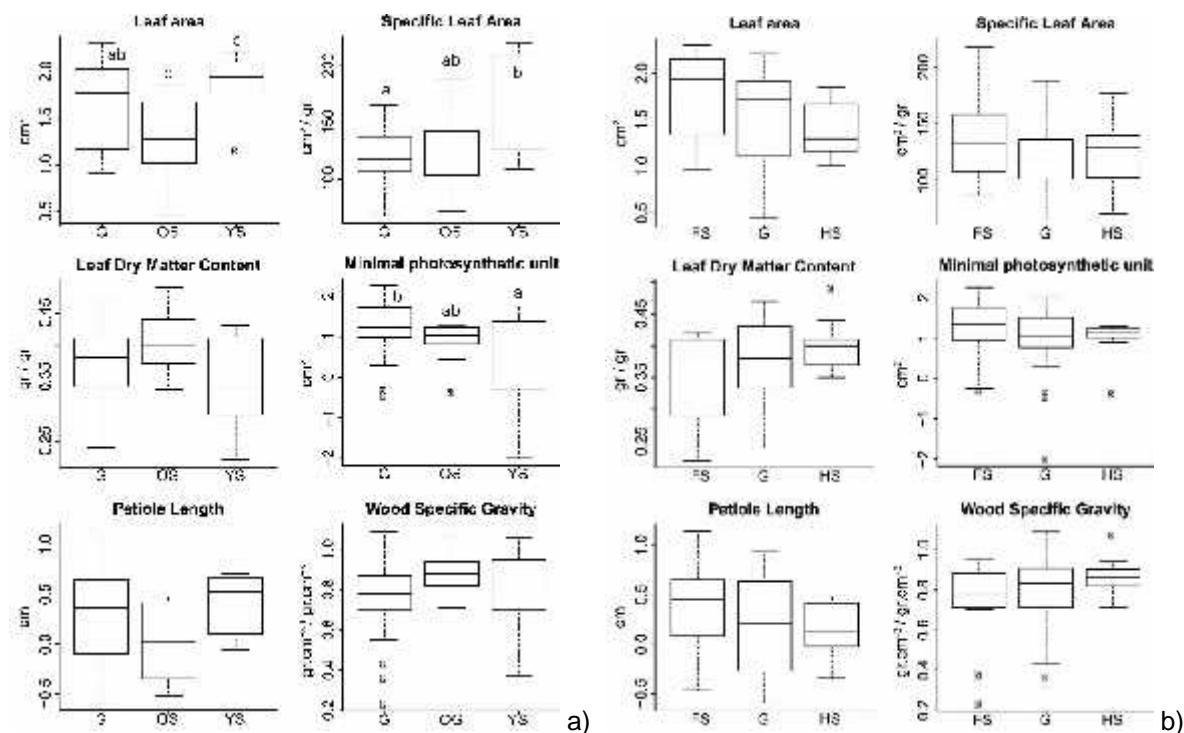
**Figure 2.1** PCA of species according to their functional traits. Symbols correspond to Plant Functional Type (PFT). Symbols represent species classification by the multinomial model: OS = old forest specialist, YS = young forest specialist; HS = hill specialist; FS = flat site specialist; G = generalist, and Too rare = too rare to classify with confidence. Functional traits are: LA = Leaf area; LP = Leaf petiole; MPU = Minimal photosynthetic unit; LDMC = Leaf dry matter content; SLA = Specific leaf area; LC = Leaf compoundness (0 = simple; 1 = compound); LD = Leaf deciduousness (0 = evergreen; 1 = deciduous); LPulv = Leaf pulvination (0 = absent; 1 = present); LPb = Leaf pubescence (0 = absent; 1 =

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present); WSG = Wood specific gravity; Ex = Plant exudates (0 = absent; 1 = present); Sp = Plant spininess (0 = absent; 1 = present), and Dis = Dispersal syndrome (0 = abiotic; 1 = biotic).

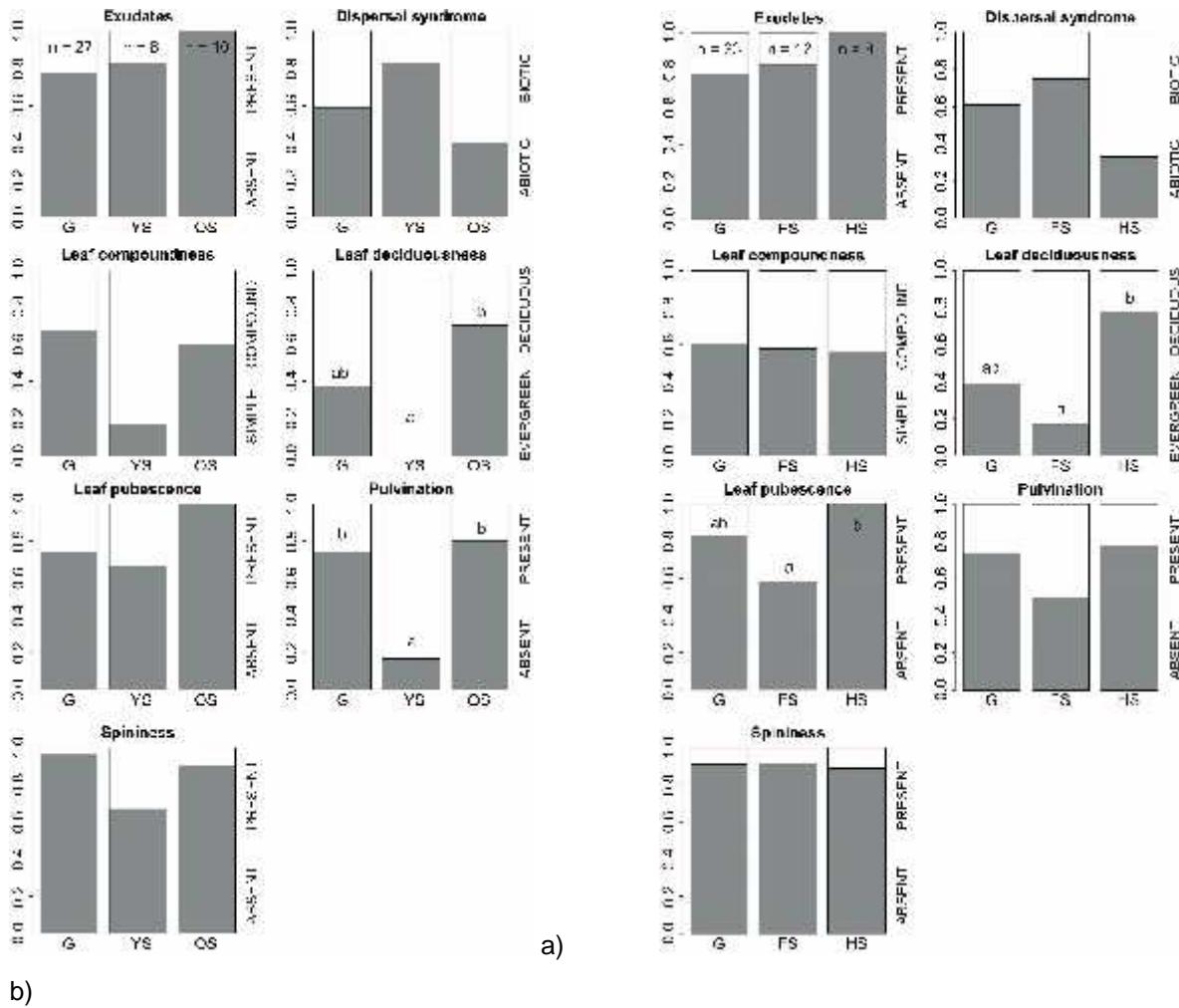
Species (in italics and abbreviated) are: *Ac.pen*, *Acacia pennatula*; *Am.pan*, *Amphilophium paniculatum var molle*; *Ap.sca*, *Aphelandra scabra*; *Ar.pub*, *Arrabidaea pubescens*; *Ba.div*, *Bauhinia divaricata*; *Ba.ung*, *B. unguis*; *Bo.pul*, *Bourreria pulchra*; *Bu.sim*, *Bunchosia swartziana*; *Bu.swa*, *Bursera simaruba*; *Ca.gau*, *Caesalpinia gaumeri*; *Ca.pal*, *Calyptanthes pallens*; *Ca.cor*, *Cardiospermum corindum*; *Ch.man*, *Chloroleucon mangense*; *Cn.aco*, *Cnidoscolus aconitifolius*; *Co.aca*, *Coccoloba acapulcensis*; *Co.spi*, *Coccoloba spicata*; *Co.vit*, *Cochlospermum vitifolium*; *Cr.rha*, *Crossopetalum rhacoma*; *Cr.ref*, *Croton reflexifolius*; *Cy.div*, *Cydista diversifolia*; *Cy.pot*, *Cydista potosina*; *Da.gla*, *Dalbergia glabra*; *Di.an*, *Diospyros anisandra*; *Di.tet*, *Diospyros tetrasperma*; *Di.yuc*, *Diospyros yucatanensis ssp. yucatanensis*; *Er.rot*, *Erythroxylum rotundifolium*; *Eu.axi*, *Eugenia axillaris*; *Eu.bux*, *Eugenia buxifolia*; *Ex.car*, *Exostema caribaeum*; *Gu.ell*, *Guettarda elliptica*; *Gy.flo*, *Gymnopodium floribundum*; *He.don*, *Heliocarpus donnellsmithii*; *He.bra*, *Heteropterys brachiata*; *Ja.gau*, *Jatropha gaumeri*; *Ka.hum*, *Karwinskia humboldtiana*; *La.fru*, *Lasianthaea fruticosa*; *Le.leu*, *Leucaena leucocephala*; *Lo.rug*, *Lonchocarpus rugosus*; *Lo.gua*, *L. guatemalensis*; *Lu.spe*, *Luehea speciosa*; *Ly.lat*, *Lysiloma latisiliquum*; *Ma.lin*, *Machaonia lindeniana*; *Ma.gla*, *Malpighia glabra*; *Ma.ver*, *Mansoa verrucifera*; *Mi.bah*, *Mimosa bahamensis*; *Ne.psy*, *Neea psychotrioides*; *Ne.ema*, *Neomillspaughia emarginata*; *Pi.pis*, *Piscidia piscipula*; *Pi.acu*, *Pisonia aculeata*; *Pl.yuc*, *Platymiscium yucatanum*; *Ps.sar*, *Psidium sartorianum*; *Ra.tru*, *Randia truncata*; *Sa.yuc*, *Samyda yucatanensis*; *Se.mex*, *Semialarium mexicanum*; *Se.gau*, *Senegalia gaumeri*; *Se.ato*, *Senna atomaria*; *Se.rac*, *S. racemosa*; *Si.obt*, *Sideroxylon obtusifolium*; *Ta.chr*, *Tabebuia chrysanththa ssp. chrysanththa*; *Ta.alb*, *Tabernaemontana alba*; *Ta.oli*, *Talisia oliviformis*; *Th.pau*, *Thouinia paucidentata*; *Vi.gau*, *Vitex gaumeri*; *Xi.ame*, *Ximenia americana*; *Za.for*, *Zapoteca formosa spp. formosa*.

PERMANOVA analysis showed that in the successional gradient, young specialists were significantly different from generalists ( $t = 1618$ ,  $p = 0.0291$ ) and from old specialists ( $t = 1.7596$ ,  $p = 0.0467$ ). We also found a significant functional difference between hill and flat specialists ( $t = 1.4671$ ,  $p = 0.0454$ ). The first two component axes of the PCA accounted for 50.8% of species variation (Figure 2.1). The first axis (which explained 28.1 % of variation) was largely related to the leaf and stem economics spectrum, as it tended to separate species with big leaves, long petioles, high specific leaf area, low wood specific gravity and abiotic dispersal from species with opposite traits. The second axis (that explained 22.7% of variation) was associated with traits related to leaf temperature control and defense, as it separated deciduous species, mainly with compound leaves, high leaf dry matter content, very small minimal photosynthetic unit, pulvinii and spines, from species with high specific leaf area, mostly simple leaves without pulvination and exudates.



**Figure 2.2** Box plot of continuous traits for generalist and specialist species a) in the successional gradient and b) in the topographical gradient. Significantly different means among PFT are shown with different letters ( $p < 0.05$ ). OS = old growth forest specialist, YS = young forest specialist; HS = hill specialist; FS = flat site specialist, and G = generalist. Significantly different means are shown

with different letters ( $p < 0.05$ ). Only leaf area, leaf deciduousness and leaf pulvination significantly differ between young specialists and generalists, while specific leaf area, minimal photosynthetic unit and leaf pulvination significantly differ between young and old specialists. With respect to topography, only leaf deciduousness and leaf pubescence differed between flat and hill specialists (Figure 2.1).

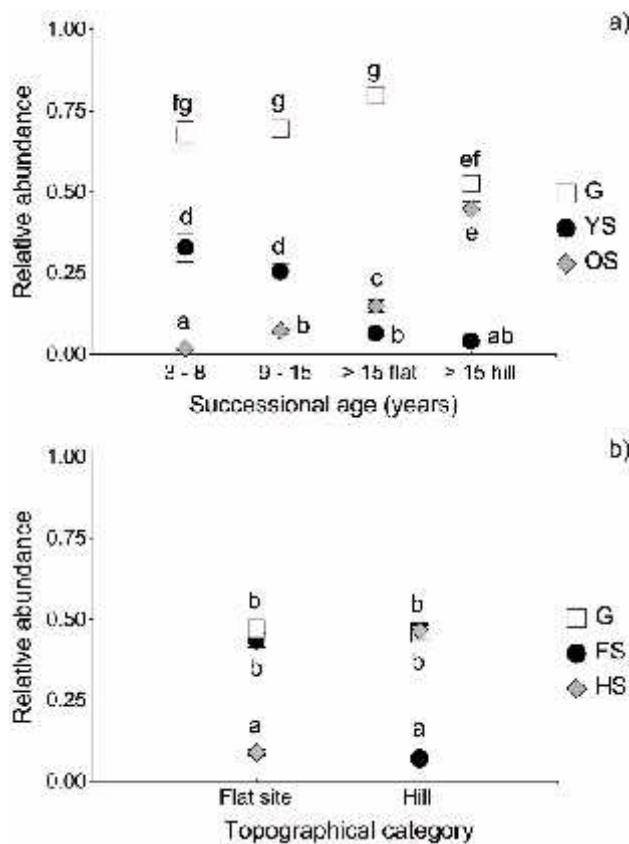


**Figure 2.3** Proportion of species with particular attributes of different binary traits for generalists and specialists a) in the successional gradient and b) in the topographical gradient. Different letters show the proportions that are significantly different among PFT with ( $p < 0.05$ ) based on Tukey-type multiple comparison testing. OS = old growth forest specialist, YS = young forest specialist; HS = hill specialist; FS = flat site specialist, and G = generalist.

When analyzed separately, several functional traits distinguished the groups: young specialists comprised species with higher specific leaf area ( $F_{2,40} = 3.39$ ,  $p = 0.0437$ ) and

lower minimum photosynthetic unit ( $F_{2,40} = 4.15$ ,  $p = 0.0231$ ) than generalists (Figure 2.2 a). Young specialists also had more deciduous ( $q = 4.410$ ,  $p < 0.01$ ) and pulvinate species ( $q = 3.398$ ,  $p < 0.05$ ) with bigger total leaf area ( $F_{2,40} = 3.84$ ,  $p = 0.0298$ ) than old specialists. Regarding topography, flat specialists showed more deciduous species ( $q = 3.921$ ,  $p < 0.05$ ) and more pubescent leaves than hill specialists ( $q = 3.598$ ,  $p < 0.05$ ) (Figure 2.3 b).

Finally, we found significant differences in dominance among groups along the successional gradient ( $H = 578.12$ ,  $p < 0.0001$ ) and according to topographical position ( $H = 365.96$ ,  $p < 0.0001$ ). In the successional gradient (Figure 2.4 a), generalists were dominant over the other functional groups in all vegetation classes except 4 (> 15 years on hills), where they co-dominated with old specialists. Regarding topography, generalists were co-dominant with flat specialists in flat sites and with hill specialists in hill sites (Figure 2.4 b).



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**Figure 2.4** Change in relative abundance of generalists and specialists a) in the successional gradient and b) in the topographical gradient. Secondary succession categories: 1 = 3 to 8 years of secondary succession on flat areas ( $n = 48$  plots), 2 = 9 to 15 years (78) on flat areas, 3 = > 15 years on flat areas (84) and 4 = > 15 years on hills (63). Significantly different means are shown with different letters ( $p < 0.05$ ). OG = old-growth forest specialist, SG = second-growth forest specialist; HS = hill specialist; FS = flat site specialist, and G = generalist.

## 2.5 DISCUSSION

Our results clearly show that secondary succession and topography are important elements influencing functional variation of woody plants in our study site, and differentiating young from old forest as well as hill from flat area specialists, in accordance with our first prediction.

On the other hand, we found only partial support for our second prediction: that specialist species would display different constellations of traits, with young specialists and hill specialists showing leaf and stem traits associated with drought resistance and avoidance, while old specialists and flat specialists would show traits associated with more mesic environments. Our results show that desiccation avoidance is indeed a key element in this semideciduous forest. Desiccation avoidance can be achieved via increased access to water (through deep roots or water storage in stems and roots) or via reduced water loss (through leaf shedding or stomatal control) (Larcher, 2003). As predicted, young specialists have drought avoidance traits, such as deciduous leaves that evade hydraulic failure when trees experience water stress (Reich and Borchert, 1984) and pulvinar movement that reduces irradiance load through fine-tuned changes in leaf orientation (Bielenberg *et al.*, 2003). A larger total leaf area found in young specialists than in old specialists (Figure 2.3 a) allow an increment in light harvest (Niinemets *et al.*, 2004; Takenaka, 1994), while pulvini and deciduousness prevent excessive water loss by transpiration (Bielenberg *et al.*, 2003; Sobrado, 1993). Although a big leaf area may seem surprising early in succession in a dry forest, as this trait declines with increasing insolation (Ackerly *et al.*, 2002), a similar result has been found in other Mexican dry forests (Lohbeck *et al.*, 2013). Besides, most of our young specialists are legumes, and have compound leaves, that in combination with deciduousness allow pioneer plants to low leaf temperature minimizing water loss by transpiration, and a rapid acquisition of light for

photosynthesis during the rainy season prior to leaf shedding (Sobrado, 1993). In contrast, small perennial leaves are associated with a more conservative strategy, with a lower acquisition of light (Sobrado, 1993).

Contrary to our expectations, however, young specialists were functionally more similar to flat specialists; while old were more similar to hill specialists (Figure 2.1). Indeed, eight out of the ten old specialists were also hill specialists, while five out of the six young specialists were also flat specialists (Table 2.1). The association between old and hill specialists was particularly strong, since only one out of the nine hill specialists was not an old specialist, whereas seven out of twelve flat were not young specialists. These results may reflect our unbalanced sampling design, since we did not include young secondary forest plots on hills. However, the scant occurrence of this combination of conditions in our study area clearly reflects the preference of Mayan farmers (with a millennial history of traditional slash-and-burn agriculture <http://www.kiuc.org/research.html>; Dupuy *et al.* 2012b) for flat areas. Thus, the oldest and least disturbed forest stands, harbouring old-growth specialists, are expected to occur on hills, while flat areas have likely been subjected to recurrent land conversion to agriculture, and are therefore dominated by generalists and young specialists.

Surprisingly, flat specialists differed from hill specialists only in two functional traits (leaf deciduousness and leaf pubescence) and in the opposite direction we predicted – deciduousness was more common among the former (Figure 2b). Previous studies on tropical dry forests have analyzed the role of leaf deciduousness as a strategy to cope with drought (Pineda-García *et al.*, 2013; Hasselquist *et al.*, 2010; Markesteijn *et al.*, 2010; Sobrado, 1997, 1995, 1993, 1991). As mentioned before, our results could be an artefact of our unbalanced sampling design. Alternatively, since deciduous species tend to be more susceptible to cavitation and loss of function, but also have higher assimilation rates and water and nitrogen use efficiency than perennial species (Hasselquist *et al.*, 2010; Sobrado, 1997, 1993, 1991), deciduous species could be more common on dryer sites such as slopes and ridges, because they maximize light and water use for rapid assimilation during the rainy season and subsequently shed their disposable leaves during dry season, thus avoiding hydraulic failure. In contrast, evergreen species could be more common on moister sites, where they can afford to produce costly leaves and keep them during dry season through a stem that is more resistant to cavitation (Méndez-Alonso *et*

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*al.*, 2013). Multiple studies have shown that slopes and hill-tops represent more stressful sites in terms of soil water availability (Markesteijn *et al.*, 2010; Daws *et al.*, 2005, 2002; Bellingham and Tanner, 2000; Becker *et al.*, 1988); it is therefore possible that evergreen species on hills in our study site are accessing deeper sources of water. Previous studies in the Yucatan have shown that tree roots take water from subsurface soil-filled cavities and in the porous limestone bedrock at approximately 2 m depth (Hasselquist *et al.*, 2010; Querejeta *et al.*, 2007); however, further studies are required to elucidate the sources of water used by perennial and deciduous species on hills and in flat sites in our study area.

Interestingly, functional groups were not differentiated by wood specific gravity (WSG) even though this trait has been directly associated with higher cavitation resistance (Méndez-Alonso *et al.*, 2012; Markesteijn *et al.*, 2011; Chave *et al.*, 2009). Previous studies in other dry forests have shown that woody plants have multiple strategies to face drought resulting from the interplay among LD, WSG, stem water storage capacity and root depth (Paz *et al.*, 2015; Pineda-García *et al.*, 2013; Sobrado, 1997). For example, species that are susceptible to drought may get established in drought-prone early successional stages or on hills through an increased capacity of roots to forage deeper for water (Paz *et al.*, 2015). An alternative strategy involves the decoupling of plant-tissue from soil hydric status through water storage in stems and roots, which can allow plants to maintain their water potential above soil levels as drought intensifies (Méndez-Alonso *et al.*, 2013; Pineda-García *et al.*, 2013). Finally, leaf shedding may be key to avoid hydraulic failure in species that are highly susceptible to cavitation (Choat *et al.*, 2005; Sobrado, 1993), and has generally been associated with low WSG (Méndez-Alonso *et al.*, 2012; Markesteijn *et al.*, 2011), but also with a high proportion of non-conductive heartwood for the particular case of legume species (Reyes-García *et al.*, 2012).

Interestingly, we found that generalist species are highly variable functionally, and we were unable to identify a set of traits that could account for their success. Moreover, and contrary to our third prediction, generalist species were neither restricted to an intermediate functional position among young-secondary/hill-specialists and late-successional/flat-specialist species nor closer to the former. Although Pineda-García *et al.* (2013) proposed that generalists may show high resistance to soil drought based on high resistance of xylem to embolism making them capable of establishing during early stages of secondary succession, we found that generalists exhibited the entire range of wood

specific gravity (Méndez-Alonso *et al.*, 2012; Markesteijn *et al.*, 2011). It is possible that other functional traits that we did not consider may prove to be more relevant for defining generalist species. In particular, traits associated with reproduction and seed dispersal capacity in open or disturbed habitats may be important, since generalists have been characterized as having high fecundity, long distance dispersal primarily by wind and abiotic pollination (Wiegmann and Waller, 2006; McKinney and Lockwood, 1999). The predominance of generalist species may also be related to sprouting capacity -an important functional trait that was not included in this study. Stem and root sprouting can be an important regeneration mechanism (Kammesheidt, 1999), especially in a context of recurrent, but spaced and low-intensity shifting cultivation, where small agricultural fields are surrounded by second growth or old-growth forests, as occurs in our study area (Dupuy *et al.*, 2012a, 2012b) Woody plant species capable of sprouting can circumvent the vicissitudes of regeneration from seed, including pollination and dispersal failure, seedling mortality from litterfall or herbivory, and asymmetric competition (Bond and Midgley, 2003). Sprouts have a well-developed root system stored with reserves, which gives them a competitive advantage over seedlings, since sprouts can occupy a larger portion of available growing space because they are taller, have larger crown area and larger basal diameter than seedlings (Kennard *et al.*, 2002; Miller and Kauffman, 1998). According to local people with a deep empirical knowledge of vegetation and extensive practice of slash-and-burn agriculture, all 65 species included in our analyses are capable of sprouting after slash and after slash-and-burn agriculture, but further studies on sprouting capacity are needed to assess the importance of this trait in defining the generalist syndrome.

Finally, our fourth prediction that generalists would dominate across succession and topography was supported only for the successional gradient. Our results show that generalists are more competitive under more mesic conditions: at intermediate-aged and old plots on flat sites (Pineda-García *et al.*, 2013; Lebrija-Trejos *et al.*, 2011; Markesteijn *et al.*, 2010). The importance of generalists in this forest deserves a more thorough functional analysis, to determine which sets of functional traits (apart from the ones included in this study) confer them competitive advantages over old forest specialists on flat sites.

## 2.6 CONCLUSIONS

Our results suggest that in our study site leaf shedding is the main mechanism allowing young forest specialist species to avoid hydraulic failure, while old forest specialists retain their leaves and consequently must use different mechanisms to cope with drought. Besides, we found that generalist species were functionally more similar to old forest and hill specialists, and consequently became highly dominant at older plots both on flat sites and on hills. In the more mesic conditions of flat sites, generalists dominate over old forest specialists, while in the more stressful conditions on hills they are co-dominant with hill-specialists. Given the millennial history of management of our study area, and the preference by Mayan farmers for flat areas to establish slash-and-burn agriculture, we hypothesize that hills may constitute important reservoirs for old forest specialists, which are likely most vulnerable to local extinction due to recurrent and pervasive human disturbance.

## 2.7 ACKNOWLEDGEMENTS

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## CAPÍTULO 3.

### FUNCTIONAL DIVERSITY OF SMALL AND LARGE TREES ALONG SECONDARY SUCCESSION IN A TROPICAL DRY FOREST

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#### 3.1 ABSTRACT

Functional Diversity is considered an important driver of community assembly in environmental and successional gradients. To understand tree assembly processes in a semideciduous tropical forest, we analyzed the variation of Functional Richness (FRic), Functional Divergence (FDiv), and Functional Evenness (FEve) of small vs large trees in relation to fallow age after slash-and-burn agriculture and topographical position (flat sites vs hills). FRic of small trees was lower than null model predicted values across the successional gradient, and decreased unexpectedly in older successional ages. FRic of large trees was higher than null model predictions early in succession and lower in late-successional stands on hills. Dominant species were more similar (low FDiv) in early and intermediate successional stands for small trees, and on hills for large trees, suggesting that species that are best adapted to harsh conditions share similar traits. We also found evidence of competitive exclusion among similar species (high FEve) for small trees in early successional stands. Overall, our results indicate that community assembly of small trees is strongly affected by the changing biotic and abiotic conditions along the

successional and topographical gradient. For large trees, hills may represent the most stressful conditions in this landscape.

**Keywords:** Competitive exclusion, environmental filtering, null models, plant functional traits, topographic position, Yucatan.

### 3.2 INTRODUCTION

Tropical dry forests (TDF), characterized by a dry period of several months, a mean annual rainfall between 400 and 1700 mm, and a ratio of rainfall to potential evapotranspiration greater than unity, is one of the most extensive ecosystems in the tropics (Gerhardt and Hytteborn, 1992; Murphy and Lugo, 1986). However, because the severe dry season facilitates vegetation removal with fire and the suppression of pests and weeds (Miles *et al.*, 2006; Sanchez-Azofeifa *et al.*, 2005; Murphy and Lugo, 1986) it is also one of the ecosystems most threatened by land conversion. This land use change has produced a mosaic of tropical dry forest patches of different successional ages, which may offer an opportunity to further our understanding of assembly patterns and processes during secondary succession in this human-modified system (Quesada *et al.*, 2009).

Young successional forest stands are dry, sunny, and hot, because early plant communities have small stature and offer little cover, have small basal area and a small leaf area index (Alvarez-Añorve *et al.*, 2012; Williams-Linera *et al.*, 2011; Lebrija-Trejos *et al.*, 2010b; Madeira *et al.*, 2009; Kennard, 2002). The increase in plant density, height, above-ground biomass and leaf area index modifies the environment over time into one that is relatively cooler and moister at later successional stages (Buzzard *et al.*, 2015; Lebrija-Trejos *et al.*, 2011). Although an increasing number of studies have analysed the recovery of species richness, and the change of structural and functional traits during secondary succession in TDF, only few have measured some of the environmental gradients involved (Buzzard *et al.*, 2015; Pineda-García *et al.*, 2013; Lebrija-Trejos *et al.*, 2011). In particular, soil water availability (Buzzard *et al.*, 2015) and air temperature (Lebrija-Trejos *et al.*, 2010a) have been described among the main filters limiting plant establishment and growth of species associated with young plots. Light may also play a role in community assembly (Buzzard *et al.*, 2015; Alvarez-Añorve *et al.*, 2012) although to a lesser extent than in wet forests, because tropical dry forests are less stratified, possess

short statured trees and have a patchy distribution of canopy that can allow higher light availability in the understory (Murphy and Lugo, 1986).

As a consequence of the harsh environmental conditions at the beginning of succession, a reduced number of species with functional traits associated with maximizing photo-protection and heat dissipation dominate (i.e. the TDF pioneer guild) (Lohbeck *et al.*, 2013; Alvarez-Añorve *et al.*, 2012; Lebrija-Trejos *et al.*, 2010b). These species are characterized by conservative traits associated with high water stress tolerance and slow growth (Buzzard *et al.*, 2015; Lohbeck *et al.*, 2015). As the environment changes, pioneers decline and other species with acquisitive traits associated with fast growth can establish and compete for resources (i.e. the TDF mature forest guild) (Buzzard *et al.*, 2015; Lohbeck *et al.*, 2015). These changes from conservative to acquisitive strategies suggest that abiotic filtering is an important process in community assembly early in TDF succession, whereas the relative importance of competitive exclusion appears to increase at later successional stages (Puschke *et al.*, 2013).

Besides succession, another source of variation in forests is topography, which covaries with multiple environmental factors (Gallardo-Cruz *et al.*, 2009; Becker *et al.*, 1988). Several studies in TDF have shown that soil water availability is lower on slopes and hill-tops compared to valleys (Markesteijn *et al.*, 2010; Gallardo-Cruz *et al.*, 2009). Environmental variation associated with topographic position may result in shifts in TDF plant species composition that are analogous to those observed along secondary succession. Thus, environmental filtering can be expected to select species with conservative traits on slopes and hill-tops, while some species having acquisitive traits may competitively exclude other species in valleys. Moreover, the effects of environmental filtering and competition along succession and across topographic positions may be size dependent, since plant function (e.g. water transport capacity or light harvest), plant responses to the environment, and plant-plant interactions (e.g. competition or facilitation) are also size dependent (Schwinning and Weiner, 1998).

The distribution of functional traits in a community (Mason *et al.*, 2008; Cavender-Bares *et al.*, 2004), and the magnitude of their differences among species, or functional diversity (Mouchet *et al.*, 2010) can shed light on the relative influence of environmental filtering (Weiher and Keddy, 1995) and competition (Tilman, 1987). Assessment of functional

organization of communities requires a multifaceted approach, and several functional diversity indices have been proposed as indicators of the processes that govern community assembly (Ricotta *et al.*, 2014; Villéger *et al.*, 2008; Mason *et al.*, 2005). Here, we consider three functional diversity indices: (1) Functional Richness (FRic), which measures the functional trait space occupied by species based on their position on trait axes, independently of their abundance; (2) Functional Evenness (FEve), which reflects the regularity in the distribution of species abundances, or the regularity in their pairwise functional dissimilarities, and (3) Functional Divergence (FDiv), which measures functional distance among the most abundant species (Villéger *et al.*, 2008). Since environmental filtering is expected to reduce the range of successful strategies among coexisting species (Weiher *et al.*, 1998; Keddy, 1992b), and FRic can be considered as a multivariate range of functional traits; low values of FRic can be interpreted as the result of environmental filtering (Cornwell *et al.*, 2006). FEve gauges how thoroughly the resources available are being exploited by the community (Ricotta *et al.*, 2014), and increases when the strategies of co-occurring species are evenly distributed in relation to resource use, which can be interpreted as an indication of niche partitioning by competitive exclusion (Kraft *et al.*, 2008). Finally, FDiv measures how species abundances are spread along functional axes, and is low when the most dominant species have low functional trait differentiation, which occurs when environmental filters favor a narrow range of functional traits (Villéger *et al.*, 2008). Conversely, high FDiv may be an indication of an increase in competitive interactions (Villéger *et al.*, 2008; Mason *et al.*, 2005), since competition may set a limit to the similarity of coexisting species (MacArthur and Levins, 1967).

The aim of this study was to use a trait-based approach to assess how environmental filtering and competition influence the assembly of large and small-sized tree communities during succession, and if this influence differs in flat areas and on hills of a tropical semideciduous forest. Specifically, we aimed to answer the following questions: (1) how do different functional diversity components (FRic, FDiv and FEve) vary along secondary succession after slash and burn agriculture, and between flat areas and hills? (2) Do functional diversity responses to successional age and topographic position differ between large- and small-sized trees? We hypothesize that abiotic conditions early in succession and on hills may represent strong filters allowing the establishment of mostly stress tolerant slow-growing species that conserve resources for longer periods of time (Lohbeck

*et al.*, 2013). Conversely, later in succession and in flat areas, where water availability is relatively less limiting, acquisitive faster-growing plants with low water use efficiencies and high photosynthetic rates may dominate, and competitively exclude other species (Alvarez-Añorve *et al.*, 2012). Therefore, we predict (1) lower FRic in early successional ages and on hills, reflecting stronger environmental filtering under these conditions compared to later successional ages and flat areas. We also expect (2) lower FRic values for small than for large trees, because the strongest filters to species establishment are known to occur at early life stages when plants are smaller (Grubb, 1977). (3) We predict that FEve and FDiv would be higher at intermediate- and late-successional ages, reflecting increasing competition, as the number of individuals and/or their size increase with successional age. Finally, (4) we predict that, compared to large trees, small trees will show higher FEve and FDiv values due to asymmetric competition for limiting resources, especially at intermediate and late-successional ages and in flat areas, where they can be suppressed by large canopy trees (Schwinning and Weiner, 1998).

### 3.3 MATERIALS AND METHODS

#### 3.3.1 Study site

The study area covers a 352 km<sup>2</sup> landscape of semi-deciduous tropical forest (50–75% of trees shed their leaves during the dry season) in the central part of the Yucatan Peninsula, Mexico (20° 01' 07" to 20° 09' 36" N latitude, and 89° 35' 59" to 89° 23' 31" W longitude). The region is characterized by a warm sub humid climate -AW1 according to the modified Köppen system (García, 1981)- with summer rains and a marked dry season from November to April. Mean annual temperature is 26°C and mean annual precipitation ranges between 1000 and 1200 mm (Orellana *et al.*, 2003). The landscape consists of valleys or flat areas with relatively deep (40–100 cm) clayey Luvisols and Cambisols and low limestone hills (elevations between 60 and 190 m asl) with shallow (5–20 cm) rocky Lithosols and Rendzines (Bautista-Zúñiga *et al.*, 2003; Flores and Espejel, 1994). Soil depth is greater in flat areas than on slopes (Bautista-Zúñiga *et al.*, 2003) whereas soil fertility shows the opposite pattern (Dupuy *et al.*, 2012a). The predominant land use has been traditional slash and burn agriculture, in which all trees are cut to grow corn, squash and beans for one or two years, followed by a fallow period; this system has been practiced by the Mayan people throughout the studied landscape for over 2000 years

(Rico-Gray and García-Franco, 1991). Consequently the vegetation is a shifting mosaic of different successional ages.

### 3.3.2 Species selection

As part of a study relating forest structure and diversity to landscape patterns of habitat types based on a supervised classification of satellite imagery (Hernández-Stefanoni and Dupuy, 2008), in the summer of 2008 and 2009 twenty three 1 km<sup>2</sup> landscape units were selected that encompassed the range of landscape conditions of disturbance and fragmentation of the area. At each unit, 12 sampling sites were established spanning four vegetation classes that could be differentiated using remote sensing: 1) 3 to 8 years of secondary succession, 2) 9 to 15 years, 3) > 15 years on flat areas and 4) > 15 years on hills –three sites per vegetation class where possible, depending on the availability of stands of each class in each landscape unit. Stand age was determined from interviews with local residents who lived in the area for at least 40 years and owned or worked on the land. Mayan farmers have a keen empirical knowledge of forest succession, and their own detailed system of classifying and distinguishing several successional stages based on their knowledge of the local disturbance regime, and the presence and size of certain species, which makes their determination of forest stand age reliable (Hernández-Stefanoni *et al.*, 2006). In total, there were 276 plots consisting of two concentric circular areas, one of 200 m<sup>2</sup> where all trees with a diameter at breast height (DBH; 1.3 m height) > 5 cm were measured, and the other one of 50 m<sup>2</sup> where all plants of tree species with DBH between 1 and 5 cm were measured (for a detailed description of sampling and vegetation characterization see (Hernández-Stefanoni *et al.*, 2011)). From this inventory, and considering only plants with DBH > 5 cm, we calculated for each vegetation class the importance value (I.V.) of each species as:

$$\text{I.V.} = (\text{relative basal area} + \text{relative density} + \text{relative frequency})/3 \times 100$$

For trait sampling we selected a total of 45 tree species (out of a total of 120) that constituted at least 80% of the cumulative I.V. in each vegetation classes. However, for this study, we categorized sites into different successional-age classes, based on a previous study in the Yucatan Peninsula, which found that abandoned agricultural fields reached a tree species composition indistinguishable from that of mature forests after

about 25 years of succession (Turner II *et al.*, 2001): 1) 3 to 10 years old (early-successional), 2) 11 to 25 years old (intermediate), 3) 26 to 70 years old (late-successional). For the last two categories we distinguished between plots on flat sites and on hills. No sites were sampled in early-successional forest stands on hills because such stands are rare in our study area, since local farmers generally prefer flat areas for slash and burn agriculture. Since the environment that plants experience and competitive interactions are influenced by plant size, and to maximize the detection of size-dependent signals of assembly processes, we restricted our analysis to data from individuals with 1 to 2.5 cm in DBH (hereafter called small trees), and individuals with DBH > 5 cm (hereafter called large trees). These groups differed significantly in height (Mann Whitney,  $p < 0.0001$ , Appendix 8.1). The group of small trees corresponds mostly to the sapling or juvenile ontogenetic phase, while the group of large trees comprises adult trees and some juveniles.

For large trees, the selected species represent  $90.95 \% \pm 9.48$  (mean  $\pm$  standard deviation) of the total richness per plot (Pakeman and Quested, 2007), whereas for small trees they represent  $83.81 \% \pm 11.87$  (Appendix 8.2). To explore the potential effect of unrepresentative samples, we performed a second analysis for small trees including only those plots with at least 80% of species (159 plots), and obtained qualitatively similar results, so we present results from all plots (236 for small trees and 264 for large trees excluding all plots with less than 3 species, which is the minimum size required to calculate the functional indices).

### 3.3.3 Functional traits

Regardless of vegetation class, during the rainy months (August-November) of 2011 and 2012 we obtained samples from at least 5 individuals per species (15 individuals per species on average, 664 individuals in total). We collected 3 to 5 young, healthy, and completely expanded leaves from sun-exposed branches of each individual. Fresh weight of each leaf was determined to 0.001 g using a digital scale (Mettler Toledo PB4002-S/FACT, OH, USA), and each leaf was digitized using a flatbed scanner, oven-dried at  $\sim 60^\circ\text{C}$  for three days, and weighed again. Petiole length and minimal photosynthetic unit (leaf or leaflet area as an average of ten leaflets) were measured with the software ImageJ 1.47b (Rasband, 2014). Specific leaf area (leaf area/dry matter) and leaf dry matter

content (leaf dry mass/leaf fresh mass) were calculated using standard methods (Cornelissen *et al.*, 2003).

Wood specific gravity was obtained from 4 individuals per species regardless of vegetation class (average DBH was 16.4 cm). A sample was taken from cortex to pith at 1.3 m height using a 5 mm diameter core borer, and samples were cut every centimeter for a more accurate calculation (Williamson and Wiemann, 2010). Green volume was measured using the water displacement method. Samples were oven dried at 100°C and weighed on an analytical scale (Ohaus Adventurer AP 2140, NJ, USA). Dry weight of each sample was divided over its green volume to obtain wood specific gravity. A weighted average per sampled tree was calculated weighing each core section by the cross-sectional area of the corresponding trunk (Muller-Landau, 2004; Williamson and Wiemann, 2010).

In addition, we obtained the following traits from field specimens, from a parataxonomist and from the literature: leaf compoundness (0 = simple, 1 = compound); leaf pulvination (0 = absent, 1 = present); leaf pubescence (0 = absent, 1 = present), dispersal syndrome (0 = abiotic, 1 = biotic); plant exudates (0 = absent, 1 = present), plant spininess (0 = absent, 1 = present) and leaf deciduousness (0 = evergreen, 1 = deciduous). The functional role of all traits is shown in Table 3.1.

**Table 3.1** Functional traits employed in this study and their functional role.

Plant trait	Functional role
Minimal photosynthetic unit	Leaf cooling
Leaf petiole	Light capture efficiency
Leaf dry matter content	Leaf cost, leaf life span, herbivory defense
Specific leaf area	Growth rate, photosynthetic rate
Leaf compoundness	Leaf cooling
Leaf deciduousness	Drought avoidance
Leaf pulvination	Photo-damage and water loss by transpiration minimization
Leaf pubescence	Herbivory defense
Wood specific gravity	Growth rate, hydraulic conductivity and safety, mechanical resistance

Plant trait	Functional role
Plant exudates	Herbivory defense
Plant spininess	Herbivory defense
Dispersal syndrome	Biotic interactions, dispersal

### 3.3.4 Statistical analyses

#### Functional indices

Functional Richness (FRic) is the volume delimited by the smallest convex hull drawn around the species positioned on trait axes according to their trait values (Cornwell *et al.*, 2006). Functional Divergence (FDiv) is the functional distance among the most abundant species (Villéger *et al.*, 2008). Functional Evenness (FEve) is the degree to which the biomass of a community is distributed in niche space (Ricotta *et al.*, 2014) (see Table 3.2 for details).

**Table 3.2** Functional diversity measures employed in this study and their ecological interpretation.

Functional component	Formula	Ecological interpretation	
		Positive values <sup>1</sup>	Negative values <sup>1</sup>
Richness (FRic) (Cornwell <i>et al.</i> , 2006; Villéger <i>et al.</i> , 2008)	Quickhull algorithm. Volume of the minimal convex hull which includes all the species considered in the community.	Favorable conditions that allow multiple combinations of traits and a more thorough use of the resources available (Villéger <i>et al.</i> , 2008; Cornwell <i>et al.</i> , 2006).	Environmental filtering favoring a narrow range of functional traits (Villéger <i>et al.</i> , 2008; Cornwell <i>et al.</i> , 2006).
Divergence (FDiv) (abundance-weighted) (Villéger <i>et al.</i> , 2008)	$FDiv = \frac{\Delta d + \bar{d}G}{\Delta  d  + \bar{d}G}$ <p>where <math>\Delta d</math> is the sum of abundance-weighted deviances from the center of gravity; <math>\Delta  d </math> is the absolute abundance-weighted deviances from the center of gravity, and <math>\bar{d}G</math> is the</p>	The most abundant species have extreme functional trait values, reflecting either niche partitioning by competitive exclusion, or local environmental heterogeneity favoring different ecological strategies	Environmental filtering favoring a narrow range of functional traits, resulting in little functional differentiation among dominant species (Villéger <i>et al.</i> , 2008).

Functional component	Formula	Ecological interpretation	
		Positive values <sup>1</sup>	Negative values <sup>1</sup>
	mean distance of the S species to the center of gravity.	(Mason <i>et al.</i> , 2005)	
Evenness (FEve) (Abundance-weighted) (Ricotta <i>et al.</i> , 2014)	The average community uniqueness U is the expected dissimilarity between one individual of species i chosen at random from a given community and all other j species in the community:  $U = \sum_{j \neq i}^N p_i \times U_i = \sum_i^N p_i \sum_{j \neq i}^N \frac{p_j}{1 - p_i} d_{ij}$ <p>Where <math>d_{ij}</math> is the functional dissimilarity between species i and j; <math>p</math> is the relative abundance of species i or j, and <math>U_i</math> is the weighted dissimilarity between species i and all other species in the community.           Functional evenness is the regularity in the distribution of single species contributions to U. With the relative contribution of species i to U (<math>\pi_i</math>), the regularity in the distributions of <math>\pi_i</math> is calculated with the index of Bulla:</p> $E_u = \sum_i^N \min \left\{ \pi_i, \frac{1}{N} \right\}$	An even dispersion of the strategies of co-occurring species in relation to resource use, it can be interpreted as an indication of niche partitioning by competitive exclusion (Kraft <i>et al.</i> , 2008)	Environmental filters favoring one or few strategies, so the species that survive are functionally more similar than expected by chance (Mouchet <i>et al.</i> , 2010; Grime, 2006).

<sup>1</sup> Compared to a null model of random assembly of species.

Before calculating functional indices, we applied a log10 transformation to those traits that departed from normality (minimal photosynthetic unit and petiole length) as recommended by Swenson (Swenson, 2014). Because all traits considered were numeric, we standardized trait values and obtained Euclidean distances among species from a species x traits matrix. FEve was calculated using this distance matrix. The calculation of the convex hull for FRic and FDiv requires more points (species) than dimensions (traits).

Since this was not always the case for every plot, we used principal coordinate analysis (PCoA) with a correction for negative eigenvalues (Cailliez, 1983), and used PCoA axes as traits, to reduce their number (Laliberté and Legendre, 2010). The number of PCoA axes used as traits ( $T$ ) was:

$$T = S_{\min} - 1$$

Where  $S_{\min}$  is the number of species in the community with the fewest species. This entails a reduction in dimensionality, and a concomitant loss of information, which was quantified via the  $R^2$ -like ratio in PCoA (Laliberté and Legendre, 2010).

The three diversity measures were calculated separately for large trees (plants > 5 cm DBH) and small trees (DBH between 1 and 2.5 cm). All diversity indices were based on the number of selected species per plot, which was tightly correlated with the total number of species per plot (Pearson correlation 0.97,  $p < 0.0001$ ). We calculated functional richness (FRic) (Cornwell *et al.*, 2006) and functional divergence (FDiv) (Villéger *et al.*, 2008) with FD package (Laliberté *et al.*, 2014), and FEve (Ricotta *et al.*, 2014) with function FeveR in R software (R Development Core Team, 2015).

To evaluate how functional components vary as a function of secondary succession, we performed linear or logarithmic regressions with successional age. We selected as the best model the one with the highest  $R^2$ . When the difference was less than 1 %, we selected the linear model.

### Null models

To account for variation in species richness among plots and vegetation classes, and to assess if functional indices obtained per plot differed from random, we constructed null models (by shuffling species names on the trait data matrix) and re-calculated functional components 999 times. These null models maintained the observed patterns of trait covariance, and changed only the trait matrix, keeping the number of species and their abundance in each plot. To assess if the observed FRic, FDiv and FEve differed significantly from random variation among plots of different successional age and topographical position, we used the two-tailed Wilcoxon signed-ranks test per vegetation class to test our empirical data against the expectation from the null model. To assess the direction of the deviation of observed values from those expected by chance, while

accounting for variation in species richness among vegetation categories, we calculated for each plot ( $i$ ) the standardized effect size (SES) as:

$$\text{SES}_i = (\text{observed value in plot } i - \text{mean of null model in plot } i) / \text{standard deviation of null model in plot } i$$

where positive values indicate an observed value higher than the average expected value and negative values indicate an observed value lower than the average expected value (Swenson, 2014). We compared the average SES of each functional index among vegetation classes using ANOVA and Tukey's post hoc test.

## 3.4 RESULTS

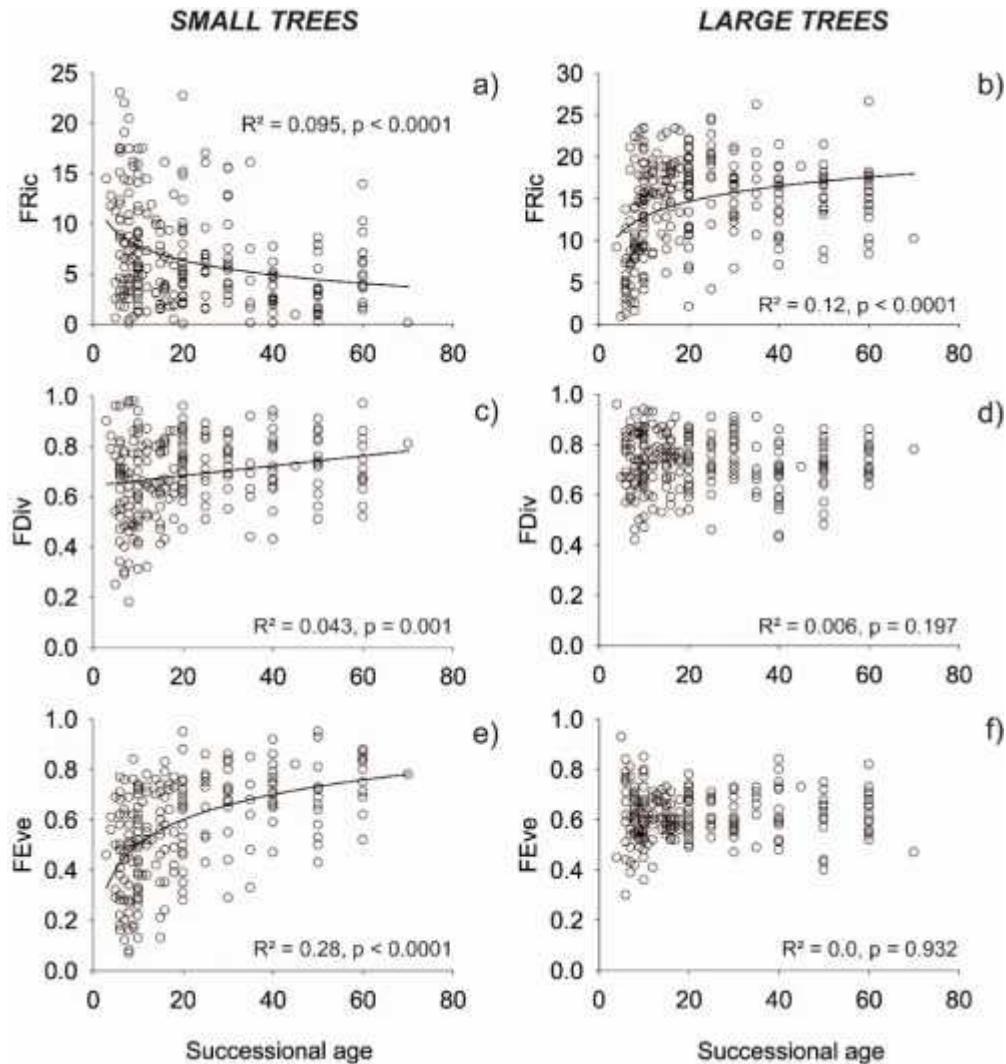
### 3.4.1 Functional indices

Principal Coordinates Analysis (PCoA) accounted for over half of the variation in functional traits of both small and large trees (54.3%). Successional age generally explained a low percentage of variation of functional indices for small trees (4 - 28%) and of FRic for large trees (12%). Functional richness (FRic) of small trees decreased logarithmically with fallow time, while for large trees FRic increased logarithmically with successional age and saturated at older ages (Figure 3.1a, b). For small trees FDiv increased linearly, while FEve increased logarithmically with successional age, whereas for large trees neither index showed any association with successional age (Fig 3.1 c-f).

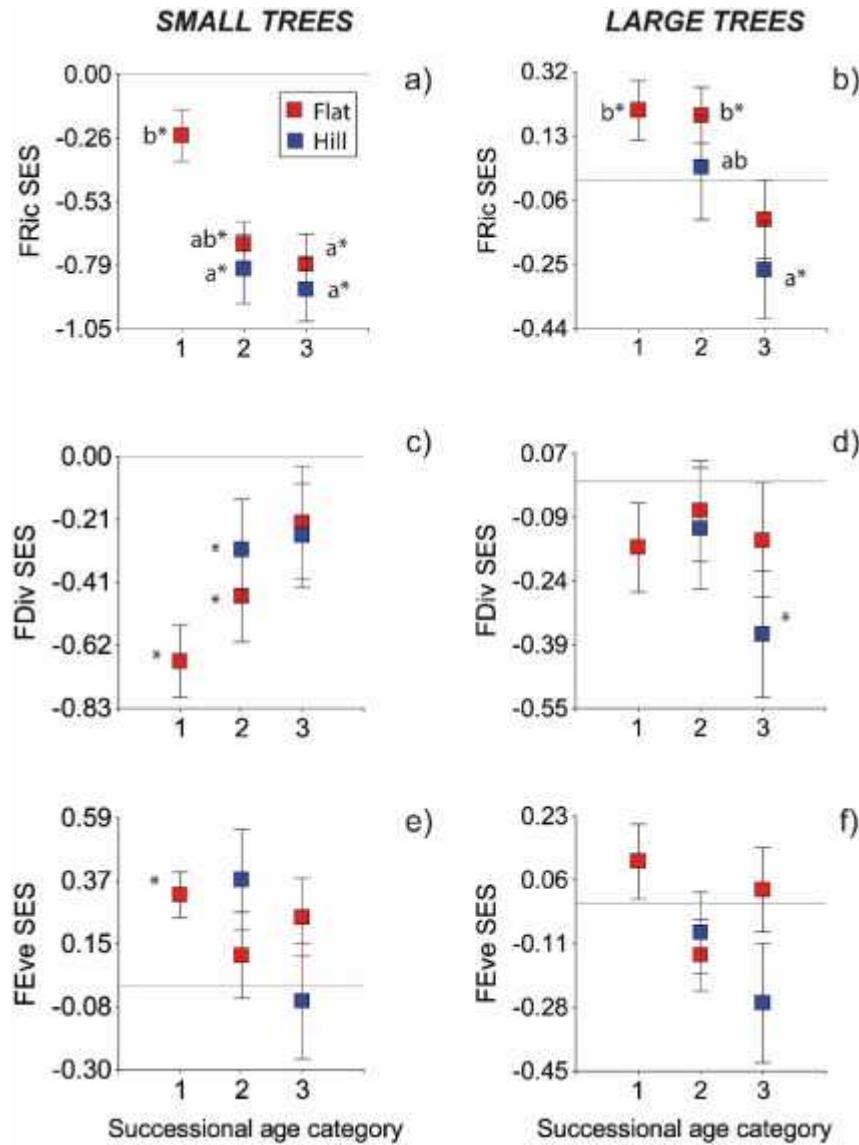
### 3.4.2 Null models

For small trees, we found that FRic differed significantly from null model expected values in all successional ages and topographic positions, while FDiv differed from the null model only in successional ages 1 and 2 and FEve only in age 1 (Table 3.3). For small trees mean FRic and FDiv that differed from null model expected values (indicated by asterisks in Figure 2) were consistently lower than expected by chance (i.e. negative values), while mean FEve that differed from null model was higher than expected by chance (positive) (Figure 3.2a, c, e). Besides, mean FRic SES of intermediate and late successional classes were significantly lower compared to the early successional class (ANOVA,  $F_{4,231} = 5.77$ ,  $p = 0.0002$ ) (Figure 3.2a). SES values of FDiv and FEve did not differ among successional age/topographic classes ( $F_{4,231} = 1.77$ ,  $p = 0.135$  and  $F_{4,231} = 1.31$ ,  $p = 0.268$  respectively).

For large trees, mean FRic differed significantly from null model values in early and intermediate successional classes on flat sites, and in the late successional class on hills (Table 3.3, Figure 3.2b). Mean FDiv only differed significantly from null model values in the late successional class on hills (Table 3.3, Figure 3.2d), while mean FEve did not differ from null model values in any successional class (Figure 3.2f). Mean FRic SES values that differed from null model (indicated by asterisks in Figure 3.2b) were higher than expected by chance at early and intermediate age classes, but lower than expected by chance in the late successional class on hills (and differed significantly among classes, ANOVA,  $F_{4,258} = 3.26$ ,  $p = 0.013$ , Figure 3.2b). Mean FDiv SES values were significantly lower than expected by chance (Figure 3.2d) only in the late successional class on hills (Figure 3.2d). Mean functional indices and SES per plot can be found in Appendix 8.3.



**Figure 3.1** Variation of functional diversity components in relation to successional age. (a) Functional Richness (FRic) of small trees; (b) Functional Richness of large trees; (c) Functional Divergence (FDiv) of small trees; (d) Functional Divergence of large trees; (e) Functional Evenness (FEve) of small trees; (f) Functional Evenness of large trees. Regression coefficients and significance values are shown.



**Figure 3.2** Mean Standardized Effect Size (SES) of observed functional diversity components (and standard error) in relation to null model randomizations by successional age category. (a) FRic SES of small trees; (b) FRic SES of large trees; (c) FDiv SES of small trees; (d) FDiv SES of large trees; (e) FEve SES of small trees; (f) FEve SES of large trees. Means with different letters are significantly different ( $p < 0.05$ ). Horizontal lines indicate mean Standardized Effect Size (SES)

equal to zero (the mean of 999 randomizations). Successional age category and number of plots for small/large trees: 1 Flat (3 to 10 years) = 85/83; 2 Flat (11 to 25 years) = 52/66; 2 Hill (11 to 25 years) = 29/30; 3 Flat (26 to 70 years) = 39/52; 3 Hill (26 to 60 years) = 31/32. Asterisks denote mean FRic, FDiv or FEve (not SES) values that differ significantly from null models (see Table 3.3).

**Table 3.3** Wilcoxon signed-rank tests evaluating differences between mean null model and mean expected values (Z) of large and small trees for each functional index and successional age/topographic class.

Successional age/ Topographic class	Functional index	Z	p	Z	p
		Large trees		Small trees	
1 Flat	FRic	1.9659	0.049	-3.148	0.002
2 Flat		2.4179	0.016	-5.155	0.000
2 Hill		0.0514	ns <sup>1</sup>	-4.054	0.000
3 Flat		-0.7012	ns	-4.577	0.000
3 Hill		-1.9821	0.046	-4.253	0.000
1 Flat	FDiv	-0.7991	ns	-4.800	0.000
2 Flat		-0.2076	ns	-2.914	0.004
2 Hill		0.0103	ns	-2.065	0.037
3 Flat		-0.4007	ns	-1.200	ns
3 Hill		-2.0756	0.037	-1.215	ns
1 Flat	FEve	0.5085	ns	2.776	0.006
2 Flat		-1.4597	ns	1.239	ns
2 Hill		-1.1210	ns	1.784	ns
3 Flat		-0.3916	ns	1.730	ns
3 Hill		-1.4959	ns	0.137	ns

<sup>1</sup> ns = not significant ( $p > 0.05$ ). Sample sizes (n) per age/topographic class: 1 Flat = 83, 2 Flat = 66, 2 Hill = 30, 3 Flat = 52, 3 Hill = 32.

### 3.5 DISCUSSION

We found that variation in functional diversity of trees in the tropical dry forest studied was influenced by successional age and topographic position, and that patterns of functional variation differed between small (DBH 1–2.5 cm) and large trees (DBH > 5 cm), depending on the functional component considered. Examining SES values and their departure from null models (Figure 2), our results generally do not support our first prediction that FRic would be lower early in succession and on hills than in late successional forests and in flat areas. This prediction was based on previous findings in tropical dry forests showing that, (1) compared to late-successional forests, early successional stages experience higher irradiance, and warmer and drier conditions, (Pineda-García *et al.*, 2013; Lebrija-Trejos *et al.*, 2011); and (2) hill tops and slopes have lower water availability than flat areas (Markesteijn *et al.*, 2010; Gallardo-Cruz *et al.*, 2009; Becker *et al.*, 1988). We found evidence of environmental filtering only for large trees in late-successional forests on hills (Figure 2b), probably due to the effect of lower soil water availability (Markesteijn *et al.*, 2010; Gallardo-Cruz *et al.*, 2009; Becker *et al.*, 1988). However, our results also suggest a thorough use of resources by large trees in early successional and intermediate forests (3 to 25 years old) on flat sites, reflecting maximum variation in ecological strategies and positive FRic values (Figure 2b), probably due to the coexistence of pioneers, generalists and (resprouts of) old-growth forest specialists. Moreover, small trees face unfavorable conditions (negative FRic SES values) in the complete successional/topographical gradient, and a stronger signal of environmental filtering at intermediate and late successional ages (Figure 2a). We believe that this successional trend may have resulted from two possibilities:

- 1) Relatively higher FRic values early in succession may reflect the coexistence of acquisitive and conservative species that show different constellations of functional traits in young stands. Pioneers (which represent the conservative strategy in dry forests) may establish from seeds of nearby forests (since slash-and-burn agriculture may destroy the seed bank) (Dalling and Denslow, 1998), whereas more acquisitive shade-tolerant species may avoid unfavorable conditions for seed establishment by getting established mainly from resprouts (Kammesheidt, 1999). The subsequent reduction in FRic over succession may result from environmental filtering associated with lower light and air evaporative demand, which would decrease the success of the conservative species (Lebrija-Trejos *et al.*, 2010a).

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- 2) Alternatively, modern coexistence theory states that functional convergence results not only from environmental filtering, but also from competitive exclusion based on hierarchical competitive abilities among species (Kraft *et al.*, 2015; Mayfield and Levine, 2010). The Functional Richness index may thus reflect the combined effect of both environmental filtering and competitive processes (Mayfield and Levine, 2010). In line with this, early in succession negative FRic values of small trees may reflect the effect of environmental filters (high irradiance load, air temperature and evaporative demand), whereas at latter successional ages the lower FRic values may reflect the elimination of poor competitors (Mayfield and Levine, 2010). Competitive hierarchy of species can be determined by multiple factors, but in a dry forests it may be defined mostly by water availability, which is the most limiting resource (Murphy and Lugo, 1986). Previous studies of microenvironment in tropical dry forests have shown that soil water content increases with successional age, as radiation load and air evaporative demand decrease with canopy development (Buzzard *et al.*, 2015; Pineda-García *et al.*, 2013; Lebrija-Trejos *et al.*, 2011). However, other studies have found a steady and sometimes marked increase in fine root biomass along succession (Vargas *et al.*, 2008; Deans *et al.*, 1996; but see Powers and Peréz-Aviles, 2013), and a decrease in soil water potential (Lebrija-Trejos *et al.*, 2011). Theoretically, the increasing importance of soil drying by transpiration as canopy closes and forests mature (Marthews *et al.*, 2008) could be a sign of stronger competitive processes, if plants pre-empt water supply from coming in contact with other species (which may be considered as a filter), or if they reduce soil water potential to low levels (Craine and Dybzinski, 2013). The effect of below-ground competition on soil water availability has been poorly quantified (Craine and Dybzinski, 2013). The relative importance of soil drying by evaporation vs. transpiration during dry forests succession, and its effects on tree community assembly need further investigation.

In agreement with our second prediction, FRic SES values were consistently lower for small trees than for large trees (see values of y axes in Figure 2a,b). The latter result also agrees with previous findings showing that the strongest filters to species establishment occur at early life stages when plants are smaller (Poorter, 2007), although our small tree category corresponds to saplings and juveniles, which are not the most sensitive

ontogenetic stage (i.e., seedlings). Differences in tree size may represent differences both in microenvironments and in competitive abilities, with smaller plants being most susceptible to both. Larger individuals are better equipped to cope with competitors and fluctuating unfavorable conditions, such as dry spells, through a more developed root system, enabling them to forage in larger areas and to store more water and nutrients, as well as a bigger trunk allowing them to store more water and to harvest more light (Niinemets, 2010). Alternatively, differences in FRic between small and large trees can arise from temporal fluctuations in environmental conditions suitable for reproduction and recruitment of species (i.e., the storage effect; Warner and Chesson, 1985). Favorable conditions could produce a strong recruitment that results in a cohort of reproductive large trees (Warner and Chesson, 1985). Under unfavorable conditions, many small trees could be filtered out (reducing their FRic), whereas large trees may be able to survive for many years and reproduce when more favorable conditions occur. In other words, lower FRic for small trees than for large ones would be expected under the storage effect, because large trees may comprise a larger number of cohorts. Resprouting capacity, which is generalized among the species studied (LSV *pers. obs.*) likely also plays a role (Kammesheidt, 1999).

Contrary to our third prediction (that competitive processes would be more important at intermediate and latter successional ages), FDiv showed partial evidence of environmental filtering (negative values, see Table 2) instead of competition. Negative FDiv values suggest a scarce functional differentiation of dominant species. Small trees showed negative FDiv SES values in early and intermediate successional forests suggesting that the small-sized trees capable of establishing and becoming dominant at these successional stages may share similar traits, probably associated with avoiding water loss, such as pinnate, deciduous, leaves (Lohbeck *et al.*, 2013). Large trees showed negative FDiv in late successional stages on hills, suggesting that environmental filtering may reduce the functional strategies present in this environment, which is also in line with the negative values of FRic found there.

In agreement with our fourth prediction, we found signs of competition only for small trees in early successional ages. Positive FEve SES values in the youngest successional class (Figure 2e) suggest that species with functional strategies that survive the filters disperse

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evenly in relation to resource use, which can be interpreted as niche partitioning by competitive exclusion. Environmental filtering is usually conceived aside of competitive processes; nonetheless both factors interact dynamically to drive community patterns (Kraft *et al.*, 2015). Moreover, although neither FEve nor FDiv departed from null model predictions in late successional ages (contrary to our third prediction), hierarchical competitive ability (reflected by low FRic values especially at late successional ages) cannot be discarded (Mayfield and Levine, 2010).

Finally, our results, especially those of FDiv and FEve, should be taken with caution, since competition in tropical dry forests is expected to be strongest for below-ground resources (water and nutrients), which are most limiting, yet we did not consider any below-ground functional traits in this study. Further studies are needed to assess the relative importance of above-ground (light availability, air temperature) vs. below-ground (water, nutrients) resources on assembly of tree communities in tropical dry forests.

### 3.6 CONCLUSIONS

Our results clearly show that assembly patterns differ between plants of different sizes. While small-sized trees showed evidence of environmental filtering and/or competition at all successional ages and topographical positions, large-sized trees showed evidence of these assembly processes only in late successional forests on hills, indicating that the former represent a more susceptible phase of development, and that small-sized tree communities are strongly affected by the changing biotic and abiotic conditions along the successional and topographical gradient. For larger plants, late successional forests on hills represent the most stressful conditions in this landscape. Moreover, small trees showed the strongest environmental filtering (lowest functional richness) in late successional forest stands, although the few studies in tropical dry forests that have analyzed microenvironmental differences during succession suggest that the most stressful conditions (hot and dry environment) occur during the early stages of succession. Our results suggest that the functional richness index may actually reflect the combined effect of both environmental filtering and hierarchical competitive ability. Future research should test this and the possibility that relatively high soil drying by transpiration in late successional forest stands may exert a stronger effect on tree community assembly than relatively low evaporative demand.

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## CAPÍTULO 4.

### AMONG AND WITHIN-COMMUNITIES PLANT TRAIT ASSOCIATIONS IN A NEOTROPICAL DRY FOREST

*Artículo en preparación.*

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Running headline: Among and within communities plant trait variation.

#### 4.1 ABSTRACT

Question(s): How do and which plant functional traits correlate at the plot scale (within plots) and at the landscape scale (among plots)? Are trait correlations at the landscape scale explained by the environmental gradient formed by soil properties, topographic position and successional age? What is the relative contribution of these three factors to explaining variation in plot trait values (community abundance-weighted means)?

Location: The Yucatan Peninsula, Mexico.

Methods: We used Trait Gradient Analysis to decompose species' functional traits into values representing the position of the species along a gradient defined by community-level mean trait values (beta values), and values representing the difference between trait values of a species and the mean of co-occurring species (alpha values). To identify trait covariation at the landscape scale (among beta values) and at the plot scale (among

values), we determined and components for six functional traits (leaf area, petiole length, specific leaf area, leaf dry matter content, wood specific gravity and seed volume) of 65 woody plant species in a tropical dry forest in the Yucatan Peninsula. We also investigated the relative contribution of environmental factors (successional age, topographical position, soil properties) to explaining variation in plot trait values (community abundance-weighted means).

**Results:** Within plots, alpha trait correlations segregated species into the rapid-slow continuum. At the landscape scale, mean trait averages of plots where each species was present ( values) were similar among species, resulting in few trait correlations –mostlt not different from random species assembly. This may be due to recurrent slash and burn agriculture leading to the selection and dominance of species capable of thriving under recurrent fire disturbance and of establishing in a wide range of conditions. Little variation in plot abundance-weighted traits was explained by environmental factors.

**Conclusions:** Alpha trait correlations suggest that, within plots, local environmental heterogeneity (likely resulting from recurrent small-scale disturbance), and possibly species competition, may play a key role in the assembly of these communities. At the landscape scale, disturbance has resulted in functionally homogeneous vegetation almost decoupled from the environment.

**Key-words.** Biotic homogenization; community abundance-weighted mean trait values; fire; functional variation within and among communities; plant community assembly; recurrent disturbance; scale; soil properties; Trait gradient analysis; Yucatan Peninsula.

#### 4.1.1 INTRODUCTION

Because functional traits affect plant fitness and mediate species responses to the environment, analysis of variation in functional traits can shed light on the factors and processes that drive community assembly (Kraft *et al.*, 2007; Weiher *et al.*, 1998). A common approach to understanding community assembly is the use of community weighted trait means (CWM) (Cornwell and Ackerly, 2009; Cingolani *et al.*, 2007; Garnier *et al.*, 2004). These reflect the functional traits of dominant species, and are directly related to the mass ratio hypothesis of Grime (1998), which postulates that the traits of the most abundant species largely determine community structure and ecosystem processes.

This approach has been used to explore patterns of variation in plant strategies along environmental gradients considering the covariation of single and multiple traits with environmental variables (De Bello *et al.*, 2013; Lebrija-Trejos *et al.*, 2010a; Garnier *et al.*, 2004). For example, CWM of specific leaf area (SLA: leaf area/dry matter) and leaf area (LA) have been found to be positively correlated in response to environmental filtering associated with rainfall and soil phosphorus gradients (McDonald *et al.*, 2003; Fonseca *et al.*, 2000; Ackerly *et al.*, 2002).

Dominant trait values in plant communities are driven by large-scale filters such as climate and temperature (Moles *et al.*, 2014), and, at finer scales, by disturbance regime and local factors such as topographic-edaphic conditions, microenvironment and biotic interactions (De Bello *et al.*, 2013; Lebrija-Trejos *et al.*, 2010a; Diaz *et al.*, 1998; Keddy, 1992b). Because spatial variation of these factors can be structured at different scales, a better understanding of community assembly using functional traits can be obtained with the explicit analysis of trait-environment covariation at different scales. Trait gradient analysis (TGA; Ackerly & Cornwell 2007) was developed as a tool for the combined analysis of functional trait variation among communities at the landscape or regional level and among species within communities. This is achieved through the decomposition of the species mean trait values ( $\bar{t}$ ) into beta (among communities) and alpha (within community) values. Thus, for species  $i$ , the beta value represents the average of the CWM where  $i$  species occurs. Since individual traits influence plant dispersal, establishment and persistence, CWMs reflect the integrated effects of disturbance, dispersal limitation and environmental filters on dominant species, and consequently values reveal the similarities or differences among species *in the environmental conditions where each species exists*. Therefore, values represent the functional position of each species within the functional space of the pool of species in the landscape or region, i.e. in the trait gradient (Ackerly & Cornwell 2007). Ecologically similar species in similar environments are expected to have similar traits, so significant correlations of beta values of different traits would reflect the turnover of species among communities in response to environmental gradients. Applying TGA to plant communities along the California Coast (USA),  $\beta$  values of SLA were positively associated with LA and maximum plant height (max height); while all three traits were negatively associated with wood density (WD) –likely in response to environmental filtering associated with soil moisture availability (Ackerly and Cornwell, 2007). Similarly, in

an Australian subtropical rain forest,  $\beta$  trait values of LA, seed size, WD and max height co-varied significantly in parallel to the dominant abiotic gradients formed by soil, topography, elevation and large natural disturbances (Kooyman *et al.*, 2010).

A simple way of measuring functional differentiation of species within communities is to determine if traits of species  $i$  are above or below the average values of co-occurring species in the communities where it is most abundant. In TGA this value is named the alpha component, and is calculated for each  $i$  species by subtracting the beta from the species mean trait value ( $t_i$ ). Correlations between values of different traits can arise from parallel co-variation of multiple traits, reflecting morfo-physiological restrictions at the species level, that allow fine partitioning of microsites and/or resources within communities. Conversely, lack of correlations between values is expected when species in a particular position in the gradient differentiate functionally from co-occurring species in different ways than other species in other parts of the gradient (for example when plants from different vegetation types are included in the analysis). Since TGA is scale dependent, we expect the first outcome if analyzing short environmental gradients where communities are more similar, while the second would be more likely in large environmental gradients with a strong species turnover, such as those sampled in the above-mentioned studies by Ackerly & Cornwell (2007) and Kooyman *et al.* (2010). In both studies, the lack of correlations between values was attributed to independent axes of ecological differentiation and coexistence of species.

TGA allows capturing the signature of ecological filters that act on plant strategies at different spatial scales, and the specific correlations of CWM with environmental variables can result in a better understanding of the fit between species and the habitat they use. This approach can be particularly useful when studying species assembly in complex swidden agricultural landscapes with a dynamic mosaic of old growth and secondary forests.

Several functional studies in tropical dry forests have found that during secondary succession, species turnover occur in response to the autogenic environmental change produced by early successional species, that show a conservative strategy characterized by traits that avoid loss of water (compound, deciduous leaves, with small area and pulvini) (Lohbeck *et al.*, 2015; Pineda-García *et al.*, 2013; Lebrija-Trejos *et al.*, 2010).

Towards older stages, conservative species are replaced by others with an acquisitive strategy, with high sapwood storage capacity, and large, perennial leaves and large seeds (Lohbeck *et al.*, 2015; Pineda-García *et al.*, 2013; Lebrija-Trejos *et al.*, 2010a). The aim of this study is to evaluate through TGA the trait co-variation of woody plants at two scales: landscape (i.e. among communities, CWM and values) and local (i.e. within communities, values) in a tropical dry forest in the Yucatan Peninsula, which has been subjected to long-term (over 2000 years) and recurrent slash and burn agriculture (Rico-Gray & García-Franco 1991). We expect strong and CWM associations (i.e. among communities, landscape scale) reflecting the functional turnover of species associated with secondary succession, and weaker or absent trait associations of values (i.e. inside communities, local scale), as a result of a scarce local environmental heterogeneity. We also expected that successional age and soil properties would explain a similar proportion of trait variation, because the gradient of soil nutrients is expected to vary with successional age (Becknell and Powers, 2014).

## 4.2 MATERIALS AND METHODS

### 3.3.1 Sampling design

In the summer of 2008 and 2009, 23 landscape units ( $1 \text{ km}^2$ ) were selected encompassing the range of disturbance and fragmentation conditions of the area. In each unit, we established 12 sampling plots differing in successional age after slash and burn agriculture and/or topographic position: 3-8 year-old, 9-15 year-old, > 15 year-old on flat areas and > 15 year-old on hills. Forest stand age was determined from interviews with local residents who lived in the area for at least 40 years and owned or worked the land. A total of 276 plots were established consisting of two concentric circular areas:  $200 \text{ m}^2$  for all woody plants with a diameter at breast height (DBH; 1.3 m) > 5 cm, and  $50 \text{ m}^2$  for all woody plants 1-5 cm DBH (for a detailed description of sampling see Hernández-Stefanoni *et al.* 2011).

### 3.3.2 Species selection

We used data from 273 plots having individuals with DBH > 5 cm to calculate the relative importance value (RIV) of all species in each stand age-topographic position category as the sum of the species' relative abundance, frequency and basal area. For each category

and separately for trees, lianas and shrubs, we selected those species representing 90% of the cumulative RIV, and obtained a total of 72 species. However, only 65 species were included for which we could collect leaf and wood samples from at least 5 individuals. Of these, 45 species were trees, 11 shrubs and 9 lianas. We could obtain seeds of only 55 species: 40 trees, 9 shrubs and 7 lianas.

### 3.3.3 Functional traits

Samples were collected from at least 5 individuals per species (14 individuals per species on average; see Appendix 8.4) during the rainy season (August-November) of 2011 and 2012. The following functional traits, reflecting key components of plant function, were selected: specific leaf area, SLA; leaf dry matter content, LDMC; petiole length, PL; leaf area, LA; wood specific gravity, WSG and seed volume, SV.

We obtained 3-5 young, healthy and completely expanded leaves from sun-exposed branches from each individual. For each leaf, fresh weight was determined to 0.001 g using a digital scale (Mettler Toledo PB4002-S/FACT, OH, USA) and samples were digitized using a scanner, oven-dried at 60°C for three days, and weighed again. Petiole length (PL) and leaf or leaflet area (the average of ten leaflets) were measured using ImageJ 1.47b (Rasband, 2014). SLA and LDMC were calculated using standard methods (Cornelissen *et al.*, 2003).

Wood specific gravity (WSG) was obtained from individuals with the largest DBH: 3.2 cm on average for lianas, 4.1 cm for shrubs, and 16.4 cm for trees. For lianas, a 4-5 cm long and 1 cm wide slice was taken from the trunk, after taking off the bark that could be manually removed. A similar procedure was used for shrubs when they had a trunk > 4 cm DBH; otherwise we cut one branch at the first ramification and took a 4-5 cm long section. For trees, a sample was taken at breast height from cortex to pith from 4 individuals per species using a 5 mm diameter core borer. Green volume was measured using the water displacement method. Samples were oven dried at 100°C and weighed with an analytical scale (Ohaus Adventurer AP 2140, NJ, USA). Wood specific gravity of each sample was obtained by dividing dry weight over green volume (Williamson and Wiemann, 2010; Muller-Landau, 2004).

Ripe fruits or seeds for 40 species were collected, in most cases from just one individual. Specimens from the Herbarium at CICY were also used to obtain fruit or seed measurements for some species. Seed volume was used as a proxy for seed mass. Height, width and length of at least 3 (and in most cases 10) seeds per individual were measured using a Vernier or obtained from botanical descriptions. Seed volume (SV) was calculated using the ellipsoid formula [(4/3) (length \* width \* height) / 8)].

### 3.3.4 Environmental variables

Three 10 cm-deep soil samples (ca. 400 g each) were taken in 2008 and 2009 at the center, northern and southern limits of each plot, and subsequently pooled to obtain a single compound sample. The following variables were obtained: pH in water (1:2 ratio), soil organic matter (combustion or Walkley-Black), cation exchange capacity (Olsen), electric conductivity (1:5 extracts), total nitrogen (Kjeldahl), available phosphorus (Bray) and interchangeable potassium (ammonium acetate). Altitude and slope were obtained using a digital elevation model (spatial resolution: 30 m) from the Mexican National Institute of Statistics, Geography and Informatics.

### 3.3.5 Statistical analyses

#### Trait Gradient Analysis

According to Ackerly & Cornwell (2007), the abundance-weighted plot mean trait value, equivalent to the widely used community abundance-weighted trait mean is:

$$\bar{P}_j = \frac{\sum_{i=1}^S a_{ij} t_{ij}}{\sum_{i=1}^S a_{ij}} \quad (1)$$

The species mean trait value is defined as:

$$\bar{t}_i = \frac{\sum_{j=1}^P a_{ij} t_{ij}}{\sum_{j=1}^P a_{ij}} \quad (2)$$

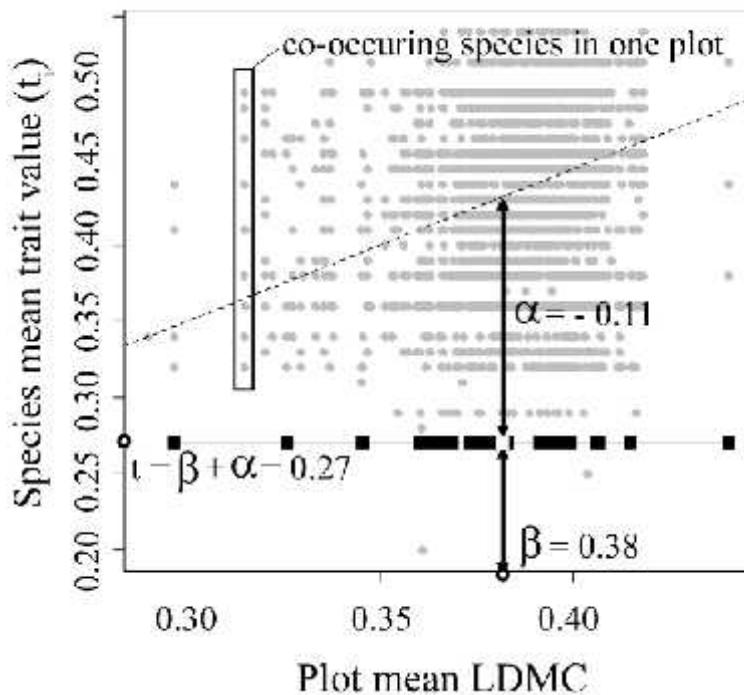
Where  $t_{ij}$  is defined as the trait value of species  $i$  in plot  $j$ ,  $a_{ij}$  is the abundance of species  $i$  in plot  $j$ ;  $S$  is the number of species in the study and  $P$  is the number of plots. The values of  $\bar{P}_j$  constitute the gradient in community structure defined by species traits (Figure 4.1), since  $\bar{P}_j$  is an integrated measure of the abiotic and biotic environment that may influence

community assembly. The range of  $\bar{P}_j$  values of occupied plots represents the niche breadth ( $R_i$ ) of the species along the gradient (Ackerly and Cornwell, 2007).

$\beta_i$  is the species' mean location along the trait gradient, defined as the abundance-weighted mean of  $\bar{P}_j$  for those plots occupied by the species (Ackerly and Cornwell, 2007):

$$\beta_i = \frac{\sum_{j=1}^P \bar{P}_j a_j}{\sum_{j=1}^P a_j} \quad (3)$$

The  $\beta_i$  value of species  $i$  is a measure of the deviation of the mean trait value of the species from the co-occurring species in the community, and it is defined as the difference between the species mean trait value and its  $\beta_i$  value (Figure 4.1) (Ackerly and Cornwell, 2007).



**Figure 4.1** Scatterplot of species trait values ( $t_i$ ) vs. abundance weighted plot mean trait values ( $\bar{P}_j$ ) for Leaf Dry Matter Content (LDMC) of woody plant communities of a tropical dry forest in the Yucatan Peninsula. The small gray circles represent species occurrences, and the dashed line represents abundance-weighted least squares regression. The vertical alignment of gray circles represents the species found in each plot. TGA parameters are illustrated for *Cochlospermum vitifolium* (Willd.) Spreng. The solid squares represent the 75 plots occupied by this species, and

their range, from 0.3 to 0.42, defines the species' niche breadth ( $R_i$ ) = 0.12 (black horizontal hair-line). The open square represents the intersection of this species's beta value (open circle on the abscissa;  $\beta = 0.38$ ) and its mean trait value (open circle on the ordinate;  $t_i = 0.27$ ). The  $\beta$  value indicates that this species is more abundant towards the mid-higher portion of the gradient. The negative  $\beta$  value (the difference between  $\beta$  and the regression or dashed line = -0.11), indicates that LDMC of this generalist species is below the values of other co-occurring species with a more conservative or slow strategy.

Two independent trait gradient analyses (TGA) were performed: one for SV using data from 55 species, and another for the other 5 traits (PL, LA, LDMC, SLA and WSG) using all 65 species. Trait data were log10-transformed when necessary. To test the potential role of habitat filtering in community assembly, we constructed a null model in which species were randomly assembled within plots, keeping species richness of each plot, and the association of species with their traits values (Ackerly and Cornwell, 2007), but not abundances. Species-trait associations were kept, because they represent the minimum possible functional differentiation among species. Both analyses were performed on R software (R Development Core Team, 2008) using Ackerly & Cornwell's (2007) script.

Pearson correlations of  $\bar{P}_j$  and beta- (landscape scale) or alpha values (plot scale) were performed to evaluate trait associations at each scale. Correlations among species mean trait values were used to infer if  $\bar{P}_j$  and beta trait correlations reflect species trait associations, or if traits are sorted independently by ecological filters.

Multiple regression models were performed to evaluate the relative contribution of soil properties, topographic variables and forest stand age to explaining variation in  $\bar{P}_j$  values. The log10[y+1] transformation was used for altitude and CE, and the logit transformation (Warton and Hui, 2011) for percentage variables (slope, stoniness, soil total nitrogen and soil matter content). For each trait, all possible subsets of independent variables were tested and the best model was selected using Akaike's criterion and hypothesis testing procedures with Infostat software (Di Rienzo *et al.*, 2013). The relative importance of explanatory variables was gauged by  $R^2$  partitioning averaging sequential sums of squares over all orderings of explanatory variables with R package relaimpo (version 2.2) (Grömping, 2006).

Finally, ANOVA was used to assess differences in functional traits among stand age-topography categories, while a principal component analysis of stand age, soil properties and topographic variables was performed to understand the relationships among environmental variables and to help interpret trait-environment associations.

#### 4.3 RESULTS

The range of alpha values exceeded the range of beta values for all traits, indicating that species vary more in their trait values relative to co-occurring species compared to the mean trait values of plots in which they occur (Table 4.1). Niche breadths ( $R_i$ ) relative to the overall range in  $t_s$  values were lower for specific leaf area (SLA) and leaf dry matter content (LDMC) than for the other traits analyzed (Table 4.1, Figure 4.2).

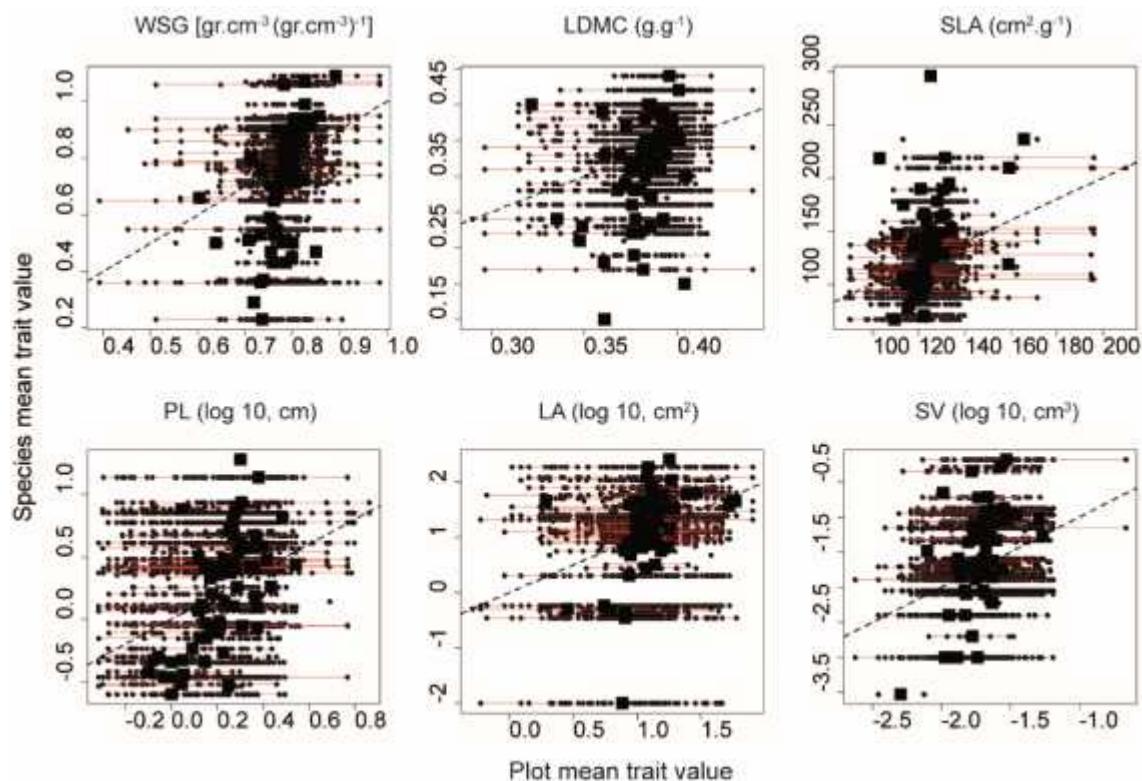
**Table 4.1** Statistics of trait gradient analysis (TGA) for six functional traits across a successional gradient in a semideciduous forest of the Yucatan Peninsula, Mexico.

	LA (cm <sup>2</sup> , log10)	SLA (cm <sup>2</sup> gr <sup>-1</sup> )	PL (cm, log10)	LDMC (gr gr <sup>-1</sup> )	WSG [gr cm <sup>3</sup> (gr cm <sup>3</sup> ) <sup>-1</sup> ]	SV (cm <sup>3</sup> , log10)
<i>Species characteristics</i>						
$t_s$ min	-2.00	67.2	-0.60	0.15	0.23	-3.52
$t_s$ max	2.40	295.7	1.28	0.49	1.09	-0.17
$t_s$ mean	1.11	137.3	0.22	0.37	0.72	-1.64
$t_s$ min	0.29	103.0	-0.10	0.32	0.60	-2.61
$t_s$ max	1.77	165.6	0.54	0.40	0.89	-1.24
$t_s$ range	1.48	62.62	0.64	0.08	0.29	1.37
$t_s$ mean	1.08	124.5	0.21	0.38	0.78	-1.85
$t_s$ min	-2.88	-52.4	-0.78	-0.21	-0.51	-1.92
$t_s$ max	1.38	170.5	0.98	0.13	0.28	1.62
$t_s$ range	4.26	222.95	1.77	0.34	0.78	3.53
$t_s$ mean	0.03	12.8	0.01	-0.02	-0.06	0.21
$R_s$ mean	1.00	37.0	0.62	0.06	0.22	1.01
$R_s$ min	0	0	0	0	0	0
$R_s$ max	2.13	105.6	1.16	0.14	0.59	1.75
$R_s$ mean / $t_s$ range	0.23	0.16	0.33	0.18	0.25	0.30
<i>Plot characteristics</i>						
$P_s$ mean	1.01	124.4	0.24	0.38	0.78	-1.85

$P_s$ min	-0.29	88.2	-0.32	0.29	0.39	-2.77
$P_s$ max	1.90	209.7	0.86	0.44	0.98	-1.02

$t_s$  = species mean trait value;  $s$  = beta value;  $s$  = alpha value;  $R_s$  = niche breadth;  $P_s$  = mean plot trait value. LA = leaf or leaflet area; SLA = specific leaf area; PL = petiole length; LDMC = leaf dry matter content; WSG = wood specific gravity, and SV = seed volume.

**Figure 4.2** Scatter diagrams of the species mean trait values and plot mean trait values for the six functional traits a) Wood Specific Gravity (WSG); b) Leaf Dry Matter Content (LDMC); c) Specific Leaf Area (SLA); d) Petiole Length (PL, log10); e) Leaf or Leaflet Area (LA, log10) and f) Seed Volume (SV, log10). The larger, solid squares represent the intersection of the mean trait value for the plots occupied by each species (the species  $i$  trait value on the abscissa) and the species mean trait value  $t_i$  (on the ordinate). The horizontal alignment of small points joined by lines represents a species occurrence across plots; the length of the line is the species niche breadth  $R_i$ .



Under the null model, all plots are expected to have the same mean plot trait values and all species are expected to have the same beta values. Considering the number of species included in our analysis, only 3 would be expected to have values significantly higher or lower than this expectation at  $p < 0.05$ . However, 5 species differed from null expectation

for wood specific gravity (WSG) and leaf area (LA), 14 for LDMC, 18 for petiole length (PL), 12 for SLA and 13 for seed volume (SV), so the null model was rejected for all traits (Appendix 8.5).

Contrary to our expectations, trait correlations were in general stronger within plots (alpha values) than among plots (plot mean trait values,  $P_j$ , and beta values; Figure 4.3). At the plot scale (alpha values), we found a negative correlation of WSG with LA and SLA, and a positive correlation between LA and PL (Figure 4.3 c). At the landscape scale, for  $P_j$  and beta values, we found a negative correlation of SLA with LA, and for  $P_j$  values a positive correlation between SV and PL. Only four out of eight correlations found among  $P_j$  values were also found among beta values (Figure 4.3 a, b). We found no associations of WSG with LA or SLA among  $P_j$  values or beta values. At both scales ( $P_j$  values and alpha values) we found negative correlations of LDMC values with SLA, LA and PL; SLA with SV; and WSG with PL; and a positive correlation between WSG and LDMC (Figure 4.3 a, c).

We found no association of SV with LA, WSG, or LDMC, or between SLA and PL at either scale. It is notable that correlations of species trait values ( $t_i$ ) showed almost the same associations and patterns as alpha values (Figure 4.3 c, d). Only the SLA-SV correlation among beta values was significantly different from null-model expectations.

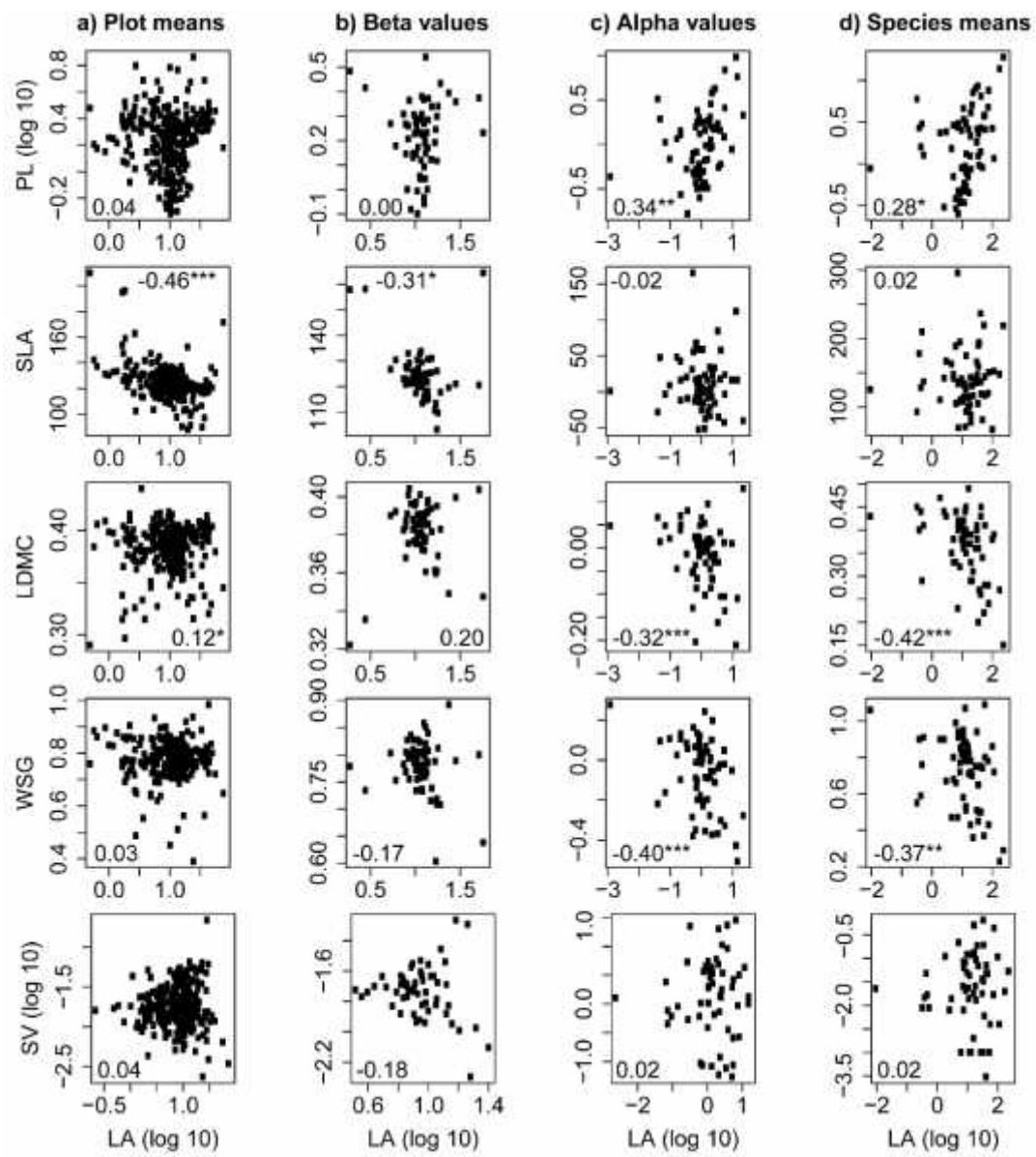
$P_j$  values differed significantly among successional-age/topographic-position categories, although stand-age/topography explained a low percentage of variation (Figure 4.4). WSG, SV, LA and LDMC had lower values in the youngest plots (3-8 year-old), while PL showed its highest values in older plots (> 15 year-old) on flat sites and hills (Figure 4.4). The lowest values of SLA were found in older plots on flat sites (Figure 4.4).

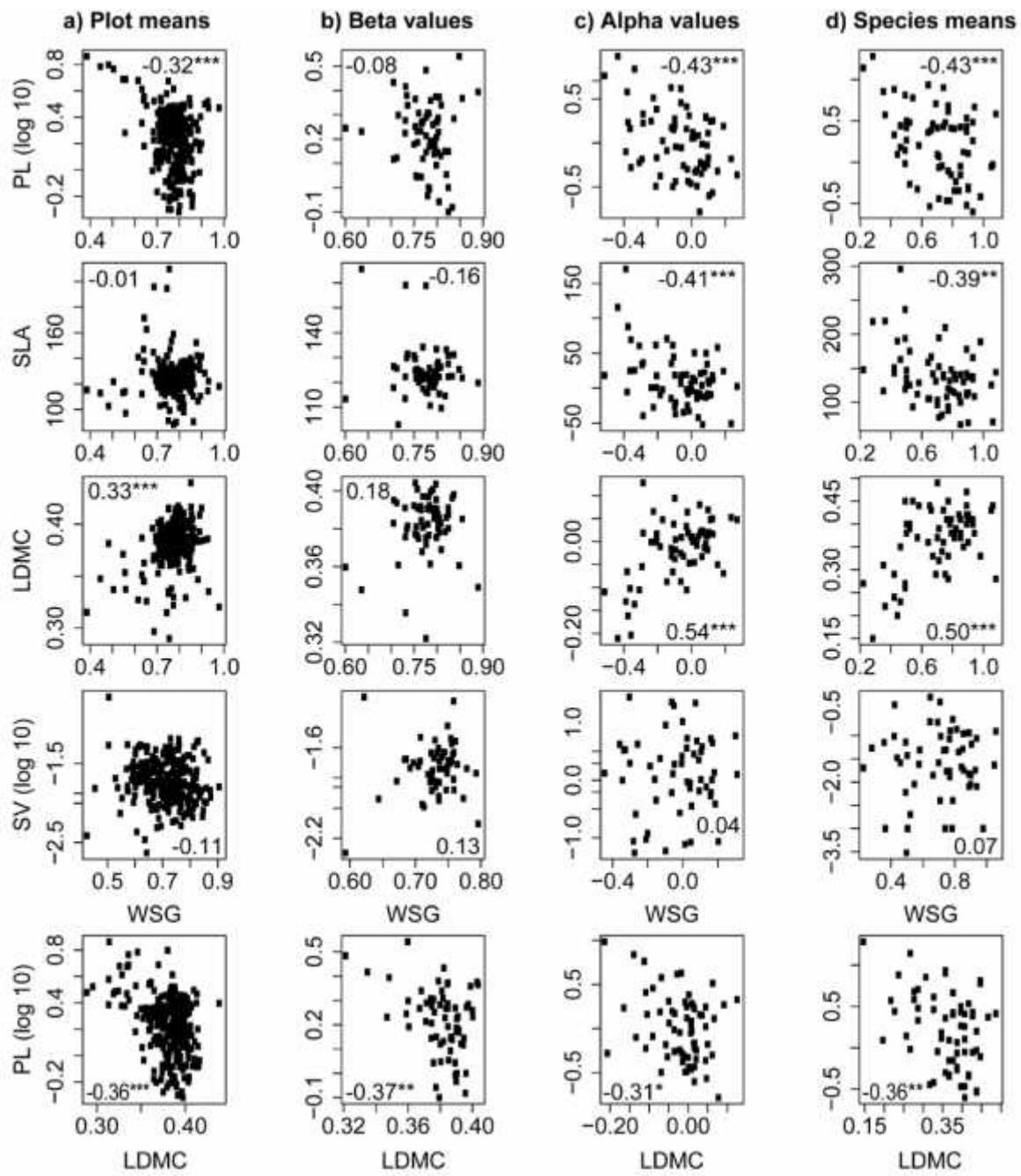
According to PCA, most of the overall variation in predictor variables was related to soil properties (first axis), mainly soil total nitrogen (N), organic matter (SOM), cation exchange capacity (CEC) and stoniness (Ston; Appendix 8.6). Some additional variation (second axis) was independently associated with soil phosphorus (P), and potassium (K), altitude and forest stand age (Appendix 8.6).

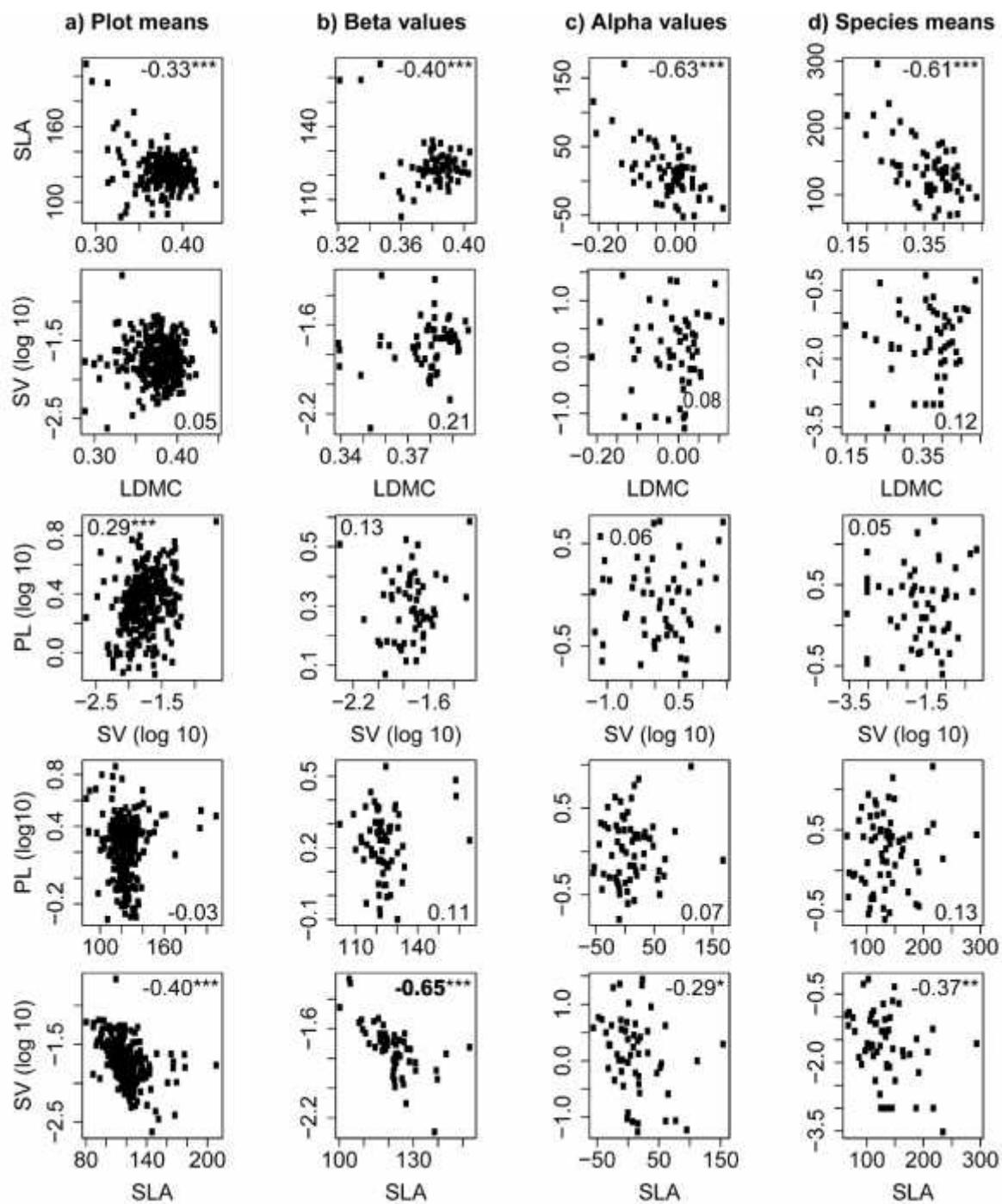
We found significant associations of functional traits with topography, soil properties and forest stand age, although the amount of variation explained was low ( $R^2$ : 0.02 - 0.27),

particularly for WSG, SLA and LDMC (Table 4.2, Appendix 8.7). LDMC and WSG were associated with CEC. PL varied with stand age, P, slope, N, SOM and Ston. LA and SLA varied with stand age, pH and N. Finally, SV was associated with stoniness, SOM, P and K. Overall, forest stand age was the main variable explaining variation in LA, LDMC and PL, while soil properties and topography were more important for SLA, SV and WSG (Table 4.3).

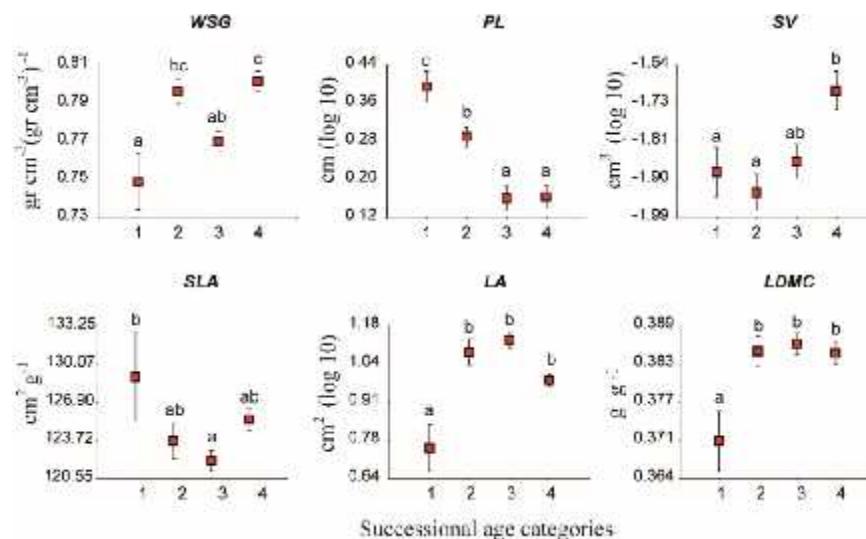
**Figure 4.3** Pearson's correlations for  $P_j$ ,  $t_b$  and  $t_s$  values.. These expected correlations of the alpha and beta components, across traits, are generally close to the correlation of the species trait values (column d). LA = leaf or leaflet area; PL = petiole length; SLA = specific leaf area; LDMC = leaf dry matter content; WSG = wood specific gravity, and SV = seed volume. Seed volume was obtained as an abundance-weighted average considering data from only 55 species. The rest of functional traits were obtained as an abundance-weighted average considering data from 65 species. \* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ .







**Figure 4.4** Average of plot mean trait values ( $\pm$  SE) by successional age category. Different letters indicate significantly different means ( $p < 0.05$ ) according to ANOVA and Tukey's *post hoc* analysis. Successional age categories: 1 = 3 to 8 years of secondary succession ( $n = 51$ ), 2 = 9 to 15 years (86), 3 = > 15 years on flat areas (74) and 4 = > 15 years on hills (62). Seed volume was obtained as an abundance-weighted average considering only data from 55 species. The rest of functional traits were obtained as an abundance-weighted average considering data from 65 species.



**Table 4.2** Reduced multiple linear regression models of plot mean trait values with successional age and environmental variables. For each trait the minimum model is shown, according to Akaike criterion and hypothesis testing procedures (\* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ ).

Trait	R <sup>2</sup>	Adj. R <sup>2</sup>	Age	pH	N	CEC	P	Slope	SOM	Ston	K
LA	0.1	0.09	***	*	***						
LDMC	0.08	0.07	***			*					
PL	0.27	0.25	***		*		*	**	*		*
SLA	0.08	0.07	**	***	**						
SV	0.23	0.22				***			*	***	**
WSG	0.02	0.02				*					

PL = petiole length; LA = leaf or leaflet area; LDMC = leaf dry matter content; SLA = specific leaf area, WSG = wood specific gravity, SV = seed volume. Age = Fallow time after slash and burn agriculture; CEC= cation exchange capacity; K = interchangeable potassium; N = Soil total nitrogen; Ston = Stoniness; SOM = Soil Matter Content; P = available phosphorus. Variables where transformed, but original names are used for clarity. n= 263.

**Table 4.3** Relative importance of regressors on variance explained of reduced multiple linear regressions models, obtained by  $R^2$  partitioning averaging sequential sums of squares over all orderings of explanatory variables.

Trait	% of variance explained by the model	Age	CEC	K	N	P	pH	Slope	SOM	Ston
LA	9.55	0.74			0.19		0.07			
LDMC	7.86	0.87	0.13							
PL	26.89	0.70			0.07	0.10		0.06	0.04	0.03
SLA	8.52	0.21			0.13		0.66			
SV	23.35			0.06		0.12			0.28	0.53
WSG	1.97		1.00							

See abbreviations meanings on Table 4.2.

#### 4.4 DISCUSSION

We evaluated through TGA the trait co-variation of woody plants at two scales: landscape (i.e. among communities, CWM and values) and local (i.e. within communities, values). We found partial support for our prediction that, at the landscape scale, beta and plot mean ( $P_j$ ) values of functional traits would be strongly correlated, reflecting turnover of functionally distinct species associated with microenvironmental change during succession; whereas, at the plot scale, alpha values would show weaker correlations, as a result of a scarce local environmental heterogeneity. We found nine functional trait correlations between alpha values, and fewer correlations between beta (four) or  $P_j$  (eight) values (Figure 4.3). Although null-model tests on beta values were rejected for all traits (Appendix 8.5), indicating that species were aggregated in plots with other species with similar trait values –which is consistent with habitat filtering (Ackerly and Cornwell, 2007; Cornwell *et al.*, 2006), this rejection was based on a reduced number of species. Consequently, only one trait correlation (involving beta values, specific leaf area-seed volume) did not differ from null model expectations. We found weak trait correlations associated with the segregation of species into the rapid-slow continuum at the plot scale (i. e.  $\beta_i$  values), and only some correlations at landscape scale (i. e.  $P_j$  and  $\beta_i$  values). By

rapid species we mean species that have great growth potential because they have “high capacity to move water and to acquire and use nutrients and light to fix carbon, but build flimsy, disposable tissues and are less tolerant to low resources” (Reich, 2014). Rapid species have been directly related with high specific leaf area (SLA) (Poorter and Garnier, 2007; Poorter and Bongers, 2006), or high leaf area (LA) and petiole length (PL) (Niinemets *et al.*, 2004; Poorter, 2009) and inversely with wood specific gravity (WSG) (Poorter and Bongers, 2006; Brodribb and Feild, 2000) and leaf dry matter content (LDMC) (Hodgson *et al.*, 2011; Wilson *et al.*, 1999).

Because in the null models species were assigned to plots at random, but the species-trait associations were maintained, the expected correlations of the  $\beta_i$  and  $\gamma_i$  components across traits in the null model are close to the traits correlations in the species (Ackley and Cornwell, 2007). Surprisingly, we found that only one trait correlation (SLA-SV) at the landscape ( $\beta_i$  values) was not different from null model expectation. This means that nearly all trait correlations we found among and inside plots did not differ from a random assembly of species. Therefore,  $\beta_i$  correlations indicate that, inside plots, species segregation may be the result of two possible processes: species morpho-physiological constraints that allow them to take advantage of fine-scale environmental heterogeneity, favoring species with ecological strategies that require or tolerate different levels of resources, and species competition that establishes a limit in species similarity (de Bello *et al.*, 2013). This fine-scale environmental heterogeneity may be partly the result of local disturbance. Firewood harvest, cutting of small trees for construction of Mayan houses, and poaching are common daily activities we witnessed during sampling, and which occur in all successional ages and topographic positions.

The correlations between  $\beta_i$  values allow to distinguish two groups of species with particular trait combinations that appear to segregate within plots: one group of species with low LDMC, WSG and SV, high SLA and variable PL and LA, and the other with low LDMC and WSG, high LA and PL and variable SV. While this combinations of traits corresponds to acquisitive or rapid species, opposite trait correlations (i.e. high LDMC and WSG, and low SLA or LA) correspond mainly to conservative or slow species. Our results suggest that the segregation of these species occurs within plots regardless of topographic position or forest stand age, which agrees with previous findings showing a high similarity

in species composition, and the coexistence of generalist, pioneer and late-successional species in all successional stages, probably as a result of the long history of disturbance in this forest (Dupuy *et al.*, 2012a; Mizrahi *et al.*, 1997; Rico-Gray and García-Franco, 1992).

Trait correlations we obtained among  $\beta$  values of WSG, LA, SLA and LDMC result from well-known associations; for example, local differentiation in relation to WSG may be the result of drought tolerance, since a relationship between high WSG and low xylem susceptibility to cavitation as has been extensively documented (Chave *et al.*, 2009). Low WSG is correlated with high water storage capacity or with high hydraulic conductivity (Poorter *et al.*, 2010; Chave *et al.*, 2009; Borchert, 1994) and with high SLA or LA, because these traits are associated with high carbon assimilation that depends on water supply (Ishida *et al.*, 2008; Santiago *et al.*, 2004). Furthermore, rapid acquisition of water and minerals that results in high photosynthetic and growth rates are associated with low LDMC (Reich, 2014). The  $\beta_{SLA}$ -PL association result from an allometric scaling relationship between these two traits (assuming PL is directly related with petiole mass), because stronger petioles are required to support bigger leaves (Li *et al.*, 2008; Niinemets *et al.*, 2007).

That  $\beta$  correlations did not differ from a random assembly is an indication that species with particular trait combinations segregate among plots, and that this segregation is unrelated to environmental differences among plots. Thus, species with particular trait associations may become dominant in some plots just because they have rapid growth, or high fecundity or are highly competitive (Kneitel and Chase, 2004). The rapid species capable of dominating in plots are those with either disposable leaves (i. e. low LDMC) and high SLA, or with low LDMC and long petioles, or with high SLA and low LA. All these trait associations are related to high photosynthetic rates (tightly associated with SLA) or efficient light capture (long petioles and big leaves), which may be an indication that light and/or moisture plays an important role in species dominance. An association of SLA and species abundance has been reported before in other systems (Cornwell and Ackerly, 2010; Cingolani *et al.*, 2007). WSG was unrelated to other traits (especially SLA and LA), probably as a consequence of the interplay between plant drought resistance vs drought avoidance mechanisms, which are fundamental in dry forests. Apart from xylem vulnerability to embolism and sapwood water reserves (both associated with WSG), other

traits, such as leaf shedding, root depth or leaf movement (paraheliotropism) may increase water use efficiency (Pineda-García *et al.*, 2013; Hasselquist *et al.*, 2010; Brodribb and Holbrook, 2003; Koller, 2000). For example, Fabace harbors more individuals (35% in 17 species) than any other family in our study site; these plants can achieve a more efficient use of water than other species irrespective of their wood density through a combination of small LA, leaf shedding and fine regulation of leaf movement by pulvini (Reyes-García *et al.*, 2012).

We found weaker trait correlations at landscape scale, and only half of them among  $P_j$  values, sometimes in opposite direction with  $P_j$  values. While  $P_j$  values reflect the integrated effects of disturbance, dispersal limitation and environmental filters on dominant species,  $P_j$  values reveal the similarities or differences among species in the environmental conditions (biotic and abiotic) *where each species exists*. In a disturbed forest as ours, many of the species are capable of establishing along most of the gradient (i.e. in most of the plots; see niche breadth as horizontal lines on Figure 4.2), and consequently the average traits of these plots (i.e. their  $P_j$  values) are similar among species, which canceled out many  $P_j$  values correlations. However, few correlations among  $P_j$  values can be also an indication that the environmental gradient among plots of different successional age is not enough to filter out specific functional strategies. This has been found previously in seedlings in a tropical dry forest (Pineda-García *et al.*, 2015). Other studies in Amazonian forests have found that species that are generalists at one scale (hundreds of square meters, Pitman *et al.*, 1999) are specialists at a bigger scale (thousands of square meters, Toledo *et al.*, 2012). Probably many of our species would show clear environmental preferences at a larger scale, as many of them distribute in geographic ranges of thousands of square kilometers, which exceeds widely the possible environmental variation of our study area.

Just one trait correlation differed from null model, and can therefore be attributed to environmental filtering: SLA-SV (Figure 4.3b). The negative correlation between SLA and SV (among  $P_j$  values) suggests the existence of filters among plots that favor species with high SLA and small seeds on one extreme, and the opposite values on the other. Species with high SLA and small seeds are associated with high photosynthetic rates and low drought tolerance (Poorter and Rose, 2005; Daws *et al.*, 2008; Baker, 1972), and they may

be favored by the environmental gradient associated to secondary succession after slash and burn agriculture.

Environmental variables explained a low proportion of variation in plot mean functional traits ( $R^2$ : 0.02 - 0.27; Table 4.3), and we found complex relationships between functional traits of dominant species and environmental variables, and partial support to our prediction that slope and soil properties would be as influential as successional age due to their co-variation. All traits (except WSG) were associated both with soil/topographic variables and with successional age; however, variation in SLA, SV and WSG was associated mostly with soil/topographic variables, whereas variation in LA, LP and LDMC was mainly associated with successional age (Table 4.4). PL has been directly associated with light capture efficiency (Niinemets *et al.*, 2004; Takenaka, 1994) suggesting that light availability, which decreases with vegetation development during succession, may be the main factor affecting this trait. In contrast, LA and LDMC were directly related to successional age, possibly reflecting greater water deficit in early successional stages (Lebrija-Trejos *et al.* 2010).

SLA was associated with the two main orthogonal axes in the landscape: total nitrogen (N), soil organic matter (SOM) and cation exchange capacity (CEC) on the one hand; and available phosphorous (P), interchangeable potassium (K) and forest stand age on the other (Table 4.3, Appendix 8.6). This is in agreement with previous findings that associate SLA with soil nutrients (Ordoñez *et al.*, 2009) and stand age (Becknell and Powers, 2014; Lebrija-Trejos *et al.*, 2010a). SV was associated with SOM, stoniness, P and K. These variables were indirectly related both with topographic position (SOM and stoniness are higher on hills than on flat areas) and with successional age (as P and K covary with stand age). Besides, mean values of SV differed between young plots in flat areas and older plots on hills (categories 1 and 4; Table 4.2), suggesting that both successional age and topographic position may indirectly and simultaneously influence SV.

The only variable that was significantly associated with WSG was CEC (Table 4.3), which is positively associated with soil fertility. However, this association explained very little variation ( $R^2 = 0.02$ ), and it is unlikely that high fertility *per se* favors species with high WSG. Other variables associated with topographic position (besides CEC) may be involved, since WSG was the only trait showing significant differences between hills and flat areas (categories 3 and 4; Table 4.2). In particular, water deficit may be an important

stressor, especially on hill tops and slopes, favoring species with high values of WSG (Markesteijn *et al.*, 2011; Choat *et al.*, 2005). Soil water potential has been found to be more negative (indicating lower water availability for plants) on hills or slopes than in valleys (Markesteijn *et al.*, 2010; Daws *et al.*, 2002; Becker *et al.*, 1988).

The low percentage of variation explained by topography, succession-related environmental conditions and soil properties, coupled with the results of null models of trait correlations, suggest that either recurrent human disturbance may have resulted in a decoupling of woody plant assembly from some environmental filters, or that the environmental factors that filter out species occur at larger scales. Further investigation is needed to determine if the scarce functional turnover seen at the landscape scale is associated with a low environmental variability among successional stages and topographical positions.

#### **4.5 CONCLUSIONS**

Our results suggest that, at the plot scale, assembly of species, as gauged by leaf, trunk and seed functional traits, is determined by local environmental heterogeneity, partially associated with fine-scale heterogeneity and/or by interspecific competition. At the landscape scale, most of species were capable of establishing in a wide range of conditions. Consequently, most trait correlations involving the functional environment of each species (i.e the trait average of those plots where each species is present) did not differ from randomness. Further investigation is needed to determine if the scarce functional turnover seen at the landscape scale is associated with a low environmental variability among successional stages and topographical positions, or from a long term management of vegetation.

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## **CAPÍTULO 5.**

### **DISCUSIÓN GENERAL**

La sucesión secundaria es uno de los escenarios más importantes para analizar los procesos que determinan el ensamblaje de las comunidades, y que permiten entender porqué las especies se establecen en donde lo hacen, en términos de tiempo y espacio. Mientras que la sucesión secundaria ha sido ampliamente descrita para bosques tropicales húmedos, los estudios en los bosques secos son más escasos (Portillo-Quintero y Sánchez-Azofeifa, 2010), y en particular los estudios que analizan la sucesión secundaria desde un punto de vista funcional. Esto ha limitado el análisis de los mecanismos sucesionales en estos sistemas, aún cuando representan el 42% de la vegetación tropical y subtropical del planeta (Murphy y Lugo, 1986), y cuando están bajo enorme presión por cambios de uso de suelo y altas tasas de deforestación (Keenan *et al.*, 2015; Miles *et al.*, 2006; Janzen, 1988).

En este contexto, la finalidad de este trabajo fue obtener, mediante el uso de caracteres funcionales de tallos, hojas y semillas, una aproximación de las características de las plantas leñosas que son clave para su coexistencia y dominancia en un paisaje particular de la Península de Yucatán, en donde los gradientes ambientales principalmente estudiados en la sucesión secundaria han sido las características del suelo y la topografía (Dupuy *et al.*, 2012a; López-Martínez *et al.*, 2012; Hernández-Stefanoni y Dupuy, 2008; White y Hood, 2004; Rico-Gray y García-Franco, 1992). Este análisis partió de tres aproximaciones distintas que se analizan en los siguientes apartados.

#### **5.1 EL CAMBIO SUCESIONAL DE LOS GRUPOS FUNCIONALES DE PLANTAS LEÑOSAS**

Con base en los pocos estudios disponibles para bosques secos, podemos describir los sitios sucesionales tempranos como lugares con una alta demanda evaporativa por la elevada irradiación y albedo, lo que produce un incremento en la temperatura del aire y una pérdida de agua superficial del suelo (Lebrija-Trejos *et al.*, 2011; Pineda-García *et al.*, 2011; Hasselquist *et al.*, 2010). De igual forma, los lugares situados en cerros, ya sea en la cima o en la pendiente, tienen una menor disponibilidad de agua en el suelo que los lugares ubicados en valles, pues por gravedad el líquido se mueve hacia las partes más

bajas (Markesteijn *et al.*, 2010; Gallardo-Cruz *et al.*, 2009; Becker *et al.*, 1988). Estas condiciones, tanto en las parcelas jóvenes como en los cerros, pueden llegar a ser severas, y producir una diferenciación de nicho que permita el establecimiento de distintos grupos de especies en cada ambiente (Chazdon *et al.*, 2010; Kraft *et al.*, 2008; Valencia *et al.*, 2004). En el sitio de estudio, se confirmó mediante un modelo multinomial basado en la estimación de las abundancias relativas de las especies, que al inicio de la sucesión en este bosque coexisten especialistas de bosque joven (< 15 años), de sitios planos y generalistas.

Se confirmó sólo parcialmente la hipótesis de que las especialistas de bosques jóvenes y cerros presentarían caracteres funcionales de hojas y tallos asociados con la evitación o con la tolerancia a la sequía, y que las especialistas de bosques viejos y sitios planos presentarían caracteres asociados con ambientes más mésicos (hipótesis b). En realidad, los grupos de especialistas más similares entre sí fueron los de bosque joven y sitios planos por un lado, y los grupos de especialistas de bosque viejo y cerros por el otro (Figura 2.1, capítulo 2).

Las plantas especialistas de bosque joven, de forma similar a lo descrito previamente en otros bosques secos (Pineda-García *et al.*, 2013; Lebrija-Trejos *et al.*, 2010a; Sobrado, 1993), mostraron caracteres primordialmente asociados al control de la temperatura en hojas mediante el movimiento a través de pulvinos, y a evitar el embolismo mediante la pérdida de hojas durante la sequía (capítulo 2), lo cual en otros trabajos se ha descrito que ocurre cuando el potencial hídrico en la planta alcanza niveles tan bajos que ponen en riesgo su integridad (Sobrado, 1993; Reich y Borchert, 1984). Las especies especialistas de sitios planos únicamente se distinguieron por tener hojas deciduas. El reducido número de caracteres altamente eficientes en las primeras etapas sucesionales (pulvinos, foliolos reducidos, hábito deciduo) explica porqué el índice de Divergencia Funcional de los briznales en parcelas jóvenes e intermedias (3 a 10 y 11 a 25 años de edad respectivamente) mostró valores más negativos de lo esperado por azar (capítulo 3), lo cual sugiere la dominancia de un reducido número de estrategias funcionales.

Las especies generalistas no mostraron una posición funcional intermedia entre las especialistas de bosque joven o de cerros y las especialistas de bosque maduro o de sitios planos, ni son más similares a las primeras (contrariamente a lo esperado en la

hipótesis c). Aunque las especies generalistas son altamente variables funcionalmente, con un número de combinaciones de caracteres propios de todos los grupos de especialistas, la mayoría fueron más similares a las especialistas de cerros y de bosque tardío. A pesar de eso, son mucho más abundantes en edades sucesionales tempranas que las especies clasificadas como especialistas de bosque joven. De esta forma los 13 caracteres funcionales empleados no resultaron suficientes o relevantes para comprender el éxito (en términos de abundancia) de estas especies, probablemente porque no se relacionan con procesos como la reproducción (las generalistas se han descrito como especies de alta fecundidad, y con dispersión y polinización abiótica; Wiegmann y Waller, 2006; McKinney y Lockwood, 1999) y la adquisición y almacenamiento de recursos subterráneos.

Algunos estudios han establecido que, en bosques secos en los que las condiciones durante la época de sequía son altamente estresantes, la sombra producida por el crecimiento de la vegetación (por hojas de especies perennes y por ramas de especies deciduas) representa un elemento facilitador para la supervivencia de las plántulas de bosque tardío durante la época seca (Lebrija-Trejos *et al.*, 2010b; McLaren y McDonald, 2003b; Gerhardt, 1996). Sin embargo, el análisis de diversidad funcional (capítulo 3) mostró el efecto del filtrado ambiental en los brizales en todas las edades de sucesión. Aunque el menor efecto negativo del ambiente ocurre en etapas iniciales de la sucesión, los valores negativos de la divergencia funcional (FDiv) en esas edades también muestran que hay condiciones ambientales favoreciendo sólo ciertas combinaciones de caracteres, pues este índice muestra que las especies son más similares de lo esperado por el azar. También se detectaron procesos de competencia en los brizales en las edades más tempranas de sucesión, lo que indica que mientras los filtros ambientales restringen las estrategias funcionales, los procesos competitivos limitan la similitud entre las especies que sobreviven a esos filtros. Esta competencia pudiera asociarse con una alta densidad de individuos jóvenes que ocurre en esta fase (Dupuy *et al.*, 2012a).

La riqueza funcional (FRic) de los árboles adultos (significativamente superior de lo esperado por azar) mostró que las condiciones de las parcelas de edades sucesionales jóvenes e intermedias, que comprenden edades de 3 a 25 años, son las más favorables para la coexistencia del máximo número de estrategias funcionales en esta fase ontogénica. El análisis de especialistas y generalistas (capítulo 2) mostró que es en el

rango de 9 a 15 años de edad sucesional cuando coexisten especies generalistas, tardías y pioneras, lo que explicaría la mayor riqueza funcional. Estos patrones son similares a lo que se esperarían bajo la hipótesis del disturbio intermedio (Connell, 1978).

A medida que continúa el desarrollo de la vegetación, las condiciones se tornan más húmedas y menos soleadas (Pineda-García *et al.*, 2013; Lebrija-Trejos *et al.*, 2011), y las especies más dominantes son las generalistas y las especialistas de bosque maduro y cerros (capítulo 2). Estas últimas (las especialistas) se caracterizan por tener hojas perennes, lo que las asocia con una estrategia de captura de recursos lenta *sensu* Reich 2014, y su conservación por un tiempo mayor (Sobrado, 1993), pero con múltiples variaciones en las combinaciones de otros caracteres. Esto conduce a pensar que las estrategias de estas especies varían entre aquellas que evitan la sequía (por ejemplo mediante raíces profundas o mediante el almacenamiento de agua en sus tejidos, lo que les permitiría desacoplar transitoriamente su estado hídrico comparado con el del suelo; Pineda-García *et al.*, 2013) y las tolerantes a la sequía (con alta densidad de madera, asociada con el mantenimiento del funcionamiento de la planta a bajos potenciales hídricos y con una alta resistencia a la cavitación; Méndez-Alonso *et al.*, 2012a; Markesteijn *et al.*, 2011; Maherli *et al.*, 2004).

Con el análisis de diversidad funcional (capítulo 3) se obtuvo que el efecto negativo del ambiente en el establecimiento o persistencia de las especies (o filtrado ambiental) es mayor en esta etapa de la sucesión (i. e. tardía) aunque sólo para los brizales (mediante un valor de FRic menor del que se esperaría por azar) tanto en sitios planos como en cerros (Figure 3.2a). En consecuencia, se comprobó el efecto de filtros ambientales en los cerros (hipótesis e), pero no en las primeras etapas sucesionales. También se corroboró la mayor susceptibilidad de los brizales a condiciones desfavorables en comparación con los adultos (hipótesis f). La disminución de la FRic de brizales en edades avanzadas de la sucesión puede deberse a que, a medida que continúa el desarrollo de la vegetación, la demanda de agua se incrementa y la disminución del potencial hídrico del suelo superficial obedece ya no a la evaporación como en fases iniciales, sino a la transpiración (Lebrija-Trejos *et al.*, 2010a; Marthews *et al.*, 2008). La luz también es un recurso limitante a medida que se desarrolla la vegetación con el tiempo (Buzzard *et al.*, 2015; Alvarez-Añorve *et al.*, 2012), a pesar de que se ha descrito como un factor menos importante porque los bosques más secos tienen una mayor apertura del dosel y es un recurso

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variable espacial y temporalmente (Lebrija-Trejos *et al.*, 2011; Huante y Rincón, 1997). Sin embargo, el área de estudio es un bosque subcaducifolio (es decir, en el extremo menos seco de los bosques estacionales), en el que un estudio reciente del microambiente muestró que durante la época de lluvias la densidad de flujo de fotones disminuye drásticamente a alturas del dosel de 3.5 y 1.5 m (de la Rosa-Manzano *et al.*, 2015), sugiriendo que la luz puede ser un filtro importante para los brizales. Lo anterior permite suponer que, contrariamente a lo esperado, en este bosque las condiciones más limitantes para las plantas jóvenes ocurren en rodales de edad sucesional avanzada, tanto en sitios planos como en cerros. No puede descartarse además, que los bajos valores de riqueza funcional de brizales en edades avanzadas reflejen también diferencias en habilidad competitiva de las especies y no sólo del filtrado ambiental (ver sección 1.1.2; Mayfield y Levine, 2010).

Por otra parte, se esperaba que los procesos de competencia (observados como una alta divergencia y equitatividad funcional) serían más importantes en edades sucesionales intermedias y tardías y en brizales, debido a que la competencia por recursos limitantes como el agua podría incrementarse con el mayor desarrollo de raíces finas de individuos cada vez de mayor tamaño (hipótesis f y g). Sin embargo, no se encontraron indicios de competencia en esas etapas de la sucesión ni en brizales ni en adultos (figura 3.2 e, f). Al parecer las condiciones más adversas para los adultos ocurren en las edades sucesionales más avanzadas en cerros, pues se obtuvieron especies funcionalmente más similares de lo esperado por azar en esa posición topográfica (bajos valores de FDiv). Como ya se mencionó antes, probablemente la competencia por el agua en este bosque ocurra por diferencias en jerarquía competitiva, lo que sería detectado mediante una reducción en la FRic, y no por exclusión competitiva, lo que se reflejaría en una mayor FEve (Mayfield y Levine, 2010). También es posible que los caracteres funcionales asociados más directamente con la competencia por agua, como los de raíces, no fueron considerados en los análisis (Craine y Dybzinski, 2013)

## 5.2 DIFERENCIACIÓN FUNCIONAL DE LAS ESPECIES EN LA ESCALA LOCAL Y DE PAISAJE

Múltiples asociaciones de caracteres funcionales y disyuntivas se han descrito como parte de los mecanismos que permiten la coexistencia de las especies vegetales (Reich, 2014;

Wright *et al.*, 2010, 2004; Chave *et al.*, 2009). En lo que se refiere a la economía de los recursos de las plantas (como el agua, la luz o los nutrientes), algunas de esas asociaciones forman un espectro o eje de variación alrededor de 4 elementos clave: las hojas, el tallo, las raíces y las semillas. Con la finalidad de analizar la variación conjunta entre pares de caracteres funcionales asociados con las hojas, el tallo, y las semillas, y compararla tanto en la escala de paisaje (entre parcelas) como en la local (dentro de las parcelas), se utilizó el método del Análisis del Gradiente de Caracteres (Trait Gradient Analysis, TGA, capítulo 4) (Ackerly y Cornwell, 2007).

Teóricamente, las limitantes en la dispersión, el filtrado ambiental o la exclusión competitiva a lo largo del gradiente considerado (en este caso entre parcelas de diferente edad de sucesión y posición topográfica) producirían un recambio de estrategias funcionales, lo que sería capturado en el TGA como un gradiente de los caracteres funcionales a escala de paisaje (en unidades de cada carácter, no en unidades geográficas) (Ackerly y Cornwell, 2007). Analizando las correlaciones de los valores beta, que representan el promedio del gradiente en donde cada especie es más abundante, se puede inferir si existe co-variación entre pares de caracteres funcionales y por tanto un recambio funcional en ejes de variación específicos. En este trabajo, se buscaba encontrar correlaciones de caracteres que mostraran el recambio de especies de una estrategia conservadora en parcelas jóvenes a una estrategia adquisitiva de recursos en parcelas de edad más avanzada (hipótesis i). Contrariamente a lo esperado, se encontraron escasas correlaciones de valores beta. Es muy posible que los largos períodos de manejo de la vegetación hayan favorecido especies generalistas capaces de establecerse en la mayor parte del gradiente ambiental, debido a disturbios continuos a una escala local que permitan la coexistencia de estrategias de crecimiento rápido, lento e intermedio en todas las edades sucesionales (capítulo 2).

Sin embargo, no fue posible probar esta hipótesis por la ausencia de vegetación que realmente pudiera considerarse “madura” como referencia. No puede descartarse además otra posibilidad importante: el método de TGA se ha utilizado para analizar el recambio funcional en áreas con una fuerte diferenciación ambiental y de tipos de vegetación (Kooyman *et al.*, 2010; Ackerly y Cornwell, 2007). Así, el gradiente ambiental del paisaje en el área de estudio puede ser muy poco contrastante, lo que también explicaría que la mayoría de las especies sean capaces de establecerse en cualquier sitio, y la escasa

relación entre las variables edáficas y de edad sucesional con los valores promedio de los caracteres por parcela (Figura 4.3). Tampoco puede descartarse la capacidad de las especies de plantas de establecerse y sobrevivir en ambientes subóptimos. Un estudio previo en bosque seco ha mostrado que las plántulas de especies pioneras y tardías no muestran una diferenciación clara a lo largo del eje de variación funcional de explotación de agua-tolerancia a la sequía, lo que sugiere que el gradiente de disponibilidad de agua entre sitios de diferente edad de sucesión no es suficiente para filtrar estrategias fisiológicas con un uso diferencial de la misma (Pineda-García *et al.*, 2015). Hallazgos parecidos fueron descritos para un área de 400 Km<sup>2</sup> de bosque tropical húmedo del Amazonas, en donde el 88% de las especies se describieron como generalistas, pues eran capaces de establecerse en tres tipos de vegetación y dos etapas sucesionales (Pitman *et al.*, 1999). Sin embargo, cuando esas mismas especies fueron analizadas en un área de 160, 000 Km<sup>2</sup>, las especies respondieron claramente a gradientes climáticos y del suelo (Toledo *et al.*, 2012). Este último trabajo mostró que las especies de plantas son capaces de distribuirse en condiciones subóptimas, pero es posible capturar sus preferencias por condiciones ambientales particulares cuando se analiza el factor ambiental adecuado a la escala correcta (Toledo *et al.*, 2012). Esto indica que es probable que las especies aparentemente generalistas en el área de estudio de este trabajo, que son la mayoría, pudieran ser especialistas al considerar un gradiente ambiental en extensiones geográficas más amplias.

Los resultados del TGA también sugieren que en este bosque la co-variación de caracteres funcionales que ocurre dentro de las parcelas puede ser igual o más fuerte que la que podría esperarse entre diferentes edades de sucesión o posiciones topográficas (es decir, entre parcelas, contrariamente a lo esperado en la hipótesis j). Estudios previos han demostrado patrones similares (De Bello *et al.*, 2009; Pavoine y Dolédec, 2005; Westoby *et al.*, 2002). Westoby y coautores (2002) propusieron que tal patrón puede ser producido por tres procesos: a) una heterogeneidad ambiental local muy amplia; b) procesos de inmigración de lugares con condiciones distintas, o, mucho más probable, c) algún proceso denso-dependiente como el efecto de almacenamiento (“storage effect”), en el que la variación temporal y espacial de las condiciones favorables permite un reclutamiento diferenciado en tiempo y espacio para especies con estrategias divergentes, además de una alterancia entre la importancia de la competencia intra vs

interespecífica, lo cual permite el mantenimiento de la diversidad a lo largo del tiempo (Chesson, 2000).

### **5.3 CONCLUSIONES Y PERSPECTIVAS**

#### **5.3.1 Conclusiones**

Los principales hallazgos de este estudio son:

1. Se analizaron los caracteres funcionales y las diferencias funcionales entre estrategias ecológicas de plantas leñosas incluyendo no sólo a especies especialistas, sino también (por primera vez en bosques secos) a las generalistas, que tienen una gran importancia en los bosques sometidos a procesos recurrentes de disturbio como los de la Península de Yucatán. Se determinó que las especies generalistas tienden a mostrar caracteres funcionales más similares a los de las especies tardías.
2. Como en otros bosques secos, en las fases iniciales de la sucesión las condiciones de alta irradiancia, alta temperatura del suelo y del aire y alta demanda evaporativa, favorecen caracteres funcionales asociados con la disminución de la pérdida de agua por transpiración y el fotodaño en las especies especialistas de bosque joven. Estas especies difieren de las generalistas en que tienen mayor área foliar específica, una unidad mínima fotosintética reducida y la presencia de pulvinos, mientras que difieren de las especialistas de bosque viejo en el hábito deciduo en las primeras.
3. Contrariamente a lo señalado en otros bosques secos, los procesos de filtrado ambiental afectan a los brizales durante toda la sucesión, pero incrementan fuertemente hacia las fases tardías, donde aparentemente las condiciones son más mésicas. En los adultos, las condiciones más desfavorables ocurren únicamente en edades tardías sobre cerros. Es probable que el principal filtro esté asociado con una desecación del suelo mediante la transpiración para los brizales, y a una menor disponibilidad de agua relacionada a la posición topográfica en los adultos, aunque en ambos casos no puede descartarse un posible efecto de la disminución de la luz.

4. Se detectaron efectos de competencia en edades tempranas de la sucesión sólo para los brizales. Sin embargo, no puede descartarse que la reducción en la riqueza funcional en brizales y adultos también muestre procesos de competencia, pues la exclusión competitiva entre especies que difieren en jerarquía competitiva también produce una reducción en el rango multivariado de los caracteres funcionales.
5. La fase regenerativa mostró ser más susceptible al filtrado ambiental y a la competencia que los adultos. Esto sugiere que los adultos tienen una mayor capacidad para competir y para afrontar peligros tales como la baja disponibilidad de recursos, daños mecánicos o el ataque de herbívoros.
6. Mediante el análisis de gradientes de caracteres, se observó que las diferencias funcionales son mayores al interior de las parcelas que entre ellas. Esto sugiere que procesos denso-dependientes, inmigración, la heterogeneidad ambiental local o el disturbio recurrente definen de forma más importante el funcionamiento de estas comunidades que el gradiente sucesional o topográfico.

### 5.3.2 Perspectivas

De acuerdo con los resultados de este estudio, se requieren varias aproximaciones de investigación adicionales para poder entender la diferenciación funcional descrita en este bosque, ya sea a nivel de estrategias ecológicas, de diversidad funcional o de covariación de caracteres a diferentes escalas:

- Micro y meso ambiente. Es necesario hacer una caracterización fina de por lo menos dos recursos que al parecer son los más relevantes en este sistema: la disponibilidad de agua en el suelo y la luz. Conocer cómo es la variación del contenido volumétrico del agua y el potencial hídrico en el suelo a diferentes profundidades, tanto en sitios planos como en laderas, o la medición mediante isótopos estables de la profundidad a la cual las especies adquieren el agua, podría ser de gran utilidad para entender la manera en la que se reparte este recurso (Kulmatiski y Beard, 2013). Además, conocer cómo difiere la disponibilidad de la luz localmente y en diferentes edades de sucesión y posiciones topográficas podría ayudar a explicar los patrones de filtrado ambiental descritos para los brizales, o el incremento de la riqueza funcional de los adultos. También

permitiría dilucidar si lo que está produciendo la diferenciación funcional dentro de las comunidades se relaciona con la heterogeneidad de recursos a escala local, o si otros procesos denso-dependientes son los que influyen en la diversidad funcional en este sistema.

- La inclusión de caracteres funcionales asociados al aprovechamiento de recursos subterráneos también es un elemento clave para entender este ecosistema. Si los patrones de filtrado ambiental en edades sucesionales jóvenes y tardías están relacionados con la capacidad de las plantas de apropiarse del recurso agua y limitar su disponibilidad a plantas vecinas (“preemption”), la competitividad de las especies podría depender de la longitud o densidad de las raíces, o de su distribución vertical (Craine y Dybzinski, 2013; Querejeta *et al.*, 2007).
- Debido a que el rebrote se ha considerado como un carácter funcional que es clave en la regeneración de los bosques secos (McLaren y McDonald, 2003a), es necesario investigar si tiene un papel relevante en el ensamblaje de las comunidades. Por ejemplo, si el reclutamiento de briznas de especies tardías en parcelas jóvenes está dado por este mecanismo; si el rebrote permite el crecimiento de las especies en ambientes que serían poco propicios para la regeneración por semilla o si se asocia con algún grupo particular de plantas (i.e. con cierta estrategia funcional) o es una característica generalizada.
- El análisis de la diversidad funcional sugirió que el filtrado ambiental es un proceso de ensamblaje importante en plantas de menor tamaño. El uso de índices con múltiples caracteres impide saber cuáles son los que están teniendo un papel más importante, e incluso podrían obscurecer patrones que se detectan en análisis de caracteres individuales (Bhaskar *et al.*, 2014). Por esto, es necesario hacer un análisis de la diversidad funcional de los caracteres más importantes por separado, lo que permitiría una mejor comparación con estudios previos en otros sistemas. También sería de utilidad analizar la variación de la diversidad funcional para los grupos de plantas con estrategia similar (i.e. especialistas y generalistas), pues sus procesos de ensamblaje difieren en diferentes etapas de la sucesión (Lebrija-Trejos *et al.*, 2010b).
- El papel del disturbio es otro tema importante por analizar. Aunque difícilmente puede medirse plenamente su impacto porque la vegetación más antigua de la

región no podría considerarse prístina (dada la larga historia de ocupación de la Península y del área de estudio), sí pueden practicarse diferentes tipos de disturbio o de daño controlado (o monitorear el que ya existe) para evaluar su efecto en las especies y la relación entre su estrategia funcional con su capacidad de recuperación. También puede analizarse la capacidad de recuperación a nivel de las comunidades. Sin embargo, permanecerá como una incógnita si las actividades humanas han seleccionado durante milenios las especies capaces de establecerse en amplios rangos ambientales, y si esto ha influido en la similitud entre comunidades del bosque en la Península.

**CAPÍTULO 6.**  
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**CAPÍTULO 7.**  
**ANEXOS**

**Appendix 7.1** Mean canopy height per successional age category and mean height of trees included in our analysis per size.

Tree size	Successional age category	Topographical position	Canopy height (m) <sup>1</sup>	SD	Tree species mean height (m)	SD
Small	1	Flat	7.32	1.64	3.97	0.59
	2	Flat	10.22	1.65	4.32	0.57
	3	Flat	11.86	1.76	4.33	0.75
	2	Hill	9.84	1.73	4.5	0.72
	3	Hill	10.36	1.97	4.32	0.57
Large	1	Flat	7.32	1.64	6.41	1.06
	2	Flat	10.22	1.65	7.93	1.01
	3	Flat	11.86	1.76	8.8	0.93
	2	Hill	9.84	1.73	7.74	1.04
	3	Hill	10.36	1.97	7.84	1.19

<sup>1</sup>Average of the 10 largest individuals per plot.

**Appendix 7.2** Total species richness and species included per plot.

Plot	Successional age category	Topography	Age	Total species				Plot				Successional age category				Topography			
				Total species small	Tree species included small	%species included small	Total species large	Tree species included large	%species included large	Total species small	Tree species included small	%species included small	Total species large	Tree species included large	%species included large	Total species small	Tree species included small	%species included small	Total species large
101	1	Flat	10	5	4	80	15	12	80	1601	1	Flat	8	9	6	66.67	12	11	91.67
102	1	Flat	7	4	4	100	8	7	87.5	1602	3	Flat	50	4	4	100	8	7	87.5
103	3	Flat	60	8	6	75	10	7	70	1603	3	Hill	40	7	6	85.71	11	10	90.91
104	3	Hill	30	12	9	75	80	13	72.22	1604	1	Flat	5	3	3	100	1	1	100
105	3	Hill	40	5	4	80	20	14	70	1605	3	Hill	40	4	3	75	17	14	82.35
106	3	Flat	40	4	4	100	13	10	76.92	1606	1	Flat	8	4	4	100	4	4	100
107	2	Hill	20	5	5	100	17	17	100	1607	1	Flat	9	6	6	100	4	4	100
108	1	Flat	7	6	5	83.33	6	5	83.33	1608	3	Hill	40	7	6	85.71	15	15	100
109	3	Flat	60	5	5	100	13	9	69.23	1609	2	Flat	12	3	3	100	9	9	100
201	2	Flat	12	6	6	100	10	10	100	1701	3	Flat	60	9	5	55.56	14	12	85.71
202	2	Flat	20	6	5	83.33	8	7	87.5	1702	2	Flat	4	3	75	8	8	100	
203	3	Hill	40	8	7	87.5	14	13	92.86	1703	3	Hill	40	6	6	100	11	10	90.91
204	2	Flat	13	2	1	50	7	7	100	1704	1	Flat	8	7	7	100	5	5	100
205	2	Flat	13	1	1	100	8	8	100	1705	1	Flat	10	8	6	75	8	8	100
206	3	Flat	40	3	2	66.67	7	6	85.71	1706	3	Flat	70	3	3	100	8	8	100
207	1	Flat	8	7	5	71.43	4	4	100	1707	3	Hill	30	11	6	54.55	11	11	100
208	1	Flat	8	4	3	75	5	4	80	1708	1	Flat	6	8	6	75	4	4	100
209	2	Hill	20	8	6	75	14	14	100	1709	1	Flat	10	3	2	66.67	4	4	100
301	1	Flat	10	4	2	50	8	7	87.5	1801	3	Hill	40	9	7	77.78	12	12	100
302	1	Flat	10	3	3	100	6	6	100	1802	3	Hill	45	4	4	100	19	16	84.21
303	2	Hill	20	8	6	75	10	6	60	1803	3	Flat	60	6	4	66.67	10	9	90
304	2	Hill	20	14	13	92.86	7	7	100	1804	3	Flat	30	7	7	100	9	8	88.89

## ANEXOS

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305	1	Flat	6	9	8	88.89	8	4	50	1805	3	Flat	60	4	4	100	9	8	88.89
306	2	Flat	25	11	6	54.55	14	11	78.57	1806	3	Hill	60	2	1	50	11	9	81.82
307	1	Flat	8	5	5	100	7	6	85.71	1807	3	Flat	50	2	1	50	10	9	90
308	2	Flat	25	15	12	80	15	14	93.33	1808	3	Hill	40	4	3	75	13	13	100
309	2	Flat	25	8	7	87.5	18	17	94.44	1809	3	Flat	50	5	4	80	10	10	100
401	2	Flat	12	8	6	75	11	11	100	1901	3	Flat	30	3	3	100	9	9	100
402	3	Flat	50	7	5	71.43	13	12	92.31	1902	2	Hill	20	2	2	100	16	14	87.5
403	3	Hill	50	6	5	83.33	18	15	83.33	1903	3	Flat	30	7	5	71.43	13	13	100
404	3	Flat	50	6	5	83.33	9	9	100	1904	1	Flat	8	5	4	80	3	3	100
405	3	Flat	50	6	5	83.33	17	15	88.24	1905	2	Flat	12	4	3	75	7	7	100
406	3	Flat	50	10	9	90	11	11	100	1906	1	Flat	9	9	6	66.67	8	6	75
407	3	Hill	50	10	8	80	13	12	92.31	1907	2	Hill	20	10	7	70	13	10	76.92
408	3	Flat	50	4	2	50	14	13	92.86	1908	1	Flat	7	7	5	71.43	4	4	100
409	3	Hill	50	6	5	83.33	15	14	93.33	1909	1	Flat	7	5	3	60	5	5	100
501	3	Hill	60	6	5	83.33	15	12	80	2001	2	Hill	25	7	7	100	15	14	93.33
502	3	Hill	60	10	8	80	15	13	86.67	2002	1	Flat	5	7	6	85.71	2	2	100
503	1	Flat	10	9	8	88.89	13	11	84.62	2003	2	Flat	15	6	4	66.67	8	7	87.5
504	2	Flat	12	15	13	86.67	11	10	90.91	2004	1	Flat	3	8	6	75	1	1	100
505	1	Flat	6	14	13	92.86	4	4	100	2005	1	Flat	10	4	1	25	8	7	87.5
506	3	Hill	60	10	10	100	17	14	82.35	2006	3	Hill	35	10	6	60	9	9	100
507	3	Hill	60	11	9	81.82	19	16	84.21	2007	3	Hill	35	6	4	66.67	13	12	92.31
508	3	Flat	60	8	6	75	17	14	82.35	2008	1	Flat	10	8	5	62.5	8	5	62.5
509	1	Flat	10	14	12	85.71	7	7	100	2009	2	Flat	25	8	7	87.5	13	12	92.31
601	1	Flat	5	8	7	87.5	4	3	75	2010	2	Hill	20	7	6	85.71	15	14	93.33
602	2	Flat	15	6	5	83.33	7	6	85.71	2011	3	Flat	40	4	3	75	10	10	100
603	2	Flat	18	5	3	60	12	11	91.67	2012	2	Flat	20	7	5	71.43	13	12	92.31
604	2	Hill	18	10	8	80	10	9	90	2101	3	Flat	30	6	6	100	14	13	92.86
605	1	Flat	6	15	12	80	6	5	83.33	2102	2	Flat	14	9	9	100	13	13	100
606	3	Flat	30	13	11	84.62	13	12	92.31	2103	2	Flat	14	3	2	66.67	9	8	88.89

## ANEXOS

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607	1	Flat	7	4	4	100	2	2	100	2104	2	Hill	20	6	6	100	13	13	100
608	2	Hill	20	8	7	87.5	11	9	81.82	2105	1	Flat	9	8	8	100	14	14	100
609	2	Flat	20	12	10	83.33	12	10	83.33	2106	2	Hill	20	7	6	85.71	16	15	93.75
701	2	Hill	20	9	7	77.78	12	12	100	2107	3	Hill	40	10	7	70	15	14	93.33
702	2	Hill	20	8	5	62.5	17	14	82.35	2108	3	Flat	40	9	7	77.78	15	12	80
703	1	Flat	7	5	5	100	4	4	100	2109	3	Flat	35	10	8	80	12	11	91.67
704	2	Flat	16	3	2	66.67	15	14	93.33	2201	1	Flat	8	9	7	77.78	7	5	71.43
705	2	Hill	16	10	8	80	15	13	86.67	2202	1	Flat	8	8	5	62.5	7	6	85.71
706	1	Flat	7	12	11	91.67	9	9	100	2203	2	Flat	20	3	2	66.67	8	8	100
707	2	Flat	14	8	8	100	15	14	93.33	2204	1	Flat	7	3	2	66.67	0	0	ND
708	2	Hill	16	11	10	90.91	9	8	88.89	2205	1	Flat	7	4	2	50	0	0	ND
709	2	Flat	17	9	8	88.89	14	14	100	2206	1	Flat	10	10	9	90	11	10	90.91
801	1	Flat	7	12	11	91.67	6	6	100	2207	1	Flat	7	4	4	100	3	3	100
802	2	Flat	12	11	9	81.82	11	10	90.91	2208	1	Flat	10	12	10	83.33	7	7	100
803	2	Flat	25	9	6	66.67	13	12	92.31	2209	1	Flat	7	10	9	90	2	2	100
804	2	Hill	17	8	7	87.5	17	15	88.24	2301	3	Flat	50	11	9	81.82	12	11	91.67
805	2	Flat	15	14	12	85.71	14	11	78.57	2302	3	Hill	50	5	5	100	13	13	100
806	1	Flat	10	2	2	100	7	5	71.43	2303	3	Flat	60	10	7	70	12	12	100
807	1	Flat	5	5	3	60	1	1	100	2304	2	Flat	15	5	4	80	11	11	100
808	3	Flat	30	2	2	100	7	7	100	2305	2	Flat	15	3	2	66.67	10	9	90
809	2	Flat	15	10	8	80	11	10	90.91	2306	2	Flat	15	6	5	83.33	10	10	100
901	1	Flat	10	7	5	71.43	5	5	100	2307	2	Flat	15	6	6	100	11	10	90.91
902	2	Flat	16	4	3	75	14	14	100	2308	3	Hill	30	10	8	80	22	19	86.36
903	2	Flat	20	4	3	75	13	13	100	2309	3	Flat	60	9	6	66.67	12	10	83.33
904	1	Flat	4	8	7	87.5	4	2	50	3010	2	Hill	20	7	6	85.71	7	7	100
905	1	Flat	10	6	5	83.33	15	12	80	3011	1	Flat	10	3	2	66.67	7	6	85.71
906	2	Flat	15	4	4	100	7	7	100	3012	1	Flat	8	4	3	75	10	9	90
907	2	Flat	20	5	4	80	11	10	90.91	4010	3	Hill	50	5	4	80	16	15	93.75
908	2	Flat	15	6	5	83.33	14	14	100	4011	3	Flat	50	6	4	66.67	9	8	88.89

## ANEXOS

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909	1	Flat	8	5	4	80	8	8	100	4012	3	Flat	50	4	4	100	11	10	90.91
1001	3	Hill	30	15	11	73.33	18	16	88.89	5010	1	Flat	10	14	11	78.57	11	11	100
1002	1	Flat	10	6	6	100	8	8	100	5011	1	Flat	8	10	9	90	5	5	100
1003	2	Flat	18	12	11	91.67	12	12	100	5012	1	Flat	6	8	7	87.5	3	3	100
1004	3	Hill	30	10	9	90	15	14	93.33	6010	1	Flat	10	11	9	81.82	10	8	80
1005	1	Flat	6	6	5	83.33	6	6	100	6011	2	Hill	13	10	9	90	14	14	100
1006	2	Hill	20	8	7	87.5	16	14	87.5	6012	2	Flat	13	1	1	100	8	8	100
1007	3	Flat	30	12	10	83.33	16	15	93.75	7010	2	Flat	16	7	7	100	16	15	93.75
1008	2	Flat	11	5	5	100	15	12	80	7011	3	Flat	40	7	5	71.43	8	7	87.5
1009	1	Flat	8	7	6	85.71	6	5	83.33	7012	1	Flat	6	11	10	90.91	6	5	83.33
1010	3	Flat	30	5	4	80	10	7	70	8010	2	Flat	20	7	4	57.14	4	3	75
1011	1	Flat	6	8	7	87.5	5	3	60	8011	1	Flat	4	13	13	100	6	6	100
1012	1	Flat	6	4	4	100	8	7	87.5	8012	1	Flat	8	14	12	85.71	9	8	88.89
1101	2	Flat	11	2	2	100	8	8	100	9010	2	Flat	14	4	4	100	8	8	100
1102	2	Hill	20	9	8	88.89	16	13	81.25	9011	1	Flat	10	4	4	100	15	12	80
1103	1	Flat	10	8	8	100	9	9	100	9012	2	Flat	20	2	2	100	7	6	85.71
1104	2	Hill	18	7	5	71.43	10	10	100	10010	2	Flat	20	7	7	100	14	14	100
1105	3	Flat	35	4	3	75	12	12	100	10011	1	Flat	7	7	6	85.71	7	6	85.71
1106	1	Flat	10	8	8	100	10	8	80	10012	2	Flat	25	9	7	77.78	14	12	85.71
1107	2	Flat	20	4	2	50	11	9	81.82	11010	1	Flat	10	5	4	80	8	8	100
1108	2	Flat	20	7	5	71.43	14	12	85.71	11011	1	Flat	10	5	5	100	10	8	80
1109	1	Flat	9	2	2	100	8	8	100	11012	1	Flat	9	5	5	100	6	6	100
1201	3	Flat	40	8	6	75	9	9	100	12010	2	Flat	15	2	2	100	8	7	87.5
1202	1	Flat	10	4	3	75	9	8	88.89	12011	3	Flat	35	3	3	100	12	12	100
1203	1	Flat	6	5	4	80	1	1	100	12012	3	Flat	40	6	2	33.33	9	5	55.56
1204	1	Flat	8	4	3	75	4	4	100	13010	1	Flat	10	7	6	85.71	9	9	100
1205	2	Hill	16	7	6	85.71	7	6	85.71	13011	2	Flat	25	8	4	50	16	14	87.5
1206	2	Hill	20	14	11	78.57	18	17	94.44	13012	2	Hill	16	13	11	84.62	7	7	100
1207	3	Flat	60	9	7	77.78	17	17	100	14010	1	Flat	6	7	6	85.71	3	3	100

1208	2	Hill	16	5	5	100	14	12	85.71	14011	1	Flat	9	9	8	88.89	10	9	90
1209	1	Flat	10	2	2	100	7	7	100	14012	1	Flat	6	4	4	100	9	9	100
1301	2	Flat	25	7	5	71.43	8	6	75	15010	2	Flat	25	6	5	83.33	16	13	81.25
1302	2	Hill	17	4	4	100	13	11	84.62	15011	1	Flat	6	8	8	100	6	6	100
1303	2	Hill	20	7	6	85.71	17	16	94.12	15012	1	Flat	10	6	4	66.67	7	7	100
1304	2	Flat	14	8	8	100	14	13	92.86	16010	3	Flat	50	1	1	100	13	12	92.31
1305	1	Flat	10	9	8	88.89	14	12	85.71	16011	1	Flat	10	7	5	71.43	5	5	100
1306	1	Flat	9	3	3	100	9	8	88.89	16012	3	Flat	60	5	2	40	8	8	100
1307	2	Flat	20	10	7	70	9	9	100	17010	3	Hill	40	7	6	85.71	9	8	88.89
1308	2	Flat	16	2	2	100	13	9	69.23	17011	3	Flat	35	4	2	50	7	6	85.71
1309	1	Flat	9	11	10	90.91	13	12	92.31	17012	1	Flat	8	5	5	100	6	6	100
1401	2	Flat	20	3	2	66.67	9	9	100	18010	3	Flat	60	11	7	63.64	12	11	91.67
1402	2	Flat	15	3	3	100	8	8	100	18011	3	Flat	60	5	4	80	12	10	83.33
1403	1	Flat	6	12	9	75	3	3	100	18012	3	Flat	40	3	2	66.67	11	10	90.91
1404	2	Hill	18	8	7	87.5	11	9	81.82	19010	1	Flat	10	8	7	87.5	5	5	100
1405	2	Flat	25	11	9	81.82	15	15	100	19011	2	Hill	25	2	2	100	13	12	92.31
1406	2	Flat	25	8	7	87.5	12	12	100	19012	3	Flat	40	2	2	100	13	11	84.62
1407	2	Flat	18	4	3	75	8	8	100	20010	3	Flat	40	2	2	100	15	13	86.67
1408	2	Flat	12	10	8	80	12	9	75	20011	3	Flat	30	4	2	50	6	6	100
1409	2	Flat	12	8	7	87.5	13	11	84.62	20012	1	Flat	6	5	4	80	1	1	100
1501	2	Hill	25	9	7	77.78	18	15	83.33	21010	2	Flat	20	8	5	62.5	12	11	91.67
1502	3	Hill	30	15	11	73.33	14	13	92.86	21011	1	Flat	8	4	3	75	12	11	91.67
1503	3	Flat	30	5	2	40	10	9	90	21012	3	Flat	30	9	8	88.89	14	12	85.71
1504	2	Flat	12	3	2	66.67	8	7	87.5	22010	1	Flat	10	11	7	63.64	6	5	83.33
1505	1	Flat	10	12	11	91.67	16	16	100	22011	2	Flat	11	13	12	92.31	9	7	77.78
1506	3	Hill	30	8	7	87.5	16	12	75	22012	2	Flat	12	10	8	80	7	6	85.71
1507	3	Flat	50	8	6	75	11	11	100	23010	3	Hill	30	8	6	75	15	12	80
1508	1	Flat	6	9	9	100	5	5	100	23011	3	Flat	35	4	3	75	10	10	100
1509	1	Flat	10	8	7	87.5	11	10	90.91	23012	3	Hill	40	11	10	90.91	15	13	86.67















**Appendix 7.4** Mean leaf area, petiole length and mean seed volume per species.**Mean leaf area and petiole length per species**

Species	Author	Family	Life form	n	Petiole Length (cm)	Leaf Area (cm <sup>2</sup> )
<i>Acacia pennatula</i>	(Schltdl. & Cham.) Benth.	Fabaceae	Tree	5	0.88	0.01
<i>Amphilophium paniculatum var molle</i>	(Schltdl. & Cham.) Standl.	Bignoniaceae	Liana	13	3.16	14.54
<i>Aphelandra scabra</i>	(Vahl) Sm.	Acanthaceae	Shrub	21	0.96	39.47
<i>Arrabidaea pubescens</i>	(L.) A.H. Gentry	Bignoniaceae	Liana	17	3.02	14.31
<i>Bauhinia divaricata</i>	L.	Fabaceae	Shrub	14	2.70	45.41
<i>Bauhinia unguis</i>	L.	Fabaceae	Tree	13	1.81	33.28
<i>Bourreria pulchra</i>	(Millsp.) Millsp.	Boraginaceae	Tree	17	4.78	78.68
<i>Bunchosia swartziana</i>	Griseb.	Malpighiaceae	Shrub	17	0.47	11.84
<i>Bursera simaruba</i>	(L.) Sarg.	Burseraceae	Tree	19	7.14	24.74
<i>Caesalpinia gaumeri</i>	Greenm.	Fabaceae	Tree	16	2.35	2.01
<i>Calyptrotheces pallens</i>	Griseb.	Myrtaceae	Tree	18	0.70	17.25
<i>Cardiospermum corindum</i>	L.	Sapindaceae	Liana	14	2.75	7.75
<i>Chloroleucon mangense</i>	(Jacq.) Britton & Rose	Fabaceae	Tree	8	1.59	0.47
<i>Cnidoscolus aconitifolius</i>	(Mill.) I.M. Johnst.	Euphorbiaceae	Shrub	5	19.12	250.50
<i>Coccocoba acapulcensis</i>	Standl.	Polygonaceae	Tree	11	2.28	37.94
<i>Coccocoba spicata</i>	Lundell	Polygonaceae	Tree	17	2.65	108.78
<i>Cochlospermum vitifolium</i>	(Willd.) Spreng.	Bixaceae	Tree	15	13.83	188.20
<i>Crossopetalum rhacoma</i>	Crantz	Celastraceae	Shrub	12	0.86	21.04
<i>Croton reflexifolius</i>	Kunth	Euphorbiaceae	Tree	16	3.83	60.54
<i>Cydistia diversifolia</i>	(Kunth) Miers	Bignoniaceae	Liana	14	2.61	34.59
<i>Cydistia potosina</i>	(K. Schum. & Loes.) Loes.	Bignoniaceae	Liana	17	1.84	33.15
<i>Dalbergia glabra</i>	(Mill.) Standl.	Fabaceae	Liana	10	1.52	4.84
<i>Diospyros anisandra</i>	S.F. Blake	Ebenaceae	Tree	18	0.25	8.01
<i>Diospyros tetrasperma</i>	Sw.	Ebenaceae	Tree	19	0.45	18.30
<i>Diospyros yucatanensis ssp. yucatanensis</i>	Lundell	Ebenaceae	Tree	26	0.78	14.55
<i>Erythroxylum rotundifolium</i>	Lunan	Erythroxylaceae	Tree	12	0.30	2.77
<i>Eugenia axillaris</i>	(Sw.) Willd.	Myrtaceae	Tree	18	0.34	9.30
<i>Eugenia buxifolia</i>	Lam.	Myrtaceae	Tree	14	0.47	8.14
<i>Exostema caribaeum</i>	(Jacq.) Schult.	Rubiaceae	Tree	15	1.31	14.75
<i>Guettarda elliptica</i>	Sw.	Rubiaceae	Tree	17	0.58	12.77
<i>Gymnopodium floribundum</i>	Rolfe	Polygonaceae	Tree	19	0.34	12.71
<i>Heliocarpus donnellsmithii</i>	Rose	Malvaceae	Tree	13	3.73	57.28
<i>Heteropterys brachiata</i>	(L.) DC.	Malpighiaceae	Liana	10	0.54	14.81
<i>Jatropha gaumeri</i>	Greenm.	Euphorbiaceae	Tree	17	0.89	10.46

<i>Karwinskia humboldtiana</i>	(Schult.) Zucc.	Rhamnaceae	Tree	11	1.39	44.44
<i>Lasianthaea fruticosa</i>	(L.) K.M. Becker	Asteraceae	Shrub	8	3.01	0.51
<i>Leucaena leucocephala</i>	(Lam.) de Wit	Fabaceae	Tree	7	4.63	11.98
<i>Lonchocarpus rugosus</i>	Benth.	Fabaceae	Tree	14	2.52	10.48
<i>Lonchocarpus guatemalensis</i>	Lundell	Fabaceae	Tree	17	1.16	122.36
<i>Luehea speciosa</i>	Willd.	Malvaceae	Tree	14	6.00	0.35
<i>Lysiloma latisiliquum</i>	(L.) Benth.	Fabaceae	Tree	15	0.38	6.57
<i>Machaonia lindeniana</i>	Baill.	Rubiaceae	Tree	13	0.50	12.00
<i>Malpighia glabra</i>	L.	Malpighiaceae	Tree	15	6.48	46.30
<i>Mansoa verrucifera</i>	(Schltdl.) A.H. Gentry	Bignoniaceae	Liana	15	1.27	0.59
<i>Mimosa bahamensis</i>	Benth.	Fabaceae	Tree	15	1.24	19.97
<i>Neea psychotrioides</i>	Donn. Sm.	Nyctaginaceae	Tree	17	2.57	62.37
<i>Neomillspaughia emarginata</i>	(H. Gross) S.F. Blake	Polygonaceae	Tree	13	4.11	20.89
<i>Piscidia piscipula</i>	(L.) Sarg.	Fabaceae	Tree	12	2.14	20.30
<i>Pisonia aculeata</i>	L.	Nyctaginaceae	Liana	15	3.39	45.42
<i>Platymiscium yucatanum</i>	Standl.	Fabaceae	Tree	10	0.45	9.40
<i>Psidium sartorianum</i>	(O. Berg) Nied.	Myrtaceae	Tree	17	0.70	5.62
<i>Randia truncata</i>	Greenm. & C.H. Thomps.	Rubiaceae	Shrub	16	0.36	9.20
<i>Samyda yucatanensis</i>	Standl.	Salicaceae	Shrub	18	0.90	50.59
<i>Semialarium mexicanum</i>	(Miers) Mennega	Celastraceae	Tree	16	7.60	82.00
<i>Senegalia gaumeri</i>	(S.F. Blake) Britton & Rose	Fabaceae	Tree	10	2.69	0.42
<i>Senna atomaria</i>	(L.) H.S. Irwin & Barneby	Fabaceae	Tree	13	5.09	23.33
<i>Senna racemosa</i>	(Mill.) H.S. Irwin & Barneby	Fabaceae	Tree	13	2.90	5.67
<i>Sideroxylon obtusifolium</i>	(Humb. ex Roem. & Schult.) T.D. Penn.	Sapotaceae	Tree	17	0.93	13.69
<i>Tabebuia chrysantha</i> ssp. <i>chrysantha</i>	(Jacq.) G. Nicholson	Bignoniaceae	Tree	10	8.00	30.02
<i>Tabernaemontana alba</i>	Mill.	Apocynaceae	Shrub	15	1.24	37.35
<i>Talisia oliviformis</i>	(Kunth) Radlk.	Sapindaceae	Tree	14	2.60	17.84
<i>Thouinia paucidentata</i>	Radlk.	Sapindaceae	Tree	19	3.03	8.13
<i>Vitex gaumeri</i>	Greenm.	Lamiaceae	Tree	19	8.60	36.32
<i>Ximenia americana</i>	L.	Olacaceae	Shrub	10	0.29	6.82
<i>Zapoteca formosa</i> spp. <i>formosa</i>	(Kunth) H.M. Hern.	Fabaceae	Shrub	9	2.42	3.20

**Mean seed volume per species and sources of information.**

Species	Author	Family	Life form	Seed Volume (cm <sup>3</sup> )	n (individuals)	Source of information
<i>Acacia pennatula</i>	(Schltdl. & Cham.) Benth.	Fabaceae	Tree	0.023	1	Field samples
<i>Amphilophium paniculatum</i> var <i>molle</i>	(Schltdl. & Cham.) Standl.	Bignoniaceae	Liana	0.001		Gentry A. H. (1982) Bignoniaceae. Flora de Veracruz (eds A. Gómez-Pompa & V. Sosa), p 26. Instituto Nacional de Investigaciones sobre Recursos Bióticos. Veracruz, Mexico.
<i>Aphelandra scabra</i>	(Vahl) Sm.	Acanthaceae	Shrub	0.006	3	CICY herbarium
<i>Arrabidaea pubescens</i>	(L.) A.H. Gentry	Bignoniaceae	Liana	0.002	3	CICY herbarium
<i>Bauhinia divaricata</i>	L.	Fabaceae	Shrub	0.049	1	Field samples
<i>Bauhinia unguifolia</i>	L.	Fabaceae	Tree	0.018	1	Field samples
<i>Bourreria pulchra</i>	(Millsp.) Millsp.	Boraginaceae	Tree	0.017	1	Field samples
<i>Bunchosia swartziana</i>	Griseb.	Malpighiaceae	Shrub	0.024		P. A. González Gutiérrez (2010) A revision of Cuban Bunchosia (Malpighiaceae), with description of a new subspecies from Hispaniola. <i>Willdenowia</i> 40(1): 55-61.
<i>Bursera simaruba</i>	(L.) Sarg.	Burseraceae	Tree	0.072	3	Field and CICY herbarium samples
<i>Caesalpinia gaumeri</i>	Greenm.	Fabaceae	Tree	0.113	1	Field samples
<i>Calyptrotheces pallens</i>	Griseb.	Myrtaceae	Tree	0.018	2	Field samples
<i>Cardiospermum corindum</i>	L.	Sapindaceae	Liana	0.026	3	Field samples
<i>Chloroleucon mangense</i>	(Jacq.) Britton & Rose	Fabaceae	Tree	0.049		Flora de Nicaragua (Trópicos): <a href="http://www.tropicos.org/name/13008139?projectid=7">http://www.tropicos.org/name/13008139?projectid=7</a>
<i>Cnidoscolus aconitifolius</i>	(Mill.) I.M. Johnst.	Euphorbiaceae	Shrub	0.054	3	Field samples
<i>Coccoloba acapulcensis</i>	Standl.	Polygonaceae	Tree	0.197	3	Field samples
<i>Coccoloba spicata</i>	Lundell	Polygonaceae	Tree	0.110	2	Field samples
<i>Cochlospermum vitifolium</i>	(Willd.) Spreng.	Bixaceae	Tree	0.020	1	Field samples
<i>Crossopetalum rhacoma</i>	Crantz	Celastraceae	Shrub	0.096	3	Field samples
<i>Cydista diversifolia</i>	(Kunth) Miers	Bignoniaceae	Liana	0.001	1	CICY herbarium
<i>Cydista potosina</i>	(K. Schum. & Loes.) Loes.	Bignoniaceae	Liana	0.037	2	CICY herbarium
<i>Diospyros anisandra</i>	S.F. Blake	Ebenaceae	Tree	0.088	3	Field and CICY herbarium samples
<i>Diospyros tetrasperma</i>	Sw.	Ebenaceae	Tree	0.135	1	CICY herbarium
<i>Diospyros yucatanensis</i> ssp. <i>yucatanensis</i>	Lundell	Ebenaceae	Tree	0.126	2	Field
<i>Erythroxylum rotundifolium</i>	Lunan	Erythroxylaceae	Tree	0.008	1	CICY herbarium
<i>Eugenia axillaris</i>	(Sw.) Willd.	Myrtaceae	Tree	0.084	3	Field samples
<i>Eugenia buxifolia</i>	Lam.	Myrtaceae	Tree	0.065		Flora Mesoamericana (Trópicos)

Species	Author	Family	Life form	Seed Volume (cm <sup>3</sup> )	n (individuals)	Source of information
<i>Guettarda elliptica</i>	Sw.	Rubiaceae	Tree	0.044	3	<a href="http://www.tropicos.org/Name/22101731?projectid=3">http://www.tropicos.org/Name/22101731?projectid=3</a> Field samples
<i>Gymnopodium floribundum</i>	Rolfe	Polygonaceae	Tree	0.001	1	Field samples
<i>Heliocarpus donnellsmithii</i>	Rose	Malvaceae	Tree	0.001	3	Field samples
<i>Jatropha gaumeri</i>	Greenm.	Euphorbiaceae	Tree	0.456	1	Field samples
<i>Karwinskia humboldtiana</i>	(Schult.) Zucc.	Rhamnaceae	Tree	0.051	3	Field samples
<i>Lasianthaea fruticosa</i>	(L.) K.M. Becker	Asteraceae	Shrub	0.0003	1	Field samples
<i>Leucaena leucocephala</i>	(Lam.) de Wit	Fabaceae	Tree	0.017	2	Field samples
<i>Luehea speciosa</i>	Willd.	Malvaceae	Tree	0.004	2	Field samples
<i>Lysiloma latisiliquum</i>	(L.) Benth.	Fabaceae	Tree	0.009	3	Field samples
<i>Machaonia lindeniana</i>	Baill.	Rubiaceae	Tree	0.001	2	Field samples
<i>Malpighia glabra</i>	L.	Malpighiaceae	Tree	0.014	1	Field samples
<i>Mansoa verrucifera</i>	(Schltdl.) A.H. Gentry	Bignoniaceae	Liana	0.072	3	Field and CICY herbarium samples
<i>Mimosa bahamensis</i>	Benth.	Fabaceae	Tree	0.009	1	Field samples
<i>Neea psychotrioides</i>	Donn. Sm.	Nyctaginaceae	Tree	0.026	1	Field samples
<i>Neomillspaughia emarginata</i>	(H. Gross) S.F. Blake	Polygonaceae	Tree	0.004	3	Field samples
<i>Piscidia piscipula</i>	(L.) Sarg.	Fabaceae	Tree	0.013	2	Field samples
<i>Pisonia aculeata</i>	L.	Nyctaginaceae	Liana	0.096		Fay J. F. (1980) Nyctaginaceae. <i>Flora de Veracruz</i> (eds A. Gómez-Pompa & V. Sosa), p 42. Instituto Nacional de Investigaciones sobre Recursos Bióticos. Veracruz, Mexico.
<i>Psidium sartorianum</i>	(O. Berg) Nied.	Myrtaceae	Tree	0.021	3	Field samples
<i>Randia truncata</i>	Greenm. & C.H. Thomps.	Rubiaceae	Shrub	0.223	1	Field samples
<i>Semialarium mexicanum</i>	(Miers) Mennega	Celastraceae	Tree	0.048	3	Field and CICY herbarium samples
<i>Senegalnia gaumeri</i>	(S.F. Blake) Britton & Rose	Fabaceae	Tree	0.015	3	Field samples
<i>Senna atomaria</i>	(L.) H.S. Irwin & Barneby	Fabaceae	Tree	0.019		P. Ubiergo & M. Lapp. (2007) Caracterización morfológica de semillas de algunas especies de los géneros Cassia L. y Senna Mill. (Leguminosae Juss.) <i>Revista de la Facultad de Agronomía</i> 24: 426-441.
<i>Sideroxylon obtusifolium</i>	(Humb. ex Roem. & Schult.) T.D. Penn.	Sapotaceae	Tree	0.123	1	Field samples
<i>Tabebuia chrysantha</i> ssp. <i>chrysantha</i>	(Jacq.) G. Nicholson	Bignoniaceae	Tree	0.001	1	CICY herbarium
<i>Tabernaemontana alba</i>	Mill.	Apocynaceae	Shrub	0.033	1	Field samples
<i>Talisia oliviformis</i>	(Kunth) Radlk.	Sapindaceae	Tree	0.524		G. E. Kantak (1979) <i>Observations on Some Fruit-</i>

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Species	Author	Family	Life form	Seed Volume (cm <sup>3</sup> )	n (individuals)	Source of information
<i>Thouinia paucidentata</i>	Radlk.	Sapindaceae	Tree	0.008	3	Eating Birds in Mexico. <i>The Auk</i> 96(1): 183-186. Field samples
<i>Vitex gaumeri</i>	Greenm.	Lamiaceae	Tree	0.670	1	Field samples
<i>Zapoteca formosa</i> spp. <i>formosa</i>	(Kunth) H.M. Hern.	Fabaceae	Shrub	0.014	2	Field samples

#### Appendix 7.5 Null models of alpha and beta components and trait correlations.

##### Null models of alpha and beta components.

"In the null model, species and their associated trait values were randomly assembled into local plots, and the trait gradient analysis was then repeated 999 times. The vector of plot numbers was resampled without replacement in the full matrix of 273 plot-species-trait observations. This approach maintained the distribution of plot diversity, the number of occurrences per species, and the intraspecific distribution of abundance" (Supplementary material of Ackerly & Cornwell 2007).

Under the null, the expectation of plot mean trait values was the same for all plots so expected beta values were the same for all species. At  $p < 0.05$ , only 3 species would be expected to have beta values that were significantly higher or lower than this shared expectation. Because alpha and beta are a linear decomposition of the trait value, either both quantities can differ significantly from the null expectation, or neither, for each species (Ackerly and Cornwell 2007).

Mean beta and alpha values confidence limits (CL) are shown, result from 999 iterations of null model. Also beta and alpha values result from our data are shown. If our values were above or under confident limits, they were considered significant (sig). Otherwise were not significant (ns).

Species	Trait	Beta.025_CL	Beta.975_CL	Alpha.025_CL	AlphaT.975_CL	Beta_our data	Alpha_our data	Beta_test	Alpha_test
SENGAU	WSG	0.78	0.82	0.08	0.12	0.80	0.10 ns	ns	ns
ACAPEN	WSG	0.77	0.83	0.23	0.29	0.78	0.28 ns	ns	ns
AMPPA1	WSG	0.63	0.78	-0.27	-0.12	0.71	-0.20 ns	ns	ns
APHSCA	WSG	0.59	0.86	-0.36	-0.09	0.80	-0.30 ns	ns	ns
ARRPUB	WSG	0.65	0.79	-0.26	-0.12	0.76	-0.23 ns	ns	ns
BAUDIV	WSG	0.70	0.83	-0.08	0.05	0.77	-0.02 ns	ns	ns
BAUUNG	WSG	0.79	0.85	0.09	0.15	0.84	0.10 ns	ns	ns
BOUPUL	WSG	0.76	0.80	-0.02	0.02	0.80	-0.02 ns	ns	ns
BUNSWA	WSG	0.70	0.80	-0.22	-0.12	0.76	-0.18 ns	ns	ns
BURSIM	WSG	0.70	0.73	-0.37	-0.34	0.73	-0.37 ns	ns	ns
CAEGAU	WSG	0.78	0.82	0.08	0.12	0.79	0.11 ns	ns	ns
CALPAL	WSG	0.77	0.83	0.03	0.09	0.82	0.04 ns	ns	ns
CARCOR	WSG	0.56	0.88	-0.41	-0.09	0.85	-0.38 ns	ns	ns
CHLMAN	WSG	0.72	0.81	-0.22	-0.13	0.75	-0.16 ns	ns	ns
CNIACO	WSG	0.54	0.87	-0.58	-0.25	0.72	-0.43 ns	ns	ns
COCACAA	WSG	0.71	0.82	-0.17	-0.06	0.76	-0.11 ns	ns	ns
COCSPI	WSG	0.78	0.82	0.04	0.08	0.81	0.05 ns	ns	ns
COCVIT	WSG	0.66	0.75	-0.52	-0.43	0.74	-0.51 ns	ns	ns
CROREF	WSG	0.85	0.93	0.16	0.24	0.89	0.20 ns	ns	ns
CRORHA	WSG	0.58	0.90	-0.18	0.14	0.81	-0.09 ns	ns	ns
CYDDIV	WSG	0.57	0.90	-0.39	-0.06	0.79	-0.28 ns	ns	ns
CYDPOT	WSG	0.57	0.89	-0.38	-0.06	0.71	-0.20 ns	ns	ns
DALGLA	WSG	0.65	0.87	-0.40	-0.18	0.76	-0.29 ns	ns	ns
DIOANI	WSG	0.80	0.85	0.09	0.14	0.83	0.11 ns	ns	ns
DIOTET	WSG	0.78	0.81	0.01	0.04	0.78	0.04 ns	ns	ns
DIOYUC	WSG	0.75	0.81	-0.03	0.03	0.80	-0.02 ns	ns	ns
ERYROT	WSG	0.76	0.83	0.07	0.14	0.77	0.13 ns	ns	ns
EUGAXI	WSG	0.75	0.80	-0.03	0.02	0.78	-0.01 ns	ns	ns
EUGBUX	WSG	0.76	0.85	0.06	0.15	0.84	0.07 ns	ns	ns
EXOCAR	WSG	0.79	0.82	0.06	0.09	0.81	0.07 ns	ns	ns
GUEELL	WSG	0.75	0.82	0.01	0.08	0.80	0.03 ns	ns	ns
GYMFLO	WSG	0.78	0.80	-0.01	0.01	0.79	0.00 ns	ns	ns
HELDON	WSG	0.66	0.78	-0.41	-0.29	0.74	-0.37 ns	ns	ns
HETBRA	WSG	0.55	0.85	-0.32	-0.02	0.73	-0.20 ns	ns	ns
JATGAU	WSG	0.71	0.80	-0.37	-0.28	0.76	-0.33 ns	ns	ns
KARHUM	WSG	0.73	0.83	0.03	0.13	0.80	0.06 ns	ns	ns
LASFNU	WSG	0.59	0.86	-0.36	-0.09	0.64	-0.14 ns	ns	ns
LEULEU	WSG	0.75	0.80	-0.04	0.01	0.73	0.03 sig	sig	ns
LONRUG	WSG	0.79	0.86	0.09	0.16	0.86	0.09 ns	ns	ns
LONGUA	WSG	0.79	0.81	0.01	0.03	0.80	0.02 ns	ns	ns
LUESPE	WSG	0.75	0.80	-0.08	-0.03	0.77	-0.05 ns	ns	ns

Species	Trait	Beta.025_CL	Beta.975_CL	Alpha.025_CL	AlphaT.975_CL	Beta_our data	Alpha_our data	Beta_test	Alpha_test
LYSLAT	WSG	0.73	0.77	-0.22	-0.18	0.77	-0.22	sig	sig
MACLIN	WSG	0.78	0.85	0.14	0.21	0.83	0.16	ns	ns
MALGLA	WSG	0.78	0.84	0.07	0.13	0.81	0.10	ns	ns
MANVER	WSG	0.56	0.90	-0.40	-0.06	0.78	-0.28	ns	ns
MIMBAH	WSG	0.81	0.83	0.08	0.10	0.80	0.11	sig	sig
NEEPSY	WSG	0.75	0.79	-0.08	-0.04	0.80	-0.09	sig	sig
NEOEMA	WSG	0.79	0.80	0.00	0.01	0.79	0.01	ns	ns
PISACU	WSG	0.69	0.84	-0.41	-0.26	0.79	-0.36	ns	ns
PISPIS	WSG	0.77	0.80	-0.02	0.01	0.79	-0.01	ns	ns
PLAYUC	WSG	0.75	0.82	0.08	0.15	0.78	0.12	ns	ns
PSISAR	WSG	0.77	0.82	0.03	0.08	0.78	0.07	ns	ns
RANTRU	WSG	0.65	0.88	-0.08	0.15	0.72	0.08	ns	ns
SAMYUC	WSG	0.67	0.85	-0.13	0.05	0.82	-0.10	ns	ns
SEMMEX	WSG	0.75	0.79	-0.05	-0.01	0.78	-0.04	ns	ns
SENATO	WSG	0.73	0.81	-0.11	-0.03	0.76	-0.06	ns	ns
SENRAC	WSG	0.72	0.81	-0.13	-0.04	0.77	-0.09	ns	ns
SIDOBT	WSG	0.79	0.84	0.23	0.28	0.83	0.24	ns	ns
TABALB	WSG	0.56	0.88	-0.43	-0.11	0.80	-0.35	ns	ns
TABCHR	WSG	0.73	0.82	-0.07	0.02	0.81	-0.06	ns	ns
TALOLI	WSG	0.73	0.81	-0.10	-0.02	0.80	-0.09	ns	ns
THOPAU	WSG	0.80	0.83	0.11	0.14	0.81	0.13	ns	ns
VITGAU	WSG	0.75	0.80	-0.15	-0.10	0.76	-0.11	ns	ns
XIMAME	WSG	0.64	0.85	-0.19	0.02	0.60	0.06	sig	sig
ZAPFOR	WSG	0.67	0.86	-0.19	0.00	0.77	-0.10	ns	ns
SENGAU	LA	0.74	0.98	-1.35	-1.12	0.91	-1.28	ns	ns
ACAPEN	LA	0.62	1.00	-3.00	-2.62	0.88	-2.88	ns	ns
AMPPA1	LA	0.76	1.37	-0.21	0.40	1.25	-0.09	ns	ns
APHSCA	LA	0.39	1.62	-0.02	1.21	0.94	0.66	ns	ns
ARRPUB	LA	0.81	1.32	-0.16	0.35	1.07	0.09	ns	ns
BAUDIV	LA	0.82	1.39	0.27	0.83	1.02	0.64	ns	ns
BAUUNG	LA	0.99	1.29	0.24	0.53	1.16	0.37	ns	ns
BOUPUL	LA	1.00	1.23	0.67	0.90	1.11	0.78	ns	ns
BUNSWA	LA	0.81	1.25	-0.18	0.26	1.07	0.00	ns	ns
BURSIM	LA	1.03	1.14	0.25	0.36	1.02	0.37	sig	sig
CAEGAU	LA	0.83	1.03	-0.73	-0.53	0.94	-0.63	ns	ns
CALPAL	LA	0.93	1.21	0.02	0.31	1.13	0.11	ns	ns
CARCOR	LA	0.18	1.66	-0.77	0.71	1.13	-0.24	ns	ns
CHLMAN	LA	0.66	1.17	-1.50	-0.99	0.80	-1.12	ns	ns
CNIACO	LA	0.34	1.74	0.65	2.06	1.25	1.14	ns	ns
COCAC	LA	0.76	1.33	0.25	0.82	1.12	0.46	ns	ns
COCSPI	LA	1.14	1.38	0.66	0.89	1.27	0.77	ns	ns

Species	Trait	Beta.025_CL	Beta.975_CL	Alpha.025_CL	AlphaT.975_CL	Beta_our data	Alpha_our data	Beta_test	Alpha_test
COCVIT	LA	1.06	1.32	0.95	1.22	1.09	1.19	ns	ns
CROREF	LA	1.14	1.43	0.35	0.65	1.39	0.40	ns	ns
CRORHA	LA	0.25	1.66	-0.34	1.07	1.16	0.16	ns	ns
CYDDIV	LA	0.21	1.62	-0.08	1.33	1.23	0.30	ns	ns
CYDPOT	LA	0.15	1.68	-0.15	1.37	1.29	0.23	ns	ns
DALGLA	LA	0.39	1.43	-0.75	0.29	0.95	-0.26	ns	ns
DIOANI	LA	0.89	1.10	-0.20	0.01	0.92	-0.02	ns	ns
DIOTET	LA	1.02	1.18	0.08	0.24	1.02	0.24	ns	ns
DIOYUC	LA	0.90	1.17	-0.01	0.26	1.12	0.04	ns	ns
ERYROT	LA	0.79	1.15	-0.71	-0.35	1.07	-0.63	ns	ns
EUGAXI	LA	0.88	1.16	-0.19	0.09	1.11	-0.14	ns	ns
EUGBUX	LA	0.78	1.24	-0.33	0.13	0.96	-0.05	ns	ns
EXOCAR	LA	0.96	1.16	0.01	0.21	0.99	0.18	ns	ns
GUEELL	LA	0.84	1.20	-0.09	0.26	1.11	-0.01	ns	ns
GYMFLO	LA	0.99	1.11	-0.01	0.11	1.04	0.07	ns	ns
HELDON	LA	0.89	1.30	0.46	0.87	1.20	0.56	ns	ns
HETBRA	LA	0.36	1.61	-0.44	0.81	1.09	0.08	ns	ns
JATGAU	LA	0.86	1.27	0.65	1.05	1.13	0.79	ns	ns
KARHUM	LA	0.76	1.26	-0.24	0.26	1.04	-0.02	ns	ns
LASFRU	LA	0.41	1.61	0.04	1.24	1.77	-0.12	sig	sig
LEULEU	LA	0.55	0.93	-1.22	-0.84	0.46	-0.75	sig	sig
LONRUG	LA	0.87	1.20	-0.13	0.21	1.11	-0.03	ns	ns
LONGUA	LA	0.98	1.09	-0.07	0.04	1.04	-0.02	ns	ns
LUESPE	LA	1.02	1.29	0.80	1.07	1.08	1.01	ns	ns
LYSLAT	LA	0.74	0.91	-1.36	-1.19	0.91	-1.36	ns	ns
MACLIN	LA	0.79	1.18	-0.36	0.02	1.04	-0.22	ns	ns
MALGLA	LA	0.86	1.22	-0.14	0.22	1.11	-0.03	ns	ns
MANVER	LA	0.22	1.67	0.00	1.44	0.29	1.38	ns	ns
MIMBAH	LA	0.58	0.75	-0.98	-0.81	0.74	-0.97	ns	ns
NEEPSY	LA	0.98	1.17	0.14	0.32	0.99	0.31	ns	ns
NEOEMA	LA	1.41	1.51	0.29	0.39	1.46	0.33	ns	ns
PISACU	LA	0.65	1.37	-0.06	0.66	1.15	0.15	ns	ns
PISPIS	LA	0.98	1.12	0.20	0.34	1.00	0.32	ns	ns
PLAYUC	LA	0.85	1.20	-0.11	0.23	1.09	-0.01	ns	ns
PSISAR	LA	0.90	1.14	-0.17	0.08	1.15	-0.17	sig	sig
RANTRU	LA	0.46	1.47	-0.72	0.29	1.19	-0.44	ns	ns
SAMYUC	LA	0.56	1.47	-0.51	0.40	1.06	-0.10	ns	ns
SEMMEX	LA	1.07	1.30	0.41	0.63	1.12	0.59	ns	ns
SENATO	LA	0.83	1.24	0.13	0.54	1.03	0.34	ns	ns
SENRAC	LA	0.78	1.19	-0.44	-0.03	0.91	-0.15	ns	ns
SIDOBT	LA	0.93	1.16	-0.02	0.20	0.99	0.14	ns	ns

Species	Trait	Beta.025_CL	Beta.975_CL	Alpha.025_CL	AlphaT.975_CL	Beta_our data	Alpha_our data	Beta_test	Alpha_test
TABALB	LA	0.26	1.69	-0.12	1.31	1.72	-0.15	sig	sig
TABCHR	LA	0.85	1.28	0.20	0.63	1.05	0.43	ns	ns
TALOLI	LA	0.86	1.23	0.02	0.39	1.01	0.24	ns	ns
THOPAU	LA	0.93	1.09	-0.18	-0.02	1.01	-0.10	ns	ns
VITGAU	LA	0.92	1.16	0.40	0.64	1.08	0.48	ns	ns
XIMAME	LA	0.45	1.45	-0.62	0.39	1.24	-0.41	ns	ns
ZAPFOR	LA	0.50	1.41	-0.91	0.00	1.14	-0.64	ns	ns
SENGAU	LDMC	0.38	0.39	0.01	0.02	0.39	0.01	ns	ns
ACAPEN	LDMC	0.38	0.39	0.04	0.05	0.38	0.05	ns	ns
AMPPA1	LDMC	0.37	0.40	0.00	0.03	0.40	0.00	ns	ns
APHSCA	LDMC	0.32	0.40	-0.13	-0.05	0.38	-0.11	ns	ns
ARRPUB	LDMC	0.37	0.40	0.00	0.03	0.40	0.00	sig	sig
BAUDIV	LDMC	0.37	0.41	0.02	0.06	0.40	0.03	ns	ns
BAUUNG	LDMC	0.38	0.40	0.01	0.03	0.40	0.01	sig	sig
BOUPUL	LDMC	0.36	0.38	-0.10	-0.08	0.39	-0.11	sig	sig
BUNSWA	LDMC	0.37	0.39	-0.02	0.00	0.38	-0.01	ns	ns
BURSIM	LDMC	0.37	0.38	-0.07	-0.06	0.38	-0.07	sig	sig
CAEGAU	LDMC	0.39	0.40	0.07	0.08	0.40	0.07	ns	ns
CALPAL	LDMC	0.37	0.39	-0.02	0.00	0.38	-0.01	ns	ns
CARCOR	LDMC	0.32	0.41	-0.18	-0.09	0.36	-0.13	ns	ns
CHLMAN	LDMC	0.37	0.40	0.04	0.07	0.39	0.05	ns	ns
CNIACO	LDMC	0.30	0.40	-0.25	-0.15	0.36	-0.21	ns	ns
COCAC	LDMC	0.36	0.40	-0.04	0.00	0.39	-0.03	ns	ns
COCSPI	LDMC	0.38	0.39	-0.01	0.00	0.37	0.01	sig	sig
COCVIT	LDMC	0.36	0.38	-0.11	-0.09	0.38	-0.11	sig	sig
CROREF	LDMC	0.33	0.36	-0.08	-0.05	0.35	-0.07	ns	ns
CRORHA	LDMC	0.33	0.42	-0.03	0.06	0.39	0.00	ns	ns
CYDDIV	LDMC	0.33	0.42	-0.04	0.05	0.36	0.02	ns	ns
CYDPOT	LDMC	0.34	0.42	-0.02	0.06	0.38	0.02	ns	ns
DALGLA	LDMC	0.35	0.41	-0.06	0.00	0.40	-0.05	ns	ns
DIOANI	LDMC	0.38	0.40	0.01	0.03	0.39	0.02	ns	ns
DIOTET	LDMC	0.37	0.38	-0.01	0.00	0.38	-0.01	ns	ns
DIOYUC	LDMC	0.38	0.40	0.05	0.07	0.39	0.06	ns	ns
ERYROT	LDMC	0.38	0.40	0.04	0.06	0.39	0.05	ns	ns
EUGAXI	LDMC	0.38	0.40	0.01	0.03	0.39	0.02	ns	ns
EUGBUX	LDMC	0.38	0.40	0.02	0.04	0.40	0.02	ns	ns
EXOCAR	LDMC	0.37	0.38	-0.03	-0.02	0.38	-0.03	sig	sig
GUEELL	LDMC	0.37	0.39	0.00	0.02	0.39	0.00	ns	ns
GYMFLO	LDMC	0.39	0.39	0.01	0.01	0.39	0.01	ns	ns
HELDON	LDMC	0.34	0.38	-0.16	-0.12	0.38	-0.16	sig	sig
HETBRA	LDMC	0.35	0.41	-0.02	0.04	0.39	0.00	ns	ns

Species	Trait	Beta.025_CL	Beta.975_CL	Alpha.025_CL	AlphaT.975_CL	Beta_our data	Alpha_our data	Beta_test	Alpha_test
JATGAU	LDMC	0.36	0.39	-0.15	-0.12	0.38	-0.14	ns	ns
KARHUM	LDMC	0.37	0.40	0.01	0.04	0.39	0.02	ns	ns
LASFNU	LDMC	0.32	0.40	-0.14	-0.06	0.35	-0.09	ns	ns
LEULEU	LDMC	0.35	0.37	-0.08	-0.06	0.34	-0.05	sig	sig
LONRUG	LDMC	0.37	0.39	-0.01	0.01	0.39	-0.01	ns	ns
LONGUA	LDMC	0.38	0.39	-0.01	0.00	0.38	0.00	ns	ns
LUESPE	LDMC	0.38	0.39	0.00	0.01	0.38	0.01	ns	ns
LYSLAT	LDMC	0.39	0.40	0.05	0.06	0.38	0.07	sig	sig
MACLIN	LDMC	0.36	0.38	-0.05	-0.03	0.38	-0.05	ns	ns
MALGLA	LDMC	0.37	0.39	-0.03	-0.01	0.38	-0.02	ns	ns
MANVER	LDMC	0.33	0.42	0.03	0.12	0.32	0.13	sig	sig
MIMBAH	LDMC	0.39	0.39	0.02	0.02	0.39	0.02	ns	ns
NEEPSY	LDMC	0.38	0.39	-0.02	-0.01	0.39	-0.02	sig	sig
NEOEMA	LDMC	0.40	0.40	0.01	0.01	0.40	0.01	ns	ns
PISACU	LDMC	0.36	0.40	-0.11	-0.07	0.39	-0.10	ns	ns
PISPIS	LDMC	0.37	0.38	-0.05	-0.04	0.38	-0.05	ns	ns
PLAYUC	LDMC	0.37	0.39	0.03	0.05	0.37	0.05	sig	sig
PSISAR	LDMC	0.38	0.40	0.02	0.04	0.40	0.02	ns	ns
RANTRU	LDMC	0.35	0.40	-0.02	0.03	0.39	-0.01	ns	ns
SAMYUC	LDMC	0.35	0.40	-0.08	-0.03	0.39	-0.07	ns	ns
SEMMEX	LDMC	0.37	0.38	-0.04	-0.03	0.37	-0.03	ns	ns
SENATO	LDMC	0.36	0.39	-0.10	-0.07	0.38	-0.09	ns	ns
SENRAC	LDMC	0.36	0.39	-0.06	-0.03	0.37	-0.04	ns	ns
SIDOBT	LDMC	0.38	0.40	0.04	0.06	0.39	0.05	ns	ns
TABALB	LDMC	0.31	0.40	-0.20	-0.11	0.40	-0.20	ns	ns
TABCHR	LDMC	0.37	0.39	-0.03	-0.01	0.39	-0.03	ns	ns
TALOLI	LDMC	0.38	0.40	0.09	0.11	0.40	0.09	ns	ns
THOPAU	LDMC	0.38	0.39	0.01	0.02	0.38	0.02	ns	ns
VITGAU	LDMC	0.37	0.39	-0.03	-0.01	0.37	-0.01	ns	ns
XIMAME	LDMC	0.36	0.42	0.02	0.08	0.36	0.08	sig	sig
ZAPFOR	LDMC	0.36	0.41	0.02	0.07	0.39	0.04	ns	ns
SENGAU	LP	0.20	0.30	0.13	0.23	0.14	0.28	sig	sig
ACAPEN	LP	0.14	0.29	-0.34	-0.20	0.31	-0.36	sig	sig
AMPPA1	LP	0.10	0.46	0.04	0.40	0.12	0.38	ns	ns
APHSCA	LP	-0.16	0.49	-0.51	0.14	0.21	-0.22	ns	ns
ARRPUB	LP	0.12	0.42	0.06	0.36	0.23	0.25	ns	ns
BAUDIV	LP	0.07	0.42	0.01	0.35	0.27	0.16	ns	ns
BAUUNG	LP	0.14	0.31	-0.06	0.12	0.28	-0.03	ns	ns
BOUPUL	LP	0.21	0.34	0.34	0.47	0.27	0.41	ns	ns
BUNSWA	LP	0.02	0.28	-0.61	-0.35	0.05	-0.38	ns	ns
BURSIM	LP	0.29	0.37	0.49	0.57	0.28	0.58	sig	sig

Species	Trait	Beta.025_CL	Beta.975_CL	Alpha.025_CL	AlphaT.975_CL	Beta_our data	Alpha_our data	Beta_test	Alpha_test
CAEGAU	LP	0.20	0.30	0.07	0.17	0.26	0.11	ns	ns
CALPAL	LP	0.06	0.23	-0.38	-0.21	0.15	-0.31	ns	ns
CARCOR	LP	-0.19	0.57	-0.13	0.63	0.54	-0.10	ns	ns
CHLMAN	LP	0.09	0.34	-0.14	0.11	0.18	0.02	ns	ns
CNIACO	LP	-0.16	0.73	0.55	1.44	0.30	0.98	ns	ns
COCACAC	LP	0.07	0.38	-0.02	0.28	0.19	0.17	ns	ns
COCSPI	LP	0.20	0.33	0.09	0.22	0.34	0.08	sig	sig
COCVIT	LP	0.26	0.44	0.70	0.88	0.38	0.76	ns	ns
CROREF	LP	0.26	0.43	0.15	0.32	0.39	0.19	ns	ns
CRORHA	LP	-0.23	0.57	-0.64	0.16	0.37	-0.44	ns	ns
CYDDIV	LP	-0.23	0.64	-0.22	0.64	0.19	0.22	ns	ns
CYDPOT	LP	-0.23	0.59	-0.33	0.50	0.43	-0.17	ns	ns
DALGLA	LP	-0.09	0.51	-0.33	0.27	0.36	-0.18	ns	ns
DIOANI	LP	-0.07	0.09	-0.69	-0.53	0.00	-0.60	ns	ns
DIOTET	LP	-0.01	0.11	-0.46	-0.34	0.15	-0.49	sig	sig
DIOYUC	LP	0.10	0.26	-0.37	-0.21	0.19	-0.30	ns	ns
ERYROT	LP	0.05	0.26	-0.78	-0.57	0.04	-0.57	sig	sig
EUGAXI	LP	-0.04	0.14	-0.61	-0.43	-0.03	-0.44	ns	ns
EUGBUX	LP	-0.03	0.24	-0.57	-0.30	-0.08	-0.25	sig	sig
EXOCAR	LP	0.14	0.26	-0.14	-0.03	0.13	-0.01	sig	sig
GUEELL	LP	0.08	0.29	-0.53	-0.32	0.09	-0.33	ns	ns
GYMFLO	LP	-0.02	0.07	-0.53	-0.45	-0.01	-0.46	ns	ns
HELDON	LP	0.15	0.39	0.19	0.43	0.34	0.23	ns	ns
HETBRA	LP	-0.27	0.42	-0.68	0.00	0.22	-0.49	ns	ns
JATGAU	LP	0.15	0.39	0.49	0.73	0.04	0.84	sig	sig
KARHUM	LP	0.08	0.35	-0.40	-0.13	0.17	-0.22	ns	ns
LASFRU	LP	-0.16	0.51	-0.37	0.31	0.23	-0.09	ns	ns
LEULEU	LP	0.20	0.36	0.12	0.28	0.42	0.06	sig	sig
LONRUG	LP	0.24	0.44	0.23	0.43	0.37	0.30	ns	ns
LONGUA	LP	0.27	0.33	0.07	0.13	0.28	0.12	ns	ns
LUESPE	LP	0.13	0.28	-0.22	-0.07	0.12	-0.06	sig	sig
LYSLAT	LP	0.26	0.35	0.43	0.51	0.27	0.51	ns	ns
MACLIN	LP	0.00	0.22	-0.64	-0.42	-0.10	-0.32	sig	sig
MALGLA	LP	0.00	0.22	-0.52	-0.30	-0.06	-0.24	sig	sig
MANVER	LP	-0.21	0.67	0.14	1.03	0.48	0.33	ns	ns
MIMBAH	LP	0.16	0.22	-0.12	-0.05	0.27	-0.17	sig	sig
NEEPSY	LP	0.15	0.26	-0.17	-0.05	0.14	-0.05	sig	sig
NEOEMA	LP	0.30	0.35	0.06	0.11	0.36	0.05	sig	sig
PISACU	LP	0.02	0.44	-0.10	0.31	0.17	0.16	ns	ns
PISPIS	LP	0.23	0.31	0.30	0.39	0.30	0.31	ns	ns
PLAYUC	LP	0.14	0.35	0.19	0.39	0.29	0.24	ns	ns

Species	Trait	Beta.025_CL	Beta.975_CL	Alpha.025_CL	AlphaT.975_CL	Beta_our data	Alpha_our data	Beta_test	Alpha_test
PSISAR	LP	0.02	0.17	-0.52	-0.36	0.00	-0.35	sig	sig
RANTRU	LP	-0.13	0.42	-0.58	-0.03	0.12	-0.28	ns	ns
SAMYUC	LP	-0.09	0.40	-0.85	-0.36	0.05	-0.50	ns	ns
SEMMEX	LP	0.10	0.23	-0.27	-0.14	0.21	-0.26	ns	ns
SENATO	LP	0.13	0.38	0.33	0.57	0.25	0.45	ns	ns
SENRAC	LP	0.13	0.36	0.10	0.33	0.27	0.19	ns	ns
SIDOBT	LP	0.13	0.26	-0.29	-0.16	0.15	-0.18	ns	ns
TABALB	LP	-0.23	0.57	-0.48	0.33	0.37	-0.28	ns	ns
TABCHR	LP	0.18	0.45	0.46	0.73	0.29	0.62	ns	ns
TALOLI	LP	0.13	0.35	0.07	0.28	0.14	0.27	ns	ns
THOPAU	LP	0.23	0.32	0.16	0.25	0.23	0.25	sig	sig
VITGAU	LP	0.19	0.33	0.60	0.75	0.31	0.63	ns	ns
XIMAME	LP	-0.24	0.35	-0.89	-0.29	0.24	-0.78	ns	ns
ZAPFOR	LP	-0.04	0.45	-0.07	0.43	0.23	0.15	ns	ns
SENGAU	SLA	126.38	133.27	44.70	51.59	128.08	49.89	ns	ns
ACAPEN	SLA	119.41	128.02	-2.46	6.15	123.16	2.40	ns	ns
AMPPA1	SLA	115.16	133.82	-6.71	11.95	126.35	0.76	ns	ns
APHSCA	SLA	111.65	156.88	36.90	82.13	133.36	60.42	ns	ns
ARRPUB	SLA	115.95	132.35	-6.96	9.44	124.80	0.59	ns	ns
BAUDIV	SLA	116.23	135.19	1.65	20.61	117.47	19.37	ns	ns
BAUUNG	SLA	127.27	139.25	26.30	38.28	131.08	34.47	ns	ns
BOUPUL	SLA	119.37	126.60	-6.39	0.84	122.38	-2.17	ns	ns
BUNSWA	SLA	115.49	128.82	-16.88	-3.55	121.64	-9.70	ns	ns
BURSIM	SLA	120.53	124.08	-7.49	-3.94	122.17	-5.58	ns	ns
CAEGAU	SLA	118.84	124.32	-13.78	-8.30	121.43	-10.89	ns	ns
CALPAL	SLA	113.68	123.46	-23.55	-13.77	114.55	-14.64	ns	ns
CARCOR	SLA	111.25	169.28	126.45	184.48	125.19	170.54	ns	ns
CHLMAN	SLA	116.45	129.62	-1.10	12.07	130.77	-2.25	sig	sig
CNIACO	SLA	105.67	158.69	60.03	113.05	102.97	115.75	sig	sig
COCAC	SLA	116.59	134.93	23.80	42.14	123.44	35.29	ns	ns
COCSPI	SLA	105.84	115.71	-48.47	-38.60	109.57	-42.33	ns	ns
COCVIT	SLA	122.79	130.68	17.22	25.11	129.85	18.05	ns	ns
CROREF	SLA	125.61	134.95	9.03	18.37	119.75	24.23	sig	sig
CRORHA	SLA	95.98	146.37	-68.41	-18.02	115.35	-37.39	ns	ns
CYDDIV	SLA	99.84	148.86	-1.94	47.08	110.65	36.27	ns	ns
CYDPOT	SLA	99.09	151.48	-16.01	36.38	117.86	17.61	ns	ns
DALGLA	SLA	107.45	143.13	19.64	55.32	129.52	33.25	ns	ns
DIOANI	SLA	123.22	129.72	4.33	10.83	127.44	6.61	ns	ns
DIOTET	SLA	118.36	123.48	-9.03	-3.91	121.64	-7.19	ns	ns
DIOYUC	SLA	114.65	124.38	-30.97	-21.24	118.17	-24.76	ns	ns
ERYROT	SLA	119.43	131.10	11.20	22.87	124.42	17.88	ns	ns

Species	Trait	Beta.025_CL	Beta.975_CL	Alpha.025_CL	AlphaT.975_CL	Beta_our data	Alpha_our data	Beta_test	Alpha_test
EUGAXI	SLA	115.92	123.87	-15.91	-7.96	115.79	-7.83	sig	sig
EUGBUX	SLA	103.52	121.95	-51.93	-33.50	122.43	-52.41	sig	sig
EXOCAR	SLA	121.89	128.12	2.09	8.32	126.19	4.02	ns	ns
GUEELL	SLA	118.61	130.73	3.45	15.57	123.83	10.35	ns	ns
GYMFLO	SLA	124.26	127.70	3.99	7.43	125.70	5.99	ns	ns
HELDON	SLA	126.26	149.89	69.39	93.02	131.41	87.87	ns	ns
HETBRA	SLA	112.13	157.44	17.59	62.90	113.46	61.57	ns	ns
JATGAU	SLA	118.20	132.17	18.46	32.43	125.27	25.36	ns	ns
KARHUM	SLA	117.18	132.35	8.36	23.53	120.00	20.71	ns	ns
LASFNU	SLA	114.12	164.40	71.88	122.16	165.58	70.70	sig	sig
LEULEU	SLA	135.29	152.06	57.59	74.36	159.09	50.56	sig	sig
LONRUG	SLA	114.40	125.02	-16.51	-5.89	121.82	-13.31	ns	ns
LONGUA	SLA	129.04	132.84	8.10	11.90	126.77	14.17	sig	sig
LUESPE	SLA	122.92	131.08	21.21	29.37	134.17	18.12	sig	sig
LYSLAT	SLA	116.75	121.58	-28.37	-23.54	120.94	-27.73	ns	ns
MACLIN	SLA	128.03	142.39	46.48	60.84	130.79	58.08	ns	ns
MALGLA	SLA	116.05	126.84	-12.90	-2.11	122.13	-8.19	ns	ns
MANVER	SLA	97.51	148.14	-29.07	21.56	158.89	-39.82	sig	sig
MIMBAH	SLA	125.95	129.45	7.89	11.39	127.00	10.34	ns	ns
NEEPSY	SLA	117.13	123.47	-20.08	-13.74	124.15	-20.76	sig	sig
NEOEMA	SLA	118.90	121.45	-4.14	-1.59	121.22	-3.91	ns	ns
PISACU	SLA	111.47	134.99	8.26	31.78	118.33	24.92	ns	ns
PISPIS	SLA	117.34	121.89	-33.66	-29.11	121.40	-33.17	ns	ns
PLAYUC	SLA	117.29	128.53	-15.57	-4.33	122.45	-9.49	ns	ns
PSISAR	SLA	116.46	124.38	-14.58	-6.66	121.93	-12.13	ns	ns
RANTRU	SLA	111.60	142.24	5.49	36.13	125.58	22.15	ns	ns
SAMYUC	SLA	113.58	147.06	47.64	81.12	133.16	61.54	ns	ns
SEMMEX	SLA	109.41	117.95	-36.61	-28.07	116.13	-34.79	ns	ns
SENATO	SLA	117.79	130.28	0.81	13.30	124.74	6.35	ns	ns
SENRAC	SLA	119.45	131.97	9.78	22.30	123.20	18.55	ns	ns
SIDOBT	SLA	112.63	121.40	-50.08	-41.31	122.30	-50.98	sig	sig
TABALB	SLA	105.54	155.23	34.68	84.37	120.73	69.18	ns	ns
TABCHR	SLA	118.93	132.78	7.80	21.65	127.48	13.10	ns	ns
TALOLI	SLA	114.43	127.36	-31.10	-18.17	122.94	-26.68	ns	ns
THOPAU	SLA	123.93	128.77	8.90	13.74	125.86	11.81	ns	ns
VITGAU	SLA	118.62	126.51	-21.39	-13.50	120.00	-14.88	ns	ns
XIMAME	SLA	105.01	137.97	-32.73	0.23	113.31	-8.07	ns	ns
ZAPFOR	SLA	111.39	139.54	27.36	55.51	122.22	44.68	ns	ns
SENGAU	SV	-1.80	-1.68	-0.15	-0.03	-1.71	-0.12	ns	ns
ACAPEN	SV	-1.79	-1.64	0.00	0.15	-1.74	0.10	ns	ns
AMPPA1	SV	-2.18	-1.53	-1.47	-0.82	-1.97	-1.03	ns	ns

Species	Trait	Beta.025_CL	Beta.975_CL	Alpha.025_CL	AlphaT.975_CL	Beta_our data	Alpha_our data	Beta_test	Alpha_test
APHSCA	SV	-2.14	-1.38	-0.84	-0.08	-1.63	-0.59	ns	ns
ARRPUB	SV	-1.98	-1.61	-1.09	-0.72	-1.78	-0.92	ns	ns
BAUDIV	SV	-1.87	-1.50	0.19	0.56	-1.72	0.41	ns	ns
BAUUNG	SV	-1.84	-1.61	-0.14	0.10	-1.88	0.14	sig	sig
BOUPUL	SV	-1.79	-1.65	-0.12	0.02	-1.74	-0.03	ns	ns
BUNSWA	SV	-1.87	-1.56	-0.06	0.25	-1.63	0.01	ns	ns
BURSIM	SV	-1.64	-1.56	0.41	0.49	-1.68	0.53	sig	sig
CAEGAU	SV	-1.65	-1.52	0.57	0.70	-1.67	0.72	sig	sig
CALPAL	SV	-1.84	-1.60	-0.15	0.10	-1.56	-0.19	sig	sig
CARCOR	SV	-2.25	-1.20	-0.39	0.67	-1.88	0.29	ns	ns
CHLMAN	SV	-1.78	-1.57	0.26	0.47	-1.69	0.38	ns	ns
CNIACO	SV	-2.22	-1.18	-0.09	0.95	-1.27	0.00	ns	ns
COCACAA	SV	-1.79	-1.50	0.79	1.08	-1.66	0.96	ns	ns
COCSPI	SV	-1.61	-1.44	0.48	0.65	-1.46	0.50	ns	ns
COCVIT	SV	-1.78	-1.65	-0.05	0.08	-1.82	0.12	sig	sig
CRORHA	SV	-2.23	-1.11	0.09	1.21	-1.29	0.27	ns	ns
CYDDIV	SV	-2.47	-1.31	-1.69	-0.53	-1.74	-1.26	ns	ns
CYDPOT	SV	-2.28	-1.20	-0.23	0.85	-1.68	0.24	ns	ns
DIOANI	SV	-1.74	-1.59	0.53	0.68	-1.71	0.65	ns	ns
DIOTET	SV	-1.65	-1.50	0.63	0.78	-1.55	0.68	ns	ns
DIOYUC	SV	-1.73	-1.54	0.64	0.84	-1.63	0.73	ns	ns
ERYROT	SV	-1.88	-1.65	-0.44	-0.22	-1.82	-0.27	ns	ns
EUGAXI	SV	-1.73	-1.53	0.45	0.65	-1.63	0.56	ns	ns
EUGBUX	SV	-1.86	-1.51	0.32	0.67	-1.77	0.58	ns	ns
GUEELL	SV	-1.79	-1.58	0.22	0.44	-1.81	0.45	sig	sig
GYMFLO	SV	-2.07	-1.96	-1.04	-0.93	-1.92	-1.08	sig	sig
HELDON	SV	-1.97	-1.75	-1.25	-1.03	-1.94	-1.06	ns	ns
JATGAU	SV	-1.74	-1.49	1.15	1.40	-1.78	1.44	sig	sig
KARHUM	SV	-1.82	-1.53	0.24	0.53	-1.64	0.35	ns	ns
LASFRU	SV	-2.25	-1.50	-2.02	-1.27	-2.30	-1.23	sig	sig
LEULEU	SV	-1.82	-1.64	-0.13	0.06	-1.72	-0.05	ns	ns
LUESPE	SV	-1.90	-1.73	-0.66	-0.49	-1.83	-0.57	ns	ns
LYSLAT	SV	-1.84	-1.76	-0.29	-0.20	-1.70	-0.35	sig	sig
MACLIN	SV	-2.02	-1.77	-1.23	-0.98	-1.94	-1.06	ns	ns
MALGLA	SV	-1.84	-1.64	-0.22	-0.01	-1.86	0.01	sig	sig
MANVER	SV	-2.25	-1.17	0.03	1.11	-1.77	0.63	ns	ns
MIMBAH	SV	-1.83	-1.74	-0.31	-0.22	-1.83	-0.22	sig	sig
NEEPSY	SV	-1.77	-1.64	0.06	0.19	-1.70	0.11	ns	ns
NEOEMA	SV	-1.95	-1.82	-0.58	-0.45	-1.95	-0.45	ns	ns
PISACU	SV	-1.92	-1.39	0.37	0.91	-1.54	0.52	ns	ns
PISPIS	SV	-1.78	-1.70	-0.18	-0.11	-1.75	-0.14	ns	ns

Species	Trait	Beta.025_CL	Beta.975_CL	Alpha.025_CL	AlphaT.975_CL	Beta_our data	Alpha_our data	Beta_test	Alpha_test
PSISAR	SV	-1.81	-1.63	-0.05	0.13	-1.69	0.01	ns	ns
RANTRU	SV	-2.05	-1.26	0.60	1.40	-1.99	1.34	ns	ns
SEMMEX	SV	-1.74	-1.59	0.27	0.43	-1.60	0.29	ns	ns
SENATO	SV	-1.76	-1.51	0.79	1.04	-1.73	1.02	ns	ns
SIDOBT	SV	-1.71	-1.56	0.65	0.80	-1.68	0.77	ns	ns
TABALB	SV	-2.26	-1.20	-0.28	0.78	-2.10	0.62	ns	ns
TABCHR	SV	-1.95	-1.69	-1.31	-1.05	-1.89	-1.11	ns	ns
TALOLI	SV	-1.70	-1.44	1.16	1.42	-1.57	1.29	ns	ns
THOPAU	SV	-1.84	-1.74	-0.35	-0.25	-1.69	-0.41	sig	sig
VITGAU	SV	-1.66	-1.50	1.33	1.49	-1.53	1.36	ns	ns
ZAPFOR	SV	-2.04	-1.43	-0.42	0.19	-1.64	-0.22	ns	ns

### Null models of trait correlations.

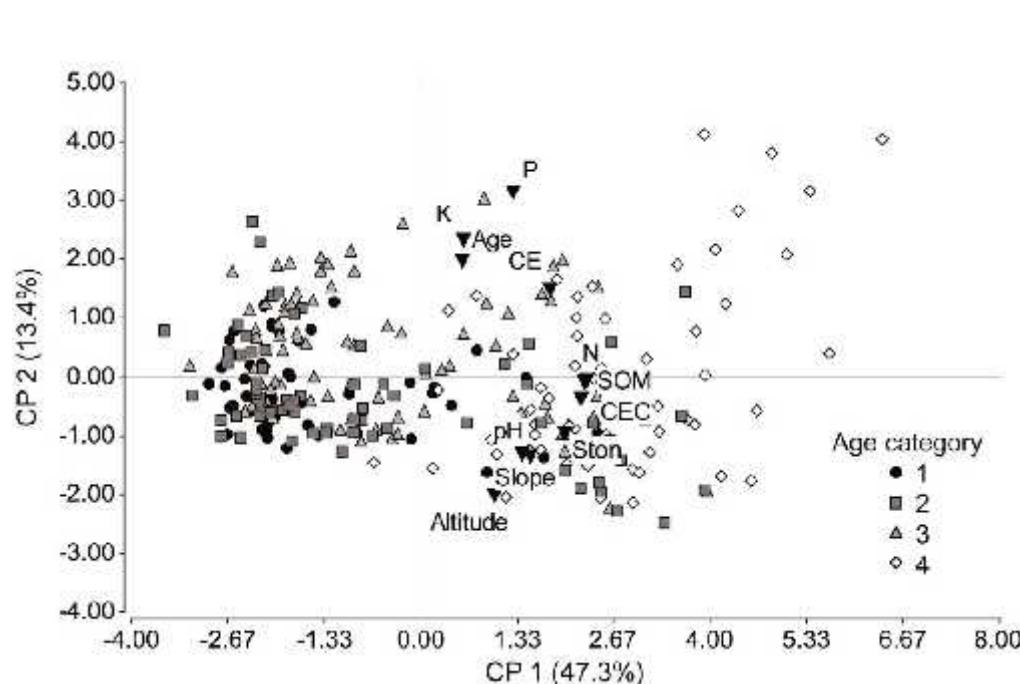
Summary data from trait correlations result from 999 iterations of null model. Correlation of our data are also shown. If our values were below percentile 2.5 or above percentile 97.5, they were considered significant (sig). Otherwise were not significant (ns).

Traits	Variable	Media	D.E.	Mín	Máx	Percentil 2.5	Percentil 97.5	Our data	p
LDMC-LA	Alpha	-0.432	0.043	-0.599	-0.266	-0.514	-0.348	-0.3245	ns
LDMC-LP	Alpha	-0.357	0.046	-0.497	-0.218	-0.441	-0.267	-0.3086	ns
LP-LA	Alpha	0.29	0.039	0.166	0.407	0.212	0.365	0.3424	ns
SLA-LA	Alpha	0.042	0.05	-0.12	0.211	-0.054	0.145	-0.0179	ns
SLA-LDMC	Alpha	-0.619	0.027	-0.702	-0.481	-0.664	-0.562	-0.6319	ns
SLA-LP	Alpha	0.117	0.051	-0.046	0.271	0.017	0.223	0.0705	ns
SLA-WSG	Alpha	-0.41	0.039	-0.542	-0.275	-0.477	-0.32	-0.4145	ns
SV-LA	Alpha	0.025	0.038	-0.109	0.207	-0.05	0.097	0.019	ns
SV-LDMC	Alpha	0.114	0.043	-0.033	0.243	0.023	0.196	0.0787	ns
SV-LP	Alpha	0.051	0.041	-0.084	0.194	-0.024	0.137	0.0642	ns
SV-SLA	Alpha	-0.361	0.037	-0.465	-0.23	-0.434	-0.285	-0.2908	ns
SV-WSG	Alpha	0.077	0.04	-0.105	0.179	-0.006	0.153	0.0439	ns
WSG-LA	Alpha	-0.397	0.037	-0.511	-0.263	-0.471	-0.326	-0.3998	ns
WSG-LDMC	Alpha	0.53	0.036	0.346	0.622	0.452	0.59	0.5364	ns
WSG-LP	Alpha	-0.446	0.037	-0.564	-0.303	-0.514	-0.371	-0.4259	ns
LDMC-LA	Beta	-0.212	0.169	-0.77	0.398	-0.525	0.117	0.1997	ns
LDMC-LP	Beta	-0.269	0.152	-0.74	0.183	-0.563	0.054	-0.366	ns

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LP-LA	Beta	0.171	0.141	-0.362	0.566	-0.12	0.442	-0.0004	ns
SLA-LA	Beta	-0.251	0.159	-0.709	0.524	-0.543	0.072	-0.3108	ns
SLA-LDMC	Beta	-0.368	0.162	-0.851	0.13	-0.666	-0.055	-0.4011	ns
SLA-LP	Beta	0.068	0.162	-0.373	0.706	-0.23	0.38	0.1084	ns
SLA-WSG	Beta	-0.006	0.178	-0.654	0.485	-0.41	0.338	-0.1635	ns
SV-LA	Beta	0.148	0.178	-0.374	0.606	-0.216	0.485	-0.182	ns
SV-LDMC	Beta	-0.126	0.189	-0.567	0.52	-0.475	0.264	0.2055	ns
SV-LP	Beta	0.269	0.185	-0.399	0.706	-0.133	0.589	0.1286	ns
SV-SLA	Beta	<b>-0.353</b>	<b>0.162</b>	<b>-0.778</b>	<b>0.24</b>	<b>-0.649</b>	<b>-0.006</b>	<b>-0.651</b>	<b>&lt;0.05</b>
SV-WSG	Beta	-0.14	0.184	-0.599	0.46	-0.481	0.235	0.1331	ns
WSG-LA	Beta	-0.099	0.161	-0.624	0.49	-0.383	0.219	-0.1671	ns
WSG-LDMC	Beta	0.252	0.212	-0.424	0.886	-0.189	0.64	0.1823	ns
WSG-LP	Beta	-0.296	0.162	-0.726	0.328	-0.599	0.052	-0.0837	ns

**Appendix 7.6** Principal Component Analysis of topography, soil variables and forest stand age.



Symbols represent age categories: 1 = 3 to 8 years of secondary succession; 2 = 9 to 15 years; 3 = plots with > 15 years on flat areas, and 4 = > 15 years on hills. Variables are shown as black inverted triangles.

Variables	PC1(47%)	Eigenvectors	PC2(13%)
Age	0.11	0.11	0.36
pH	0.26	0.26	-0.24
EC	0.33	0.33	0.27
P	0.23	0.23	0.57
K	0.11	0.11	0.42
CEC	0.40	0.40	-0.07
Altitude	0.19	0.19	-0.37
Slope	0.28	0.28	-0.25
Ston	0.36	0.36	-0.18
SOM	0.41	0.41	-0.02
N	0.42	0.42	-0.01

Age = Fallow time after slash and burn agriculture; EC = electric conductivity; P = available phosphorus; K = interchangeable potassium; CEC= cation exchange capacity; Ston = Stoniness; SOM = Soil Matter Content; N = total nitrogen. n= 263.

**Appendix 7.7** Reduced multiple linear regressions models of plot mean trait values with successional age and environmental variables. For each trait the minimum model is shown, according to akaike criterion and hypothesis testing procedures.

Trait	R <sup>2</sup>	Adj. R <sup>2</sup>	AIC	Coef	Est.	SE	T	p-value
LA	0.1	0.09	240.67	const	-3.64	1.56	-2.34	0.0199
				Age	0.41	0.08	5.05	<0.0001
				pH	3.84	1.58	2.44	0.0156
				N	-0.17	0.05	-3.39	0.0008
LDMC	0.08	0.07	-1258.16	const	0.39	0.01	27.56	<0.0001
				Age	0.02	0.0044	4.56	<0.0001
				CEC	-0.02	0.01	-2.19	0.0293
PL	0.27	0.25	-110.49	const	-0.02	0.25	-0.09	0.9275
				Age	-0.32	0.04	-7.74	<0.0001
				P	-0.08	0.04	-2.11	0.0358
				Slope	-0.22	0.09	-2.6	0.0100
				SOM	0.06	0.03	2.28	0.0236
				N	-0.13	0.06	-2.34	0.0198
				Ston	0.23	0.11	2.12	0.0352
SLA	0.08	0.07	2130.41	const	379.57	56.51	6.72	<0.0001
				Age	-8.4	2.91	-2.88	0.0040
				pH	-256.99	57.29	-4.49	<0.0001
				N	4.81	1.86	2.58	0.0100
SV	0.23	0.22	175.59	const	-1.76	0.1	-17.81	<0.0001

Trait	R <sup>2</sup>	Adj. R <sup>2</sup>	AIC	Coef	Est.	SE	T	p-value
WSG	0.02	0.02	-647.04	P	-0.27	0.07	-3.8	0.0002
				K	0.26	0.09	2.83	0.0050
				Ston	0.73	0.17	4.26	<0.0001
				SOM	0.06	0.03	1.98	0.0490
				const	0.68	0.04	15.1	<0.0001
				CEC	0.06	0.03	2.3	0.0200

PL = petiole length; LA = leaf or leaflet area; LDMC = leaf dry matter content; SLA = specific leaf area, WSG = wood specific gravity, SV = seed volume. Age = Fallow time after slash and burn agriculture; CEC= cation exchange capacity; K = interchangeable potassium; N = Soil total nitrogen; Ston = Stoniness; SOM = Soil Matter Content; P = available phosphorus. Variables where transformed, but original names are used for clarity. n= 263.