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Mecanismos que afectan la diversidad beta (β) de especies leñosas en un bosque tropical seco

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Por medio de la presente, hago constar que el trabajo de tesis titulado "Mecanismos que afectan la diversidad β de especies leñosas en un bosque tropical seco", fue realizado en los laboratorios de la Unidad de Recursos Naturales del Centro de Investigación Científica de Yucatán, A.C. bajo la dirección de los Drs. José Luis Hernández Stefanoni y Juan Manuel Dupuy Rada, dentro de la Opción Ecología, Sistemática y Evolución, perteneciente al Programa de Posgrado en Ciencias y Biotecnología de Plantas de este Centro.

Atentamente,

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A la vida,

que me ha dado tanto, me ha dado la marcha de mis pies cansados,
con ellos anduve ciudades y charcos,
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RESUMEN

Determinar los mecanismos que originan y mantienen la diversidad β (la variación en la composición de especies) es un tema intensamente debatido en la ecología de comunidades. Dos de las principales teorías que han tratado de explicar esta variación son la teoría de la segregación de los nichos o filtrado ambiental, la cual se basa en el principio de exclusión competitiva y establece que dos especies que comparten el mismo nicho ecológico no pueden coexistir indefinidamente; y la teoría neutral de la biodiversidad, la cual se basa en el supuesto de que todas las especies son competitivamente iguales, pero tienen una capacidad de dispersión limitada para colonizar un sitio. Se ha demostrado que ambos mecanismos influyen en la diversidad β, pero su influencia varía en función de la escala espacial del estudio. Así mismo, la influencia relativa de cada mecanismo puede variar en función de los caracteres funcionales de cada especie. El objetivo de este estudio fue evaluar la importancia relativa del filtrado ambiental vs la capacidad de dispersión limitada a diferentes escalas (tamaños de grano), así como para tres diferentes síndromes de dispersión y formas de vida. Para ello muestreamos la vegetación leñosa en 276 sitios distribuidos en un paisaje de selvas secas, así como varios atributos del suelo; determinamos la edad sucesional de cada sitio y el síndrome de dispersión y la forma de crecimiento de cada especie; y analizamos la influencia de cada grupo de variables (del suelo, de la estructura del paisaje, de la estructura espacial de los sitios de muestreo, de la edad sucesional), a través de la partición de la varianza. La magnitud de la diversidad β fue mayor en el grano local que en el del paisaje, decreció con la edad sucesional y varió entre las formas de crecimiento y los síndromes de dispersión. Concluimos que la importancia relativa del filtrado ambiental y la dispersión limitada depende del tamaño de grano y que el filtrado ambiental es el factor más importante para la diversidad β de los síndromes de dispersión y las formas de crecimiento. También concluimos que los caracteres funcionales son elementos importantes a incorporar para entender los patrones de distribución de la diversidad β.

ABSTRACT

Determining the mechanisms that generate and maintain β diversity (the variation in species composition) is a subject of intense debate in community ecology. Two major theories put forward to explain this variation are the niche theory or environmental filtering, which is based on the principle of competitive exclusion, which states that two species that share the same ecological niche cannot coexist indefinitely; and the neutral theory of biodiversity, which is based on the assumption that all species are competitively equal, but have a limited dispersal ability to colonize a site. It has been shown that both mechanisms influence β diversity, but their relative influence varies depending on the spatial scale of the study, as well as on the functional characteristics of each species. The aim of this study was to assess the relative importance of environmental filtering vs limited dispersal ability at different scales (grain sizes), and for three different dispersal syndromes and growth forms. We sampled woody vegetation at 276 sites distributed over a landscape of tropical dry forests, and measured several soil attributes; we also determined the successional age of each site and the dispersion syndrome and growth form of each species, and analyzed the influence of each group of variables (soil, landscape structure, spatial structure of the sampling sites, successional age) through variance partitionig. The magnitude of β diversity was higher at the local grain size, decreased with successional age and varied among growth forms and dispersal syndromes. We conclude that the relative importance of environmental filtering and dispersal limitation depends on grain size, and that environmental filtering is the most important factor influencing β diversity of dispersal syndromes and growth forms. We also conclude that functional traits are important elements to incorporate to understand the distribution patterns of β diversity.

INTRODUCCIÓN GENERAL

El mundo natural es sumamente complejo; miles de especies interactúan juntas formando comunidades y ecosistemas. Por ejemplo, imaginémonos inmersos en medio de un bosque tropical o sumergidos en un arrecife de coral. En ambos escenarios estaremos rodeados por cientos de especies interactuando entre ellas. Ante esto, surge la siguiente pregunta: ¿cómo pueden todas estas especies coexistir? Por otro lado, si nos movemos en cualquier dirección en nuestros escenarios hipotéticos observaremos que algunas de las especies presentes varían, algunas desaparecen y otras nuevas aparecen en escena con respecto a nuestro sitio original; esta variación es llamada diversidad β. Esta variación en la composición nos lleva a la siguiente pregunta: ¿por qué cambian las especies a través del espacio? Responder estas preguntas ha sido una de las principales tareas de la ecología de comunidades desde sus inicios y ha sido tema de intensos debates (Shmida y Wilson, 1985; Leibold, 1995; Tuomisto *et al.*, 1995; Hubbell, 2001; Tuomisto *et al.*, 2003a, 200b; Leibold *et al.*, 2004; Legendre *et al.*, 2005).

Se han propuesto numerosas teorías para explicar la variación en la composición de especies o diversidad β, tales como la segregación de los nichos (también conocida como partición de los nichos o filtrado ambiental) (Hutchinson, 1957; Grubb, 1977), la facilitación (Schluter y Ricklefs, 1993), la complejidad trófica (Tilman y Pacala, 1993), los factores históricos (Gardner y Engelhard, 2008) y la teoría neutral (Hubbell, 2001; Condit *et al.*, 2002; Chave, 2004; Hubbell, 2005, 2006). Una de las teorías ecológicas que más apoyo ha recibido es la de la segregación de los nichos, la cual afirma que la composición y la abundancia de las especies son el resultado de las respuestas de cada especie a la heterogeneidad biótica y abiótica (Lu, 2011). Otra teoría más reciente es la teoría neutral unificadora de la biodiversidad y la biogeografía (Hubbell, 2001), la cual se basa en la equivalencia ecológica de las especies; es decir, asume que todos los individuos son competitivamente iguales, pero su probabilidad de colonizar un sitio está limitada por su capacidad de dispersión. En la última década se ha generado un amplio debate acerca de la importancia relativa de la segregación de los nichos *versus* la capacidad de dispersión limitada, de aquí en adelante, dispersión limitada.

Entre los numerosos factores ambientales que afectan la variación en la composición de especies se encuentran la topografía (Gallardo-Cruz *et al.* 2009; Svenning *et al.* 2010), las propiedades físico-químicas del suelo (Paoli, 2006), la sucesión secundaria (Dupuy *et al.*, 2012), la fragmentación (Fahring, 2003; Cayuela *et al.*, 2006; Debuse *et al.*, 2007), el clima (Early y Sax, 2011; Dobrovolski *et al.*, 2012; Golicher *et al.*, 2012) y la estructura espacial –causada por la dispersión de los

propágulos, la agregación de las poblaciones o los disturbios (Bacaro y Ricotta, 2007; Beck y Vun Ken, 2007; Morlon *et al.*, 2008; Gallardo-Cruz *et al.*, 2010; Bonada *et al.*, 2012; Brownstein *et al.*, 2012)– entre otros.

Los organismos y el ambiente están autocorrelacionados espacialmente (Legendre, 1989; Fortin, 2005), es decir, los valores de cualquier variable muestreada no son independientes de la distancia geográfica entre las muestras –mientras más cercanas, son más similares (autocorrelación positiva) ó menos similares (autocorrelación negativa) de lo que se esperaría al azar. Este fenómeno es inherente a todos los procesos ecológicos y se observa en todas las escalas espaciales. Si bien la autocorrelación espacial es un factor bien conocido, pocos estudios la han tomado en cuenta. Recientemente se ha utilizado la autocorrelación espacial como una manera indirecta de estimar la importancia relativa de la dispersión limitada de las especies para evaluar la importancia relativa de la teoría neutral (Chust *et al.*, 2006).

La habilidad de la plantas para dispersarse es un elemento crítico en su historia de vida y tiene implicaciones en la persistencia, la migración y el reclutamiento de las especies (Howe y Smallwood, 1982; Levin *et al.*, 2003). Se ha observado que el síndrome de dispersión y la morfología de las semillas están fuertemente asociadas con la distribución espacial de cientos de especies de árboles, y por lo tanto con la conformación de las comunidades (Seidler, 2006). Asimismo, Grubb (1977) sugirió que la complementariedad en la utilización de los recursos es el resultado evolutivo de las respuestas de las especies a las variaciones ambientales, lo que le permite a las especies segregar sus nichos a fin de evitar la exclusión competitiva. En este contexto, Medina (1995) observó una fuerte relación entre las formas de crecimiento y la heterogeneidad ambiental en bosques secos.

Considerando que los procesos ecológicos ocurren a diferentes escalas espaciales y temporales, Levin (1992) sugirió prestar atención a la escala como un medio para entender la variación en los patrones naturales. De acuerdo con esta idea, algunos autores como Nekola y White (1999), Gravel *et al.* (2006) y Leibold (2006) han sugerido que diversos mecanismos actúan de modo conjunto dependiendo de la escala espacial en la cual se observan. Por ejemplo, a escala local, factores como los nutrimentos del suelo, la topografía y la sucesión secundaria son elementos clave en la variación en la composición de especies leñosas (Tuomisto *et al.*, 2003a; Paoli *et al.*, 2006), mientras que a meso-escala, también llamada de paisaje, se ha sugerido que la fragmentación es un promotor de la variación en la composición a través de mecanismos como el efecto de borde o el aislamiento de las poblaciones.

El conjunto de mecanismos propuestos para explicar el mantenimiento de la diversidad de especies en comunidades ecológicas de organismos sésiles, tales como la segregación de los nichos

ecológicos y la dispersión limitada, deben incluir características intrínsecas de las especies que nos ayuden a entender el papel de la segregación de los nichos, así como de los procesos de dispersión propios de la teoría neutral. Aunque se ha demostrado que ambos mecanismos intervienen en la composición de las comunidades (Gravel, 2006), aún queda mucho por aprender acerca de su importancia relativa.

La mayoría de los estudios sobre los mecanismos que afectan la diversidad β han sido desarrollados en bosques templados o tropicales húmedos (Hubbell, 2001; Condit *et al.*, 2002; Chust *et al.*, 2006; Paoli *et al.*, 2006). Sin embargo, la marcada estacionalidad hídrica de los bosques tropicales secos (BTS) les confiere una dinámica totalmente diferente a la de los bosques tropicales húmedos, ya que afecta el crecimiento de las plantas, su supervivencia, su fenología y su distribución (Poorter, 2006). Por lo tanto, es importante determinar la influencia relativa de los mecanismos potencialmente responsables de la variación en la composición de especies leñosas a diferentes escalas espaciales, así como para diferentes síndromes de dispersión y formas de crecimiento en los bosques secos, para establecer esquemas de conservación así como para contribuir a entender la dinámica ecológica de dichos bosques.

El objetivo general de esta tesis fue evaluar la importancia relativa de la heterogeneidad ambiental y la estructura espacial de las comunidades de plantas sobre la diversidad β a diferentes escalas espaciales (considerando el tamaño de la unidad de observación –grano–) y para tres diferentes síndromes de dispersión y formas de crecimiento. Para ello se plantearon las siguientes preguntas: ¿cuál es la importancia relativa de la edad sucesional, la heterogeneidad ambiental, la estructura del paisaje y la autocorrelación espacial sobre la diversidad β en un bosque tropical seco?, ¿cómo varía la magnitud de la diversidad β y la influencia relativa de los factores, procesos y mecanismos que influyen en ella a diferentes resoluciones de grano espacial?, ¿cuál es la importancia relativa de la edad sucesional, la heterogeneidad ambiental y la autocorrelación espacial de las muestras sobre la diversidad β de especies con diferentes síndromes de dispersión y formas de crecimiento?, ¿qué diferencias hay en la riqueza de especies de tres diferentes síndromes de dispersión y formas de crecimiento con respecto a la edad sucesional?

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Capítulo 1

Antecedentes, hipótesis y objetivos

1.1 ANTECEDENTES

1.1.1 Diversidad β

Los ecólogos de comunidades, al analizar la diversidad de especies desde una perspectiva espacial, tradicionalmente reconocen tres componentes de la diversidad de especies: la diversidad alfa (α), la diversidad beta (β) y la diversidad gama (γ). La diversidad alfa describe el número de especies en una parcela o hábitat, mientras que la diversidad gama describe el número de especies observado en el conjunto total de parcelas o comunidades que integran un paisaje (Halffter, 2003; Legendre *et al.*, 2005). A diferencia de los conceptos anteriores, la diversidad β describe la diferencia en la composición de especies entre al menos dos unidades de muestreo diferentes y captura una faceta fundamental de los patrones espaciales de la diversidad (Whittaker, 1960, 1972; Wilson y Schmida, 1984; Schmida y Wilson, 1985).

A pesar de que se ha propuesto un gran número de medidas de diversidad β, no existe un consenso general acerca de la función matemática más apropiada para responder las preguntas ecológicas (Arita y Rodriguez, 2002). Por ejemplo, Wilson y Shmida (1984) y Koleff *et al.* (2003) en sus revisiones sobre este concepto encontraron 8 y 24 diferentes formas de medir la diversidad β, respectivamente. Actualmente, los ecólogos de comunidades agrupan las medidas de diversidad β en dos grandes conjuntos, (1) las métricas clásicas de diversidad β calculadas a partir de las diversidades γ (regional) y α (local) y basadas únicamente en el número de especies; y (2) las medidas multivariadas calculadas con base en la comparación de la similitud o disimilitud entre unidades de muestreo, que puede incorporar la abundancia, la cobertura o la biomasa de las especies (Anderson *et al.*, 2010).

Dentro del grupo multivariado se distinguen dos conceptos esenciales: *recambio* (cambio direccional) y *variación* (cambio no direccional). Por un lado, el *recambio* evalúa el cambio en la composición o la abundancia de la comunidad de una unidad de muestreo a otra, a lo largo de un gradiente espacial, temporal o ambiental, y puede ser expresado como la velocidad de caída en la similitud con la distancia entre sitios (Nekola y White 1999; Qian y Ricklefs, 2007). Por otro lado, la *variación* corresponde al cambio en la composición o abundancia de especies entre sitios de muestreo dentro de una extensión espacial dada, sin hacer referencia a un gradiente

ambiental o dirección, y tiene una correspondencia directa con la dispersión multivariada o varianza en la composición de especies (Legendre *et al.*, 2005; Anderson *et al.*, 2006, 2010).

Las medidas clásicas de la diversidad β no ofrecen información sobre los factores que la afectan. Por el contrario, las medidas multivariadas pueden ser analizadas a través de la partición de la varianza con regresiones múltiples de matrices que representan relaciones entre ellas (Borcard *et al.*, 1992, 2011), tales como el análisis de redundancia canónica (RDA). Los análisis matriciales consisten en el análisis simultáneo de dos matrices, una matriz de respuesta (Y) que está relacionada con una matriz explicativa (X), y brindan elementos estadísticos para cuantificar los efectos relativos de diferentes grupos de variables explicativas (ter Braak, 1986; Legendre, 1993; Borcard *et al.*, 2004). Dicho planteamiento ha dado origen a dos enfoques: el primero de ellos plantea la utilización de matrices conformadas por datos crudos en el análisis, por ejemplo la abundancia de las especies en un conjunto de sitios, mientras que el otro plantea la utilización de matrices de distancia o disimilitud (Borcard *et al.*, 2004; Tuomisto y Ruokolainen, 2006). Esta disyuntiva ha llevado a un debate en los últimos años acerca de cuál es el mejor enfoque para evaluar la variación en la diversidad β (Legendre *et al.*, 2005; Tuomisto y Ruokolainen, 2006; Arias-González *et al.*, 2008; Legendre, 2008; Tuomisto y Ruokolainen, 2008).

Tuomisto y Ruokolainen (2006) argumentan que ambos enfoques son válidos, e incluso complementarios; sin embargo, responden a preguntas diferentes. Para entender mejor este argumento, plantean tres niveles de abstracción (similares a los planteados por Legendre *et al.* (2005), excepto por el primer nivel de abstracción). El primer nivel está formado por la composición de una población o comunidad representada por matrices de datos crudos, las cuales consisten en la abundancia de una o más especies en más de un sitio de estudio, en los que se tomaron las coordenadas geográficas y algunas variables ambientales. Con este nivel de abstracción se pueden responder preguntas como las siguientes: ¿puede la variación en la abundancia de una o más especies ser explicada por su posición geográfica o por las variables ambientales? El segundo nivel de abstracción deriva directamente del primero y consiste en la variación de la composición entre sitios (diversidad β), es decir, la identidad o la abundancia de las especies, y nos ayuda a responder las siguientes preguntas: ¿cuáles son los factores que afectan la diversidad β? El tercer nivel, a su vez, se deriva del segundo. Sin embargo, en este nivel se utiliza el enfoque de distancia o disimilitud y responde a la variación en la variación en la composición de especies. Por lo tanto, la secuencia es la siguiente: 1) composición de la comunidad → diversidad β (variación en la composición) → variación en la diversidad β (variación en la variación en la composición). En el presente trabajo nos

enfocamos en el segundo nivel de abstracción ya que nos interesa determinar qué factores afectan la variación en la composición de especies o diversidad β.

1.1.2 Teoría neutral

El principio de exclusión competitiva de Gausse establece claramente que dos especies que comparten el mismo nicho ecológico no pueden coexistir indefinidamente; por lo tanto, debe haber una diferenciación o división en sus nichos para que puedan coexistir (Etienne y Alonso, 2007). Sin embargo, algunos ejemplos en la naturaleza presentan un gran número de especies que coexisten a pesar de que utilizan los mismos recursos de formas muy similares. Un ejemplo de esto es la paradoja del plancton, donde cientos de especies de plancton sobreviven en unos pocos litros de agua de mar. Hubbell (2001) planteó una posible solución a dicha paradoja, argumentando que la coexistencia de especies en una escala regional es el resultado de un equilibrio estocástico entre la especiación y la extinción, y a una escala local es el resultado de procesos de inmigración y extinción local –ya sea por muerte o por migración–.

La teoría neutral unificadora de la biodiversidad y la biogeografía puede definirse de la siguiente manera: la presencia conjunta de especies de un mismo nivel trófico en un sitio es el resultado de una oportunidad aleatoria de dispersión, en donde se supone que todos los individuos inmersos en la comunidad presentan las mismas probabilidades de nacer, morir, migrar o sufrir especiación, sin que estos eventos estén afectados por las interacciones entre ellos, siendo la capacidad de dispersión limitada el factor clave en la colonización y el establecimiento de las especies, y por consecuencia, en la diversidad biológica (Hubbell, 2001). Sin embargo, varios estudios han evidenciado que la dispersión limitada no es el único mecanismo que actúa sobre la composición y la abundancia de las especies, y es evidente que la segregación de los nichos ecológicos juega un papel fundamental en la diversidad β (Tuomisto y Poulsen, 1996; Ruokolainen y Tuomisto, 2002; Tuomisto *et al.*, 2003a, 2003b, 2012).

1.1.3 Segregación de los nichos ecológicos

Muchas de nuestras ideas acerca de la variación espacial en la composición de especies se basan en la premisa mecanicista de la teoría de la segregación de los nichos ecológicos. El papel de este proceso ha sido invocado con frecuencia como la principal fuerza generadora de biodiversidad. Esta teoría propuesta inicialmente por Grinnell (1917) ha tenido una larga lista de revisiones y adhesiones por numerosos autores (Grinnell, 1917; Hutchinson, 1957; Vandermeer,

1972; Grubb, 1977; Leibold, 1995; Amarasekare, 2003), todas ellas fundamentadas en el mecanismo de exclusión competitiva y en la heterogeneidad como fuente de variación en el uso diferencial de los recursos limitantes (Tilman, 1994).

La segregación de los nichos involucra un gran número de factores bióticos y abióticos, así como interacciones positivas y negativas, que actúan en diferentes planos, o como lo definiría Hutchinson (1957) en diferentes ejes de un espacio n-dimensional. La segregación puede ocurrir de tres formas básicas: (1) especies diferentes pueden especializarse en distintos recursos (partición clásica de los nichos); (2) diferentes especies pueden ser limitadas por los mismos recursos o enemigos naturales, pero difieren en términos de cuándo ellas explotan los recursos o responden a los enemigos naturales (segregación temporal de los nichos); y (3) difieren en cuanto al sitio en el que responden o son limitadas por los enemigos o los recursos respectivamente (segregación espacial de los nichos) (Chesson 2000). Así, para la coexistencia de las especies se requiere que respondan diferencialmente tanto ante los recursos y las condiciones limitantes como ante los enemigos naturales en algunas de estas tres formas básicas, de modo que la presión de competencia sea más fuerte a nivel intraespecífico que a nivel interespecífico (Tilman, 1994; Chesson, 2000).

Cada vez más se acepta la idea de que el ambiente está espacialmente estructurado, es decir, que los factores ambientales presentan variaciones asociadas significativamente con la distancia espacial (Wiens, 1989). Por ejemplo, algunos autores han sugerido que las características del suelo están espacialmente estructuradas y pueden ser un factor determinante en la modelación de las comunidades de plantas (Tuomisto y Poulsen, 1996; Clark *et al.*, 1999; Bell *et al.*, 2000; Tuomisto *et al.*, 2003a; Costa *et al.*, 2005; Mejía-Domínguez *et al.*, 2012), debido a que las características del suelo varían continuamente en el espacio, y ofrecen un amplio conjunto de posibilidades para el establecimiento de una gran diversidad de especies. Asimismo, estudios como los realizados por Lapin y Barnes (1995) y Nichols *et al.* (1998) muestran que la variación en la estructura física (*e.g.* textura, tipos de suelo, drenaje del suelo), dentro y entre hábitats, proporciona elementos útiles en la predicción de la riqueza de especies de plantas.

Numerosos estudios apoyan el papel de la heterogeneidad en las propiedades del suelo como un elemento clave para entender la diversidad β (Ruokolainen *et al.*, 1997; Sabatier *et al.*, 1997; Clark *et al.*, 1998; Tuomisto *et al.*, 2003b; Costa *et al.*, 2005; Paoli *et al.*, 2006). Sin embargo, se ha argumentando que algunos factores tales como disturbios, la dispersión de las semillas, la herbivoría, las enfermedades o el azar son factores más importantes para entender la variación en la composición de especies leñosas (Duivenvoorden, 1995; Condit *et al.*, 2002). Levin (1992) sugiere poner atención a la escala espacial como un

medio para entender la variación en los patrones naturales. Por lo tanto, de acuerdo con Levin (1992), algunos autores como Nekola y White (1999), Gravel *et al.* (2006) y Leibold (2006) sugieren que diversos mecanismos actúan de modo conjunto para explicar la diversidad β y que su importancia relativa varía según la escala espacial a la que se observen.

1.1.4 Sucesión secundaria

Entre los procesos que promueven la heterogeneidad, tanto biótica como abiótica, se encuentra la sucesión secundaria, la cual puede ser definida como el cambio direccional a largo plazo en la composición de una comunidad después de un evento de perturbación (Chazdon 2008). Dicho proceso puede ser desencadenado ya sea por eventos naturales (e.g. huracanes, inundaciones, deslizamientos de tierra, tormentas, ciclones y/o incendios), o por actividades humanas como el cambio de uso de suelo –conversión a otros usos humanos como agricultura o ganadería– (Chazdon 2003).

En el último siglo, las altas tasas de deforestación y fragmentación en las regiones tropicales han transformado gran parte de la cobertura forestal en vegetación secundaria con diferentes edades de sucesión después del abandono (Murphy y Lugo, 1986; Miles *et al.*, 2006; Pennington *et al.*, 2009). Esto ha llevado a que los bosques tropicales sean los ecosistemas más amenazados del mundo (Miles *et al.*, 2006), por lo que el entendimiento de la dinámica sucesional y su influencia sobre la variación en la composición de especies leñosas tiene implicaciones importantes en el desarrollo de estrategias de conservación de los bosques tropicales (Sánchez-Azofeifa, *et al.*, 2005).

Muchos estudios han abordado el tema de la sucesión secundaria a fin de entender y modelar los cambios que ocurren durante este proceso, tanto en la estructura y la composición de la comunidad (Guariguata, 1997; Peña-Claros, 2003; Lebrija-Trejos *et al.*, 2008, 2010a, 2010b; Toledo, 2011), como en el ambiente asociado (Breugel *et al.*, 2007, Chazdon, 2008), entre otros tópicos. Todos estos estudios han contribuido de manera importante al desarrollo de la teoría de sucesión ecológica, así como al desarrollo de prácticas de manejo y restauración de los bosques tropicales. Sin embargo, la mayoría de los estudios acerca de la sucesión secundaria se han realizado en bosques templados y en bosques tropicales húmedos (Finegan 1996; Chazdon *et al.* 1998), a pesar de que los BTS cubren un área mayor y se encuentran menos protegidos (Miles *et al.*, 2006; Quesada *et al.*, 2009). La marcada estacionalidad de los BTS hace imposible extrapolar los avances obtenidos en la teoría sucesional de los bosques tropicales húmedos (Ewel, 1980; Finegan, 1996; Chazdon 2008); los procesos y las rutas de la sucesión varían entre estos dos tipos de bosque

reflejando diferencias en cuanto al ambiente, la estructura, la composición y las formas de crecimiento (Guariguata, 1997; Vieira, 2006; Lebrija-Trejos *et al.*, 2010b; Dupuy *et al* 2012). A diferencia de los bosques húmedos, la estructura de las selvas secas es más simple, ya que presentan una estatura baja y pocos estratos de dosel, además de que la diversidad de especies es menor (Murphy y Lugo, 1986). Además, un gran número de especies presentan dispersión anemócora (Ceccon *et al.*, 2006) y una alta capacidad de rebrote después de un disturbio (Murphy y Lugo, 1986; Vesk y Westoby, 2004), lo que podría conferirles una mayor resiliencia –capacidad de un sistema de regresar a un estado previo o de mantener características estructurales y funcionales ante un disturbio (Holling, 1973; Lebrija-Trejos *et al.*, 2008)–.

1.1.5 Escala espacial

La escala espacial se define como la dimensión física de un objeto o proceso ecológico en el espacio (Turner, 1989). Los ecólogos han reconocido durante décadas la importancia de la escala, así como sus implicaciones en los procesos y patrones ecológicos. Sin embargo, no fue sino hasta finales de la década de 1970 cuando comenzó a recibir más atención (Wiens, 1989).

Para entender el concepto de escala hay que tener en cuenta que diferentes elementos ecológicos ocupan diferentes extensiones y tienen distintos radios de acción. Por ejemplo, el área que requiere una salamandra para desarrollarse será varios cientos de metros mayor que el área requerida por un ácaro, pero varios miles de metros menor que el ámbito de acción de un puma. De igual forma, al referirnos a la asimilación de CO_2 hablamos de micromoles por metro cuadrado, mientras que si hablamos de cobertura de paisaje será en hectáreas o kilómetros cuadrados (Turner, 1989; Turner *et al.*, 1989; Turner, 2005a, 2005b). Por lo tanto, se puede asegurar que todo proceso ecológico se encuentra enmarcado en el concepto de escala y la variabilidad que este factor le confiere al proceso en cuestión (García, 2006). Es decir, todos los fenómenos ecológicos muestran (en alguna medida) una dependencia de la escala (Farina y Belgrano, 2006), lo que ha atraído la atención de muchos ecólogos en los últimos tiempos (Schneider, 2001).

Para evaluar la importancia de la escala espacial debemos descomponerla en dos componentes, que son el grano y la extensión. El grano se define como la unidad mínima de resolución en el muestreo utilizado en un estudio (por ejemplo: el tamaño del pixel para datos en formato raster o el tamaño de la unidad de observación) y deberá ser lo suficientemente reducido para evitar que las variaciones finas de un fenómeno pasen desapercibidas. A su vez, la extensión es la dimensión espacial o la superficie máxima cubierta por el muestreo en el estudio y deberá ser lo suficientemente amplia como para albergar toda la variabilidad del fenómeno estudiado, ya que una extensión reducida en

relación a la escala real del fenómeno podría capturar sólo una pequeña parte de la variación (Turner, 2005a; García, 2006; García y Chacoff, 2006). Es importante tomar en cuenta que, desde una perspectiva estadística, no es posible extrapolar resultados más allá de la población o la comunidad muestreada, ni tampoco es posible inferir diferencias entre objetos más pequeños que la unidad experimental misma. En síntesis, cuando se evalúan patrones del paisaje, no es posible detectarlos más allá de la extensión del paisaje o por debajo de la resolución del grano (Wiens, 1989).

En las últimas décadas se han desarrollado trabajos con enfoques multi-escalares, pero la mayoría de ellos están abocados al análisis de la variación en los patrones de la diversidad de especies (Bond y Chase, 2002; Økland *et al.*, 2006; Szabo y Meszéna, 2007; Costanza *et al*,. 2011), o al efecto de la fragmentación en la diversidad de especies (Holmes *et al.*, 2005; Økland *et al.*, 2006; Honorio-Coronado *et al.*, 2009; Pickett y Siriwardena, 2011).

Se ha observado de modo sistemático que la variación en la composición depende de la escala. Sin embargo, aún se discute la escala a la que actúa cada mecanismo. Por ejemplo, Girdler y Berrie (2008) sugieren que en comunidades de plantas y a escalas pequeñas el mecanismo principal que afecta la diversidad β es la capacidad de dispersión limitada. Del mismo modo, Condit *et al.* (2002) y Chust *et al.* (2006) encontraron que la dispersión limitada explicó la variación en la composición en un estudio llevado a cabo en Barro Colorado, Panamá. Sin embargo, Keil *et al.* (2010, 2012) observaron a la misma escala en diferentes taxones que el filtrado ambiental es el mecanismo principal que promueva la diversidad β.

1.1.6 Estructura del paisaje

La ecología del paisaje evalúa la respuesta de los organismos, las poblaciones o las comunidades frente a condiciones y recursos que son heterogéneos en el espacio, así como la autocorrelación, definida como la propiedad estadística de la mayoría de las variables ecológicas que representa la relación entre los valores de una variable dada a diferentes distancias geográficas (Legendre, 1993; Turner, 2005a). Uno de los principales aportes de la ecología del paisaje ha sido la incorporación de la variación espacial para entender la complejidad de los procesos ecológicos que ocurren en la naturaleza (Wagner y Fortin, 2005); ya que los patrones espaciales son un aspecto fundamental en el estudio de las comunidades de plantas debido a que pueden afectar su establecimiento así como el de los organismos con los que interactúan (Turner *et al.*, 1989).

En el marco de esta disciplina, un paisaje puede ser visto como un mosaico de elementos o fragmentos de diferentes tipos de hábitat

(Dale, 1999), cuyas propiedades básicas son la composición (el número y la frecuencia relativa de los tipos de hábitats) y la configuración (el arreglo espacial de los elementos) (Gustafson, 1998). Usualmente, el arreglo espacial de la distribución de las plantas no es aleatorio, lo cual sugiere que existe una serie de factores que causan los patrones espaciales. Por ejemplo, Hill y Curran (2003) afirman que la fragmentación del bosque provoca una disminución en el número de especies y altera la composición de la comunidad como resultado de un incremento en el aislamiento de los fragmentos de bosque remanentes, lo cual tiene repercusiones importantes en las interacciones establecidas en la comunidad, así como en el sistema de metacomunidades adyacente (Laurance *et al.*, 2002; Benítez-Malvido y Martínez-Ramos, 2003; Chust *et al.*, 2006) –definido como el conjunto de comunidades locales conectadas a través de la dispersión de al menos algunas de las especies que las componen (Leibold *et al.*, 2004)–.

Las métricas del paisaje son índices diseñados para evaluar la estructura del paisaje, los cuales son calculados con base en el área, el perímetro, la distancia y el número de parches que integran el paisaje. Estas métricas a menudo son utilizadas como medidas de heterogeneidad ambiental y suelen ser asociadas con procesos ecológicos (Gustafson, 1998; Turner *et al.*, 2001; Hernández-Stefanoni, 2005; Farina, 2006). Esta asociación se basa en el supuesto de que los patrones espaciales y las características de los elementos del paisaje pueden ser buenos predictores de la diversidad. A pesar de la influencia que tiene la heterogeneidad espacial sobre los patrones de diversidad, la mayoría de las métricas se han utilizado como variables predictivas de la diversidad α, al igual que ha sucedido con la heterogeneidad ambiental, mientras que la diversidad β ha sido considerada sólo ocasionalmente en los estudios de ecología del paisaje.

Una de las ventajas de las métricas de paisaje es que son fáciles de obtener y su cálculo es menos demandante en términos de tiempo y dinero que recolectar de modo detallado datos sobre la abundancia y distribución de las especies (Schindler *et al.*, 2008). En las últimas dos décadas ha habido una proliferación de medidas o índices de la estructura del paisaje (Gustafson, 1998; He *et al.*, 2000), lo cual ha generado cierto grado de incertidumbre con respecto a cuál puede ser la mejor forma de medir la estructura del paisaje; de hecho, en la actualidad hay muchas métricas que son funcionalmente redundantes, es decir, que índices diferentes ofrecen la misma información. Esto se debe a que la mayoría de dichos índices se construyen con base en el diámetro y el área de los elementos del paisaje (Cushman *et al.*, 2008). Entre las métricas más utilizadas que presentan menor grado de correlación entre sí se encuentran las que ofrecen información sobre el grado de agregación de los tipos de elementos del paisaje, así como sobre la diversidad y equidad de los elementos (Contagion/diversity), el

grado de dominancia de un tipo de elemento (Large Patch dominance), el grado de contraste entre los elementos (Edge constrast), y la variación en la forma del elemento (Path shape variability), entre otras muchas métricas (McGarigal *et al.*, 2002; Cushman *et al.*, 2008).

1.1.7 Síndromes de dispersión y formas de crecimiento

El síndrome de dispersión y la forma de crecimiento son características que varían entre las especies vegetales, y se ha postulado que juegan un papel importante en el mantenimiento de la biodiversidad (Chase, 2003). Por un lado, la dispersión es el mecanismo predominante por medio del cual las especies de plantas pueden moverse a través del espacio (Harper, 1977), pero además es un elemento crítico para la supervivencia de las mismas bajo los actuales niveles de fragmentación del hábitat y aislamiento entre fragmentos remanentes, así como ante el cambio climático (Vittoz y Engler, 2007).

Para que una planta se reproduzca con éxito, una vez formadas sus semillas éstas deben escapar de la competencia intra- e interespecífica y de la depredación, por lo que es necesario que se dispersen. Por lo anterior, los mecanismos de dispersión de semillas juegan un papel fundamental en la colonización de nuevos hábitats (Strykstra *et al.*, 2002). La dispersión genera un nuevo patrón espacial en la distribución de los individuos, el cual tendrá repercusiones en las áreas potenciales de reclutamiento, sentará bases para procesos como la depredación y la competencia, y tendrá implicaciones en la conformación de la composición, la diversidad y la estructura de las comunidades (Nathan y Muller-Landau, 2000; Strykstra *et al.*, 2002; Nathan *et al.*, 2008, 2011). Aunque la dispersión de semillas debería ser incluida como un elemento importante en la modelación de la distribución de especies, no ha sido tomado en cuenta con frecuencia (Guisan y Theurillat, 2000; Guisan y Thuiller, 2005; Thuiller *et al.*, 2008).

No todas las especies leñosas tienen la misma estrategia de dispersión. Por el contrario, cada una de ellas presenta diferencias como resultado de la selección natural, las cuales posiblemente les confieren ventajas en el reclutamiento de nuevos individuos y en la colonización de nuevos sitios (Moreno-Casasola, 2002). En la naturaleza se ha distinguido una gran variedad de síndromes de dispersión, cuyas diferencias radican en el tamaño de la semilla, las estructuras morfológicas de las mismas, las características químicas, el color, la presencia de pulpa y la fenología de la producción de frutos, entre otros factores (Moreno-Casasola, 2002). Moreno-Casasola (2002) propone que la dispersión de las especies no es aleatoria sino que este proceso está íntimamente ligado al concepto del "sitio seguro", definido por Harper *et al.* (1995) como un área que presenta condiciones apropiadas para la germinación y el establecimiento.

En este trabajo nos abocamos a tres grandes grupos de síndromes de dispersión: la anemocoria –especies que presentan estructuras especiales que les permiten usar las corrientes de viento para dispersarse –, la autocoria –especies que no requieren de la ayuda de un vector externo para su dispersión –, y la zoocoria –especies que son dispersadas por algún animal, ya sea de modo voluntario (a través de la ingesta del fruto) o de modo involuntario (a través del transporte en el cuerpo, e.g. semillas con espinas)–.

Por otro lado, las formas de crecimiento de las plantas expresan una diversificación en las estrategias de apropiación de los recursos y son un elemento clave a tomar en cuenta para entender la influencia del filtrado ambiental en la configuración de las comunidades de plantas (Grubb, 1977). La complementariedad entre las formas de crecimiento puede ser el mecanismo a través del cual se puede explicar la coexistencia de muchas especies de plantas que no difieren en el uso de los recursos básicos de luz, agua y nutrientes, pero que a través de su variación morfológica evitan o reducen la competencia (Silvertown, 2004). En resumen, se puede decir que las diversas formas de crecimiento representan una respuesta morfo-fisiológica a las variaciones ambientales. Asimismo, se ha observado una fuerte asociación entre las formas de crecimiento y la sucesión secundaria, y en consecuencia con el filtrado ambiental (Bazzaz, 1998). Sin embargo, no existe evidencia de cuál pueda ser la influencia relativa de la dispersión limitada y el filtrado ambiental sobre la forma de crecimiento.

1.1.8 Bosques tropicales secos

Los bosques tropicales cubren aproximadamente 40% del área total de la Tierra, proporción de la cual 42% está clasificado como bosques tropicales secos (BTS) (Murphy y Lugo, 1986). Mooney *et al.* (1995) definieron a los BTS como los bosques distribuidos en regiones tropicales donde se presenta una marcada estacionalidad hídrica y, en consecuencia, una fuerte sequía estacional.

Estudios como los de Janzen (1988) y Miles *et al.* (2006) reportan que los BTS son los bosques más amenazados del mundo, ya que, por un lado, menos de 2% de su área total se encuentra bajo algún estatus de protección y por otro lado, gran parte de su cobertura ha sido transformada a una compleja matriz de agricultura y pastizales, mientras que los remantes se encuentran sujetos a una fuerte presión antropogénica (Janzen, 1988; Miles *et al.*, 2006; Quesada *et al.*, 2009). Sin embargo, aun con esta problemática, la mayoría de los estudios que abordan los patrones y mecanismos que afectan la diversidad de especies han sido desarrollados en bosque templados o tropicales húmedos (Hubbell, 2001; Condit *et al.*, 2002; Chust *et al.*, 2006; Paoli *et al.*, 2006).

A diferencia de los bosques húmedos, los bosques tropicales secos (BTS) presentan una marcada estacionalidad hídrica, la cual tiene profundas implicaciones en la estructura y composición de estos bosques. Dichas características tienen una fuerte influencia sobre el crecimiento de las plantas, la supervivencia, la fenología, las interacciones, sus formas de crecimiento y sus síndromes de dispersión, así como en su distribución (Poorter *et al.*, 2006). Por lo tanto, determinar la influencia relativa de los mecanismos que afectan la variación en la composición de especies leñosas a diferentes escalas espaciales, y para diferentes síndromes de dispersión y formas de crecimiento tiene fuertes implicaciones en el desarrollo de la teoría ecológica en este tipo de ecosistemas, así como para el planteamiento de estrategias de manejo y conservación.

1.2 JUSTIFICACIÓN

El estudio de la diversidad β de plantas leñosas es un tema que ha despuntado con renovado interés en la última década por dos razones, (1) la creciente preocupación que ha generado el aceleramiento del cambio climático y la necesidad de entender sus efectos sobre la biodiversidad, y (2) por el replanteamiento de la teoría neutral unificadora de la biodiversidad y la biogeografía de Hubbell (2001). Dichas razones ha motivado la realización de numerosos estudios que contraponen procesos mecanicistas (segregación de los nichos) vs. procesos estocásticos (dispersión limitada) en casi todos los taxones biológicos, pero con una marcada tendencia hacia los bosques templados y tropicales lluviosos (Nekola y White, 1999; Tuomisto *et al.*, 2003b; Gilbert y Lechowicz, 2004; Soininen *et al.*, 2007; Kembel, 2009; Vergnon *et al.*, 2009; Stokes y Archer, 2010; Adler *et al.*, 2012; Kristiansen *et al.*, 2012; Tuomisto *et al.*, 2012). Ambos mecanismos pueden actuar de manera combinada pero a diferentes escalas espaciales lo cual hace imprescindible entender la escala espacial de acción de cada mecanismo (Shmida y Wilson, 1985; McGill, 2010).

Además, se ha observado que propiedades inherentes a las especies como los síndromes de dispersión y la forma de crecimiento pueden tener fuertes implicaciones en la dinámica de poblaciones y de las comunidades, por ejemplo en la probabilidad de dispersión asociada a cada síndrome o la capacidad de explotar los recursos de cada forma de crecimiento. Por lo tanto, es necesario incorporar estos dos factores para alcanzar un entendimiento más detallado de los mecanismos que generan y mantienen la diversidad de especies leñosas (Sobral Griz y Machado, 2001; Vittoz y Engler, 2007; Muller-Landay *et al.*, 2008; Jacobi y Carmo, 2011).

1.3 OBJETIVOS

1.3.1 Objetivo general

Evaluar la importancia relativa de la heterogeneidad ambiental (como medida indirecta de la segregación de los nichos) y la estructura espacial (como medida indirecta de la dispersión limitada) en la diversidad β de plantas leñosas de un bosque tropical seco a diferentes escalas espaciales (tamaños de grano) y en función de tres diferentes síndromes de dispersión y formas de crecimiento.

1.3.2 Objetivos específicos

1. Determinar la diversidad β de especies leñosas a escala local y de paisaje en un paisaje de bosque tropical seco.
2. Determinar la configuración de los elementos del paisaje y el grado de fragmentación del paisaje de estudio.
3. Analizar la contribución relativa de la edad sucesional, la heterogeneidad ambiental, la estructura del paisaje y la autocorrelación espacial sobre la diversidad β de plantas leñosas en dos tamaños de grano espacial (local y de paisaje).
4. Determinar los síndromes de dispersión y la forma de crecimiento para cada una de las especies leñosas del sitio de estudio.
5. Determinar la contribución relativa de la heterogeneidad ambiental, la edad sucesional, así como la autocorrelación espacial sobre la diversidad β de tres síndromes de dispersión y tres formas de crecimiento.
6. Analizar cómo varía la riqueza de especies de los diferentes síndromes de dispersión y formas de crecimiento en función de la edad sucesional.

1.4 HIPÓTESIS

H1. Dado que la escala espacial afecta a los procesos ecológicos que generan y mantienen la diversidad de especies (Levin 1992) esperamos que la variación en la composición de especies leñosas (diversidad beta) varíe con la escala espacial. En particular y con base en el planteamiento original de Whittaker (1972) acerca de la diversidad β como el cociente γ/α (α=diversidad local, γ=diversidad a nivel de paisaje o región), predecimos que la magnitud de la diversidad β será mayor en el tamaño de grano local en comparación con el del paisaje, siempre y cuando la diversidad γ se mantenga constante.

H2. Dado que, a escala local, el gradiente de variación ambiental es menor que a escala de paisaje y que, por lo tanto, el número de nichos disponibles es menor en comparación con la escala de paisaje (Cadotte 2006, Paoli 2006), esperamos que el principal mecanismo promotor de la diversidad β sea la dispersión limitada a escala local y la segregación de nichos a escala de paisaje. Por lo tanto, predecimos que el mayor porcentaje de la variación total de la diversidad β será explicado por la estructura espacial a escala local y por el ambiente (calculado a través de las métricas del paisaje) a escala de paisaje.

H3. Se ha postulado que las características de las plantas, tales como las formas de crecimiento y los síndromes de dispersión son estrategias evolutivas desarrolladas en respuesta a los filtros ambientales (Grub, 1977; Howe y Smallwood, 1982; McGill *et al*, 2006; Webb *et al*, 2010). Por lo tanto, esperamos que la segregación de los nichos sea el principal mecanismo que explique la diversidad β de las formas de crecimiento y síndromes de dispersión. Asimismo, predecimos que las variables ambientales explicarán un porcentaje mayor de la diversidad β de las diferentes formas de crecimiento y síndromes de dispersión que la estructura espacial.

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Capítulo 2

Partitioning the variation of woody plant β-diversity in a landscape of secondary tropical dry forests across spatial scales [1]

2.1 ABSTRACT

Question: What is the relative importance of forest successional age, environmental heterogeneity, landscape structure and spatial structure of sampling sites on β-diversity of tropical dry forests? How does the magnitude of β-diversity as well as the relative influence of factors, processes and mechanisms on β-diversity differ at different spatial grains? What are the effects of stand age on β-diversity?
Location: Yucatán peninsula, México.
Methods: Floristic composition was obtained from a hierarchical survey performed in 276 sites distributed across 23 sampling landscapes [SL] (12 sites per SL). Land cover classes were derived from the classification of multi-spectral Spot 5 satellite imagery. We calculated landscape metrics of patch type and landscape for each SL, and characterized local soil conditions for each sampling site. A principal coordinates of neighbor Matrices (PCNM) analysis was performed to estimate spatial variables, and partial Redundancy Analysis (RDA) was used to decompose variation into spatial, stand age, and landscape structure components.
Results: The magnitude of β-diversity varied with spatial scale (grain size), and was larger at the local than at the landscape grain. The magnitude of β-diversity also decreased slightly but significantly with successional age. There were significant differences in species composition among vegetation classes. Environmental factors (local soil conditions, as well as landscape structure), and spatial structure both contributed to woody plant β-diversity in our Tropical Dry Forest landscape, but their relative importance was scale-dependent. At the local grain size, both the environment (mainly soil conditions) and spatial structure strongly affected β-diversity, while at the landscape grain, environmental factors (variation in soil conditions, as well as landscape configuration) played a more prominent role.
Conclusions: The magnitude of β-diversity decreased with increasing spatial grain and successional age, while the relative importance of

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mechanisms influencing β-diversity was scale-dependent: both niche partitioning and dispersal limitation affect β-diversity at the local grain size, while niche partitioning prevails at the landscape grain.
Keywords: dispersal limitation; landscape structure; niche partitioning; spatial structure of samples; species turnover; succession; tropical dry forests.

Nomenclature: APG II (2003)

2.2 INTRODUCTION

One of the fundamental goals of ecology, as well as a cause of intense debate during the last decades, is to unravel the factors, processes and mechanisms that drive β-diversity (Tuomisto *et al.*, 1995, 2003; Tuomisto 2010). This debate has been partly confounded by the diversity of concepts, methods and measures of β-diversity that have been used in the last few decades (Anderson *et al.*, 2010). There are two fundamental concepts of β-diversity: turnover and variation (Vellend, 2001; Anderson *et al.*, 2010). In this study we focus on β-diversity defined as a variation in community composition among sample units within a spatial extent, without any reference to a particular gradient or direction. Regardless of the concept used, there are two main types of measures of β-diversity: (1) classical metrics that consider only the number of species (presence-absence data) and provide a direct link between local (α) and regional (γ) diversity (Whittaker, 1960, 1972; Blackburn & Gaston, 1996), (2) multivariate measures, based on pairwise resemblances among sample units, which take into account species composition (abundance, biomass or cover). Since these two types of measures can yield very different results, it is essential to employ both to address different and complementary aspects of β-diversity. Clearly defining and measuring β-diversity as well as understanding the factors that affect it is important because it allows us to comprehend how species share the habitat (Condit *et al.*, 2002), and can guide and help evaluate management and conservation strategies at the local, landscape and regional level (Halffter, 1998; Nekola & White, 1999).

Different theories about the origin and maintenance of species diversity, such as the niche and the neutral theories, postulate contrasting underlying causes of variation in community composition –β-diversity (Pitman *et al.*, 1999; Condit *et al.*, 2002; Ruokolainen *et al.*, 2002; Tuomisto *et al.*, 2003). The niche theory (Hutchinson, 1957; Leibold, 2008) states that β-diversity is positively associated to environmental heterogeneity and that some species consistently perform better than others under certain environmental conditions. Consequently, species abundance is an indicator of how suitable the environmental conditions are for the species to grow and reproduce. Conversely, the

neutral theory establishes that all species are competitively equal and able to grow equally well in a range of environmental conditions, and that species composition fluctuates owing to dispersal limitation; if species assemblages are assumed to be spatially structured, it follows that sites that are close together will be more similar in composition than sites that are far apart (Hubbell, 2001; Condit *et al.*, 2002). More recently, some authors have suggested that the niche and neutral perspectives are endpoints of a continuum, and that variation in species composition cannot be explained completely either by the neutral or by the niche theory (Gravel *et al.*, 2006; Leibold & McPeek, 2006); therefore the challenge is to understand the relative contribution of these two processes (niche partitioning vs. dispersal limitation) to ecosystems β-diversity.

Landscape structure, measured as a function of the size, shape, similarity, contrast and other metrics of the geometry of patches (Gustafson, 1998; McGarigal *et al.*, 2002), can influence β-diversity through multiple processes such as deforestation, fragmentation, and the associated reduction of habitat, change in the amount of habitat edge, and increase in fragment isolation (Fahrig, 2003). Most studies on the effects landscape patterns on plant communities, however, focus on local number of species (α-diversity), while few studies address the effects of landscape structure on community composition (Hernández-Stefanoni *et al.*, 2011).

Secondary forest succession can also influence β-diversity, through changes both in species richness -classical metrics- and in species composition –multivariate measures– (see reviews by Guariguata & Ostertag (2001), Chazdon *et al.* (2007), Chazdon (2008), and Quesada *et al.* (2009) for tropical wet and dry forests). However, very few studies have explicitly explored successional changes in β-diversity or examined the influence of successional age on β-diversity of tropical forests (Chao *et al.*, 2005, 2006).

Moreover, the degree to which environmental factors affect variation in community composition depends on processes occurring at different spatial scales (Shmida & Wilson, 1985; Levin, 1992; McGill, 2010). For example, local species composition is influenced by species' abilities to compete for limited resources like water or nutrients (Tilman, 1994). In turn, at the landscape level (mosaic of different patches), species composition is influenced by dispersal and the existence of different habitats that allow the co-existence of species with different niches (Bell *et al.*, 2006). Therefore, the study of β-diversity should focus not only on the relative effects of different factors, but it should also evaluate how their relative influence changes across different spatial scales. Yet most studies examining the effects of environmental and spatial factors on β-diversity have focused on a single spatial scale (Balvanera *et al.*, 2002; Duivenvoorden *et al.*, 2002). Here, we examine one component of the scale, namely the grain (i.e. the size of the

observation unit), using two different sizes: 200 m^2 and 1 km^2, henceforth referred to as local and landscape grains, respectively.

Evaluating the relative influence of factors, processes and mechanisms on β-diversity at different spatial scales is especially relevant for tropical dry forests (TDFs) because of their particularly high levels of endemism, coupled with high rates of deforestation, degradation and fragmentation, and low levels of protection (Hoekstra *et al.*, 2005; Miles *et al.*, 2006; Pennington *et al.*, 2009; Portillo-Quintero & Sánchez-Azofeifa, 2010). The main objectives of this study were (1) to assess the effect of variation in spatial grain and forest successional age on the magnitude of β-diversity and (2) to evaluate the relative importance of environmental heterogeneity, forest successional age, landscape structure and spatial structure of sampling sites on variation in TDF species composition at two contrasting spatial grains (local and landscape). We used the same types of explanatory variables at both spatial grains. Through this procedure we were able to indirectly gauge the relative importance of niche segregation and of dispersal limitation on β-diversity in a TDF.

Several theoretical principles guided us in making four predictions to be examined in this investigation. First, we predicted that the magnitude of β-diversity would be greater at the local grain size compared to the landscape size –as long as gamma diversity remains constant (P1). This prediction is based on the widely accepted notion of β diversity as the gamma diversity/alfa diversity ratio, i.e. the division of the total number of species in a landscape or region by the mean number of species in a locality or plot (Magurran, 2004). Second, we predicted that the correlation between β-diversity and the explanatory variables would be stronger at the landscape grain than that at the local grain (P2). This prediction relies on the tenet that grain size produces a strong stochastic error component on the analysis of β-diversity: the smaller the grain, the larger the noise or stochastic error (Nekola & White 1999). Third, we predicted significant differences in species composition among successional age classes, and a decline in β-diversity as successional age increased (P3). This prediction is based on the well established changes in species composition, and increase in α diversity during Neotropical forest succession (Guarigata & Ostertag, 2001; Chazdon, 2008; Quesada *et al.*, 2009), which implies a corresponding decline in classical measures of β-diversity. Fourth, we predicted that the relative importance of environmental heterogeneity and landscape structure (which are indirect indicators of niche partitioning) vs. spatial structure of samples (an indirect indicator of dispersal limitation) would depend on the spatial grain: at the local grain, the influence of spatial structure of samples would dominate, whereas at the landscape grain environmental heterogeneity and landscape structure would have a greater influence on β diversity (P4). This prediction is based on the recently-observed scale-dependence of the relative importance of niche

partitioning and dispersal limitation (Bell, 2005; Cottenie, 2005); at the local scale, environmental gradients tend to be shorter thus providing less room for the packing of species with different niches, thereby increasing the relative importance of dispersal limitation and stochastic variation (He & Legendre, 2002; Dugue *et al.*, 2009). Conversely, moving to a larger spatial grain often results in an increase in environmental heterogeneity and a concomitant increase in among-site species similarity (reduction in β-diversity), thereby enhancing the importance of niche partitioning relative to dispersal limitation (Bell, 2005; Laliberté *et al.*, 2009; Borcard *et al.*, 2011).

2.3 METHODS

2.3.1 Study area

The study area (*ca* 22 × 16 km) is centrally located in the Yucatán Peninsula, Mexico (89°39'- 89°60'W, 20°01'-20°16'N). Climate is warm subhumid, with summer rains (May-October) and a marked dry season (November-April). Mean annual temperature is *ca* 26°C, and mean annual precipitation ranges from 1000 to 1200 mm. The landscape consists of Cenozoic (Eocene) limestone hills with moderate slopes (10-25°) alternating with flat areas; elevation ranges from 60 m to 160 m a.s.l. (Flores & Espejel, 1994). Soil heterogeneity is strongly associated with topography, with shallow, rocky Lithosols and Rendzines dominating the hills, and deeper, clayey Luvisols and Cambisols prevailing in the flat areas (Bautista-Zúñiga *et al.*, 2003). Prevailing vegetation is seasonally dry tropical forest (50-75% of the species drop their leaves during the dry season) with stands of different ages, i.e. time since abandonment after traditional slash-and-burn agriculture (Fig. 1). The forest is relatively low (canopy height ca. 8-12 m), with a few prominent trees attaining 15-18 m in the oldest (60-70 y-old) stands.

2.3.2 Remotely sensed data and image processing

A SPOT 5 satellite image (10 m spatial resolution) acquired in January 2005 was geo-referenced as well as radiometrically and atmospherically corrected to reduce the effect of atmospheric scattering. A false colour composite image was created from bands 2 (red), 3 (near infrared), and 4 (mid infrared) to identify suitable training sites for the different land-cover types, located in the field using a global positioning system (GPS) unit. At least three training sites were selected for each of the following land-cover types: (1) 3-8 y-old secondary forest (vegetation class 1: VC1); (2) 9-15 y-old secondary forest (vegetation class 2: VC2); (3) >15 y-old secondary forest on flat areas (vegetation class 3: VC3); (4) >15 y-

old secondary forest on hills (vegetation class 4: VC4), (5) agricultural fields; (6) urban areas and roads. The training areas and the false colour

2.3.3 Vegetation and environmental data

A hierarchical survey was performed to obtain field data during the rainy seasons of 2008 and 2009. First, we selected 23 sampling landscapes (SL) of 1 km^2 following a random design that encompassed the whole range of forest fragmentation conditions. Second, we randomly selected three sampling sites of 200 m^2 for each of the four vegetation classes (VC1-VC4) in each SL (12 sampling sites per SL, 276 sampling sites in total). If one or more vegetation classes were absent or highly under-represented in a given SL, additional sampling sites were randomly located in the existing vegetation classes in order to obtain 12 sampling sites per SL. Each sampling site was located using a GPS unit and consisted of a circular 200 m^2 plot where all woody plants > 5 cm in DBH (diameter at breast [1.3 m] height) were recorded and a concentric 50 m^2 subplot where all woody plants ≥ 1 cm in DHB were recorded. Stand age was determined for each site by interviewing local residents who had lived in the area for > 40 yr and owned or worked the land. Of the total number of sampling sites, 53 belonged to VC1, 75 to VC2, 86 to VC3, and 62 to VC4.

Local soil conditions were characterized by estimating percent surface stoniness and collecting three 10 cm-deep soil samples (*ca* 400 g each), at the centre and northern and southern limits of each sampling site. The three samples from each site were pooled to form a single

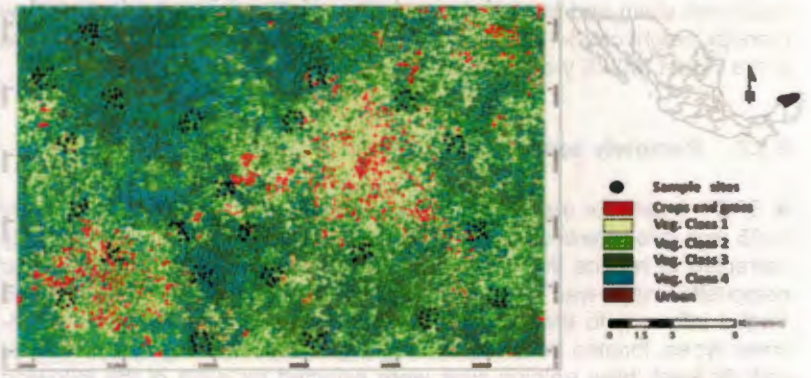

Figure 1.1 ***Location and land cover thematic map of the study area showing the location of sample plots.***

sample for physico-chemical analyses: pH in water (1:2 ratio), electric conductivity (EC; 1:5 extracts), cation exchange capacity (CEC; Olsen), soil organic matter (SOM, combustion or Walkley-Black), total nitrogen (N, Kjeldahl), available phosphorous (P, Bray), interchangeable potassium (K; with ammonium acetate), and soil texture (percent lime, clay and sand content, Bouyoucos). At the landscape level, we calculated the coefficient of variation for each soil variable and stand age using all sites within each SL. Finally, we obtained altitude and slope for each plot using a Digital Elevation Model (DEM) from the Instituto Nacional de Estadística, Geografía e Informática (INEGI).

2.3.4 Spatial data

A set of explanatory spatial variables was generated for each studied spatial grain using the principal coordinate of neighbor matrices (PCNM) analysis (PCNM, Borcard *et al.*, 2004) as well as the geographical coordinates of both the sampling sites and the sampling landscapes for the local and landscape grain respectively. The PCNM vectors (spatial variables) represent the spatial structure or spatial dependence among the sampling sites or among the sampled landscapes –without considering species composition, or any explanatory (environmental) variable. PCNM vectors are also uncorrelated variables that can be used as predictors in regression or another analysis to describe spatial relationships in community data, because they are not subject to multicollinearity troubles (Borcard & Legendre, 2002; Borcard *et al.*, 2004; Legendre *et al.*, 2005).

The general procedure to obtain the set of explanatory spatial variables involves the following steps: (a) Calculation of a Euclidean distance matrix comprised of geographical distances between site or landscape locations, (b) Modification of the Euclidean distance matrix by replacing distances greater than the larger distances between adjacent sites or landscapes with an arbitrary large number as suggested by Borcard *et al.* (2004), (c) Performing a principal coordinate analysis on the modified distance matrix and (d) the principal coordinate axes that correspond to positive eigenvalues are retained as the set of explanatory PCNM variables. The PCNM function from the R software 'spacemakeR' library was used to perform this analysis (version 2.10.1, The R foundation for Statistical Computing). The PCNM analysis produced 136 and 10 eigenvectors (PCNM vectors), among which 36 and 6 eigenvectors, at the local and landscape grain respectively, had positive values and a significant autocorrelation ($p>0.001$) tested by Moran's I (Bocard *et al.*, 2004). Only these positive and significant vectors were used in the analyses.

2.3.5 Calculation of landscape-pattern metrics

We calculated different landscape metrics for each vegetation cover in each of the 23 sampling landscapes using FRAGSTATS (McGarigal *et al.*, 2002). This patch-type approach requires calculation of individual metrics for each given patch-type, regardless of how many individual patches make up that particular patch-type. Since many of these indices are redundant or represent an alternative formulation of the same information, Pearson correlation coefficients between each pair of metrics were computed to select those metrics to be included in this study (Hargis *et al.*, 1998). Metric selection was done by considering variables that quantify different aspects of landscape configuration, the potential explanatory power of a given metric for plant species composition, and how common such measurements are in the landscape ecology literature (Mazerrolle & Villard, 1999). On this basis we selected: PLAND (Percentage landscape) for the local grain analysis; LPI [largest Patch Index), SHEI [Shannon's Evenness Index], SIDI [Simpson's Diversity Index] for the landscape grain analysis; and Shape_AM (Shape area-weighted mean), TECI (Total Edge Contrast Index), and LSI (Landscape shape Index) for both spatial grains. A description of the metrics is given by McGarigal *et al.*, (2002) (http://www.umass.edu/landeco/research/fragstats/documents/Metrics/Metrics%20TOC.htm).

2.3.6 Data analysis

To estimate actual species richness per vegetation type and to assess sampling effort, we computed the non-parametric estimator Chao 1 with 95% CI in EstimateS V7.5 (Colwell, 2005). This estimator has been shown to perform particularly well with ecological data (Chazdon *et al.*, 1998; Gotelli & Colwell, 2001).

We examined the relative magnitude of variation in woody species composition at both spatial scales using Detrented Correspondance Analysis (DCA), which assumes a Gaussian model as the species response model, employs the chi square dissimilarity index, and provides a standardized measure of variation in species composition (Jongman *et al.*, 1987). Additionally, we estimated the magnitude of β-diversity at the two spatial scales with Whittaker's effective species variation index (Whittaker, 1972; Tuomisto, 2010):

$$\beta_{pt} = (\gamma - \alpha_t) / \gamma$$

where β_{Pt} is effective species variation, γ is total richness, α_t is the average richness of all sampling sites at both spatial scales. This equation quantifies the effective proportion of total species that is not

contained in each sampling unit, which is an adequate measure since gamma is constant at both spatial scales (Tuomisto, 2010). Since this measure of β-diversity is strongly dependent on α-diversity, and the latter is strongly influenced by differences in sample size (Gotelli & Colwell, 2001), we used individual-based rarefaction in EcoSim v7 to standardize sample size: 22 individuals for the local grain size. The sample size at the landscape grain was obtained by pooling the 12 samples of the lower level (264 individuals).

To test for the effects of sucessional age class on β-diversity we used two types of measures. For the classic measure, we used Whittaker's effective species variation index to estimate the magnitude of β-diversity in each vegetation class, and we applied individual-based rarefaction to standardize sample size (3700 individuals). In the case of multivariate measures, we used an analysis of similarity (ANOSIM) in PRIMER-E 6.1.12 (Clarke & Warwick, 1994) to assess differences in species composition among vegetation classes at the local grain, by applying the Bonferroni correction for post-hoc comparisons. The response variable was β diversity (Bray-Curtis dissimilarity index among pairs of sampling sites).

At the landscape grain, we also calculated differences in species composition among fragmentation classes. These classes were obtained using the area of a sampling landscape covered with > 15 y-old forests. Four classes of fragmentation were identified: FC1 refers to sampling landscapes with > 75% of the area covered by > 15 y-old forests, whereas FC2, FC3 and FC4 correspond to SL with 50 to 75%, 25 to 50%, and < 25% of area covered by > 15 y-old forests, respectively. At this scale, the response variable was also β diversity using Bray-Curtis dissimilarity index, and individual-based rarefaction was also applied to standardize sample size (4500 individuals).

To evaluate the relative contribution of environmental, spatial and landscape structure variables, as well as of stand age, on β-diversity, we performed variation partitioning analyses (Borcard *et al.*, 1992). The total variation in species composition was dissected into five components: a pure environmental effect, a pure effect of spatial structure, a stand age effect, a landscape structure effect, the combined variation explained by all components, as well as the unexplained variation. To this end, we first transformed species abundance using Hellinger's transformation, which allows using species abundance data in redundancy analysis (Legendre & Gallager, 2001), and down-weighted the most abundant species in the analysis (Jones *et al.*, 2008). It should be noted that all multivariate measures of β-diversity employed in this study (chi square (DCA), Bray-Curtis (ANOSIM) and Hellinger (Euclidean on proportions, RDA), as well as Whittaker's effective species variation index exclude joint absences and are therefore comparable (see Anderson *et al.*, 2010).

To determine the amount of variation in plant species composition attributable to environmental factors and to the spatial structure captured by the PCNM vectors, we performed a Partially Constrained Ordination using multiple Redundancy analysis (RDA) on Hellinger's dissimilarity, in CANOCO 4.0 (ter Braak & Smilauer, 1988); we recorded the proportion of the variation (R^2) explained by all significant variables of each component, selected by using the forward procedure with unrestricted Monte-Carlo permutations. At the local grain, fractions considered were: (1) soil environmental variables (EC, pH, K, SOM, CEC, soil texture, percent stoniness) and elevation; (2) stand age, (3) landscape structure metrics (TECI, PLAND, SHAPE_AM, LSI), and (4) spatial structure (all 36 significant PCNM vectors for the sampling sites), whereas at the landscape grain, the fractions were: (1) standard deviation of soil variables, (2) standard deviation of stand age, (3) landscape structure (LSI, LPI, SHAPE_AM, TECI, SHEI and SIDI), and (4) spatial dependence (all 6 significant PCNM vectors for the SL).

2.4 RESULTS

2.4.1 Land cover map

Figure 1 shows the land cover thematic map constructed for the study area. The total area analyzed was 37,243 ha, of which the large majority (94.3%) corresponded to tropical dry forest in any of the four vegetation classes, whereas the remaining portion (5.7%) corresponded to agricultural and urban areas. The overall accuracy in the supervised classification was 73.3% and the Kappa index was 0.7. Vegetation class 4 (> 15 yr-old forests on hills) was the largest land cover type covering 11,545 ha (> 31% of the study area). Vegetation class 3 (> 15 yr-old forests on flat areas) occupied 10,158 ha (27.3%), whereas vegetation classes 2 (8 to 15 yr-old forests) and 1 (3 to 8 yr-old forests) covered 6,900 (18.5%) and 6,525 ha (17.5%), respectively. The urban and agriculture classes combined covered 2,144 ha.

2.4.2 Species composition

A total of 22,262 individuals belonging to 204 species and 52 families were recorded in 276 plots. Of the total number of species identified 60.9% were trees (90.2% of total abundance), 20.6% were shrubs (4% of abundance), and 19.1% were lianas (5.8% of abundance). The number of species recorded in each of the four vegetation classes represented 69% to 95% of the richness predicted by the Chao 1 estimator (Table 1). Observed species richness was lower in VC1 compared to all other vegetation classes. VC1 also had the lowest

sampling size (53 samples, 3834 individuals) and the lowest percentage of estimated richness that was observed (69%), and it was the only class for which the 95% CI for observed richness did not overlap that for estimated richness.

Variation in floristic composition was much greater at the local grain (the first two DCA ordination axes represented close to 4 SD) than at the landscape grain (< 2 SD; data not shown). Furthermore, β-diversity, measured through Whittaker's effective species variation, showed a 95% confidence interval (CI) of 90 - 91% of effective turnover using local grain, and 60 - 63% using the landscape grain (Table 1). This general pattern held even after standardizing Whittaker's effective species variation to a comparable number of individuals (CI at the local grain: 94.7 - 95.0, CI at the landscape grain: 73.2 – 75.3%).

The magnitude of β-diversity decreased slightly but significantly with successional age class (Table 1). Although observed β-diversity did not differ between VC3 and VC4, standardized β-diversity was VC3 < VC4, indicating that differences in the number of individuals sampled masked real differences between topographic positions. The analysis of similarity (ANOSIM) revealed significant differences between vegetation classes, except for VC1 vs. VC2. Although VC3 and VC4 shared the same successional age class, they showed greater variation in composition than vegetation classes that were contiguous in stand age (VC1 vs. VC2, and VC2 vs. VC3). At the landscape grain, there were no statistical differences between fragmentation classes, using either measure of β-diversity (Tables 1, 2).

2.4.3 Variation Partitioning

At the local grain, the RDA analysis retained 23 significant predictors ($P < 0.05$): seven soil variables, one landscape metric, stand age, and fourteen spatial variables (PCNM's), which together accounted for 21% of the total variation in species composition. The most important environmental variables associated with the first ordination axis were soil organic matter (SOM), pH, percent soil-surface stone content, K, and clay. Species composition of VC1 was associated with high values of clay content and low values of SOM, and VC4 showed the opposite pattern, whereas VC2 and VC3 showed large variation in species composition and no clear pattern of association with environmental variables (Fig. 2). However, the spatial component also explained a large portion of the variation in species composition (42% of the variation explained by the model vs. 45% for soil variables), whereas stand age and landscape structure combined, and the variation shared by all variables accounted for less than 7% of the variation explained by the model (Table 3).

Table 2.1 Observed (obs.), estimated (est.) and rarefied (raref.) species richness and β-diversity for all woody plants ≥ 1 cm in diameter at breast height, at the local and landscape scale, as well as among vegetation classes (VC) and fragmentation classes (FC).

Factors	Total number of samplings	Total number of individuals	Obs. Species richness	95% CI (Mao Tau)	Est. Species richness	95% CI (Chao 1)	% Richness obs./est.	*Raref. species richness	95% CI	Obs. β-diversity	95% CI	Raref. β-diversity	95% CI
Local scale	276	22262	204	192.6 – 215.8	231.2	215.0 – 270.0	88	10	10.1 - 10.8	90	89.9 - 90.1	95	94.7 – 95.0
Landscape scale	23	22262	204	191.4 – 216.6	227.0	213.6 – 263.3	90	52.6	50.3 - 54.7	62	60.2 - 63.2	74	73.2 – 75.3
VC1	53	3935	110	99.8 – 120.1	150.6	125.9 – 213.7	73	108.0	105 – 110	46	41 - 51	47	46 - 49
VC2	75	6378	149	138.0 – 159.9	156.8	151.5 – 173.0	95	135.6	130 – 141	27	22 - 32	34	31 - 36
VC3	86	6018	157	146.4 – 167.5	175.8	164.1 – 206.5	89	144.4	139 – 150	23	18 - 28	29	26 - 32
VC4	62	5931	139	129.6 – 148.4	171.5	155.3 – 225.2	81	127.5	122 – 132	32	27 - 36	37	35 - 40
FC1	6	5973	152	137.7 – 166.2	183.5	164.3 – 232.3	83	144.1	139 – 148	29.4	19 - 33	29	27 - 32
FC2	5	4705	145	130.4 – 159.6	166.4	153.1 – 201.7	87	143.9	142 – 145	29.5	22 - 36	29	29 - 30
FC3	6	5821	154	139.8 – 168.2	175.0	161.5 – 213.0	88	135.8	131 – 140	33.4	18 - 31	33	31 - 36
FC4	6	5763	144	130.0 – 157.9	160.2	149.7 – 190.0	90	138.7	134 – 142	32.0	23 - 36	31	30 - 34

*Rarefaction was calculated for 22 individuals at the local scale, 264 individuals at the landscape scale, 3700 individuals for the vegetation classes, and 4500 individuals for the fragmentation classes.

Table 2.2 Results of ANOSIM comparisons of community composition among vegetation classes (local grain) and among fragmentation classes (landscape grain), showing test statistics for global and pair-wise comparisons. The Bonferroni-corrected significance value is P = 0.008.

		Local spatial grain			Landscape spatial grain	
		R	*P*		*r*	*P*
All vegetation classes		0.18	0.001		0.09	> 0.05
Pairwise comparisons	2, 1	0.027	0.12	2, 1	0.003	0.46
	2, 3	0.113	0.001	2, 3	0.125	0.18
	2, 4	0.255	0.001	2, 4	0.069	0.26
	1, 3	0.224	0.001	1, 3	0.172	0.24
	1, 4	0.409	0.001	1, 4	0.085	0.19
	3, 4	0.139	0.001	3, 4	0.113	0.15

At the landscape grain, the RDA analysis retained five significant predictors ($P < 0.05$): two soil variables, two landscape metrics and one spatial variable (PCNM's); together they explained 31% of the variation in species composition. The most important variables associated with the first ordination axis were LPI and CV of pH. At this scale, soil variables explained 40% of total variation, followed by landscape metrics, which explained a further 38%. The spatial component came third (18% of the variation), and was less important compared with the local grain (Table 3).

Table 2.3 Variation partitioning of woody species composition at the local and landscape grains through partial Redundancy analysis (RDA). Shown values are percentage of variation explained from the total inertia of selected variables (vars.).

	Local grain	Landscape grain
Group	Percent Explained	Percent Explained
Total explained variation	21	31
Total unexplained variation	79	69
Variables groups	Percent contribution of the total explained variation	Percent contribution of the total explained variation
Soil variables	45.07	40.26
Stand age	3.29	
Landscape Structure	2.82	37.99
Space	42.25	18.18
Shared variation	6.57	3.57
Explanatory variables		
SOM	28.64	
K	3.76	
Clay	2.82	
pH	2.82	
Stone content	2.82	
Elevation	2.35	
Slope	1.88	
Stand age	3.29	
TECI	2.82	
PCNM7	3.76	
PCNM5	3.76	
PCNM8	3.76	
PCNM4	3.29	
PCNM2	3.29	
PCNM15	3.29	
PCNM14	2.82	
PCNM3	2.82	
PCNM11	2.82	
PCNM6	2.82	
PCNM9	2.35	
PCNM10	2.82	
PCNM12	2.35	
PCNM28	2.35	
CV_Elevation		20.78
CV_pH		19.48
LPI		17.53
SHEI		20.45
PCNM2		18.18

Coefficient variation = CV; Variables included in the analysis with $P < 0.05$

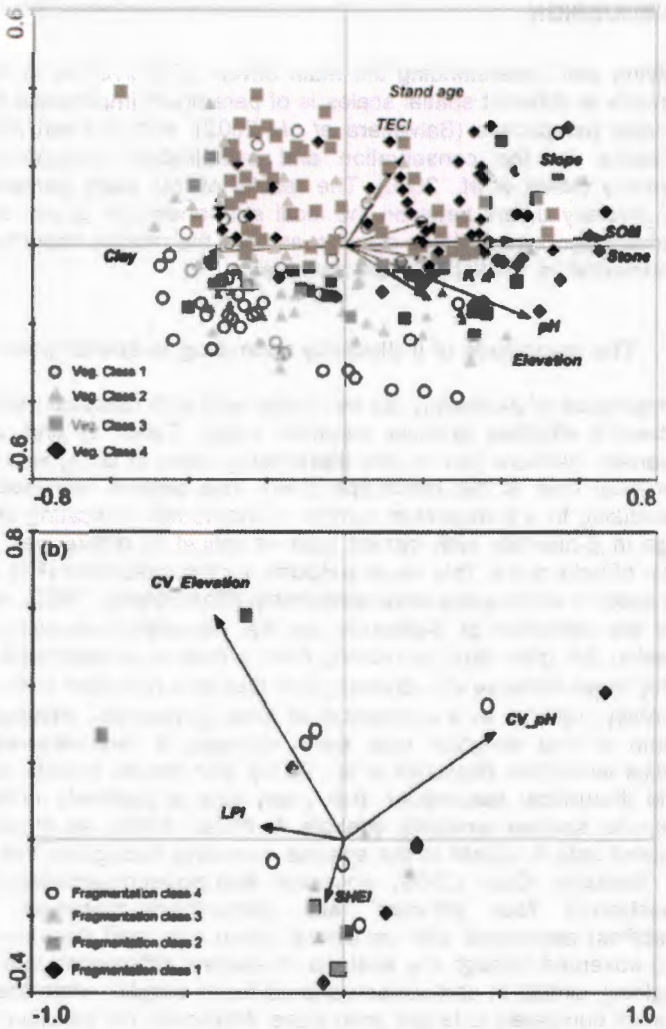

Figure 2.2 *RDA biplots for the first and second axes at two spatial grains. (a) local grain, showing stand age, percent soil-surface stone content (stone), soil organic matter content (SOM), pH, elevation, clay, potassium (K) and total edge contrast index (TECI); (b) landscape grain, showing the coefficient of variation (CV) for elevation and pH, Shannon's Evenness Index (SHEI) of patch types and the large patch index (LPI).*

2.5 DISCUSSION

Identifying and understanding the main drivers of β-diversity in tropical dry forests at different spatial scales is of paramount importance from a theoretical perspective (Balvanera *et al.*, 2002), and of great practical significance for the conservation and sustainable management of biodiversity (Miles *et al.*, 2006). The results of this study demonstrate that β-diversity differs between the local and landscape grains studied and among successional age classes, as does the relative importance of environmental vs. spatial structure variables.

2.5.1 The magnitude of β-diversity according to spatial grain

The magnitude of β-diversity, as estimated both with classical measures (Whittaker's effective species variation index, Table 1) and with a multivariate measure (chi square dissimilarity index in DCA) was larger at the local than at the landscape grain. This pattern remained after standardizing to a comparable number of individuals, indicating that the change in β-diversity with spatial grain is robust to differences in the number of individuals. This result supports our first prediction (P1), which was based on the species-area relationship (Rosenzweig, 1995), as well as on the definition of β-diversity as the γ-diversity/α-diversity ratio. Increasing the grain size by moving from a local to a landscape scale resulted in an increase in α-diversity and thus in a reduction in this ratio (β-diversity) relative to a constant total area (γ-diversity). Although the outcome of this equation may seem obvious, it has received little empirical evaluation (Rocchini *et al.*, 2010). Our results provide support for the theoretical assumption that grain size is positively related to among-site species similarity (Nekola & White, 1999), as small sites harboured only a subset of the species occurring throughout the entire area. Similarly, Qian (2009) observed that global dissimilarity in the composition of four different taxa (amphibians, mammals, birds and reptiles) decreased with increasing grain size, and Rocchini *et al.* (2010) observed through the analysis of spectral differences that areas ecologically similar in composition shared fewer species when the grain was small compared to larger grain sizes. Moreover, our results of DCA indicate that (abundance-based) species composition also contributed to the differences in the magnitude of β-diversity between grain sizes.

Additionally, and in agreement with our second prediction (P2), the correlation between explanatory variables and β-diversity was stronger for the landscape grain size compared to the local grain. Steinitz *et al.* (2006) reported similar results in analyzing the correlation between the assembly of snail species and rainfall. This shift in the correlation between explanatory variables and β-diversity at different spatial grains can be attributed to the strong stochastic error (large

noise) associated with small grain sizes (Nekola y White, 1999) and may indicate that the average level of variation in species composition may be a local-scale consequence associated with the random nature of species occurrences.

2.5.2 The effect of successional age classes on β-diversity

We found a significant effect of successional age classes on β-diversity using both classical and multivariate measures. For Whittaker's effective species variation (classic measure), we found a decline in β-diversity with increasing age, which is in agreement with our third prediction (P3). This result is based on the well established increase in α diversity during Neotropical forest succession (Guariguata & Ostertag, 2001; Chazdon, 2008; Quesada *et al.*, 2009; Dupuy *et al.*, 2012), which implies a corresponding decline in classical measures of β-diversity. This is due to a reduction in this ratio (β-diversity) relative to a constant total diversity (γ-diversity). Although the difference in magnitude decreased when we standardized to a comparable number of individuals, the general pattern remained, indicating that the decline in β-diversity with successional age class was robust to variation in sample size.

On the other hand, the significant differences in multivariate measures (Bray-Curtis dissimilarity index) among successional age classes indicate that species composition changes during secondary forest succession. Previous studies document dramatic changes in composition, from early stages of succession highly dominated by a few pioneer species (Laurance *et al.*, 2006) to advanced stages represented by a diverse array of shade-tolerant species (Laurance *et al.*, 1999; Michalski *et al.*, 2007). In this study, the changes in species composition with succession were small (though significant), due to a marked dominance of a few species that combine high dispersal ability (anemochory) with a high coppicing capacity (Dupuy *et al.*, 2012).

The effect of successional age classes on β-diversity varied with the measure employed. Thus, although the magnitude of β-diversity differed significantly between VC1 and VC2 (Table 1), species composition (as gauged by Bray Curtis dissimilarity), did not differ (Table 2). This result clearly illustrates the importance of specifying the measure of β-diversity used, and of considering different measures that quantify different aspects of β-diversity. Thus, classical measures are based on presence-absence data and are therefore strongly influenced by variation in α-diversity (Table 1), whereas multivariate measures are based on species abundance (cover or biomass), and therefore take into account species composition, which can yield different results.

2.5.3 Variation partitioning

In agreement with our fourth prediction (P4), the relative contribution of environmental variables vs. spatial structure on β-diversity varied with grain size. Contrary to our prediction, however, at the local grain, the relative contribution of the environmental variables combined was similar to that of spatial structure (PCNMs) — 48% vs. 42% of the total variation explained by the model (Table 3). This result suggests that, at this scale, both dispersal limitation and niche partitioning bear a significant influence on β-diversity, which is at odds with the findings of Duque *et al.* (2009) and He y Legendre (2002) that dispersal limitation has a greater influence on β-diversity than niche partitioning at local scales, but agrees with the findings of Tuomisto *et al.* (2003) in Amazonia, and with Gravel *et al.* (2006) conclusion that both processes contribute to community assembly. Bell *et al.* (2006) suggested that the effect of these two processes can be interpreted in two ways: (1) as a spatially structured environment, which has an influence on β-diversity, or (2) as a neutral effect acting on the β-diversity in a heterogeneous environment. In agreement with Li *et al.* (2011), we favor the notion of a spatially structured environment having an influence on β-diversity, given the comparatively larger contribution of the environmental variables.

Among the examined environmental variables, organic matter had the largest influence on β-diversity, followed by K (Table 3, Fig.3a). Organic matter contributes to soil fertility by increasing water retention capacity and nutrient availability, and by catalyzing cationic exchange (Guariguata & Ostertag, 2001). Studies conducted at small scales in Amazonia (Tuomisto *et al.*, 2003; Costa *et al.*, 2005) and Indonesian (Paoli *et al.*, 2006) have also found that soil nutrients, as well as topography and slope, are important factors affecting β-diversity.

Contrary to previous findings, both in tropical humid forests (Finegan, 1996; Guariguata & Ostertag, 2001: Peña-Claros, 2003) and in tropical dry forests (Lebrija-Trejos *et al.*, 2008), here successional age explained a very small percentage (3.3%) of β-diversity at the local-grain size (Table 3). Dupuy *et al.*, (2012) found in the same study area that successional age explained most of the variation in forest structural attributes such as basal area and canopy height, but not in species composition, and attributed this result to a process of biotic homogenization caused by the dominance in the study area of a few species that combine a high dispersal ability (anemochory) with a high coppicing capacity. These species are thus able to dominate across succession, since they can colonize early in succession and can persist for several decades, thereby decreasing species turnover during succession. Lôbo *et al.* (2011) and Tabarelli *et al.* (2008) also found that tropical forest floras may be susceptible to a taxonomic homogenization (increasing similarity) in landscapes subjected to frequent human

disturbance due to the proliferation of generalist and ecologically plastic species, such as pioneers.

Topographic position strongly influenced β-diversity, as evidenced by the comparatively high percentage (21%) of total variation in species composition explained by the CV in elevation at the landscape grain size (Table 3), and the significant differences both in the magnitude of β-diversity (Table 1), and in species composition (Table 2) between vegetation classes VC3 and VC4 at the local grain –since these classes shared the same successional age but differed in topographic position. This topographic effect at the local grain size could be mediated by very distinct soil conditions on hills, compared to plains (Dupuy *et al.*, 2012). White & Hood (2004) also found a strong effect of topography and soil attributes on the distribution and abundance of woody species in the Yucatan Peninsula, whereas Gallardo-Cruz *et al.* (2009) reported a strong influence of slope aspect and elevation on woody species composition in Oaxaca, Mexico. At the landscape grain, our results agree with those of Swenson *et al.* (2011), who observed that woody species β-diversity was strongly determined by an elevation gradient in Puerto Rico.

At the local grain size, β-diversity was strongly influenced by environmental heterogeneity and weakly influenced by landscape structure (Table 3). In a *Eucalyptus populnea* semiarid forest, Debuse *et al.* (2007) also found that within-patch environmental variation was more strongly correlated with variation in the ant assembly than with landscape configuration. However, at the landscape grain, environmental heterogeneity and landscape structure had a similar, strong influence on β-diversity (Table 3). This shift in the relative influence of landscape structure suggests that habitat fragmentation has a stronger influence on β-diversity at the landscape grain than at the local grain.

The positive correlation of β-diversity with patch diversity (SHEI) and the inverse correlation with LPI at the landscape grain suggest that more fragmented landscapes are more variable in their species composition, since both measures are considered to be indicators of fragmentation. In landscapes that are not dominated by urban or agricultural land covers (as is the case in this study), fragmentation has been shown to promote β-diversity through the creation of barriers for dispersal, the modification of patch size and shape, and the generation of variation in microclimatic effects, all of which favour the arrival and establishment of species with different competitive abilities (Laurence *et al.*, 1998, 2002; Honnay *et al.*, 1999; Bascompte & Rodríguez, 2001).

In agreement with our fourth prediction (P4), environmental variables (soil conditions and landscape structure combined) had a much stronger influence on β-diversity at the landscape grain than spatial structure (78% vs. 18%; Table 3). This result suggests that, at this spatial scale, niche partitioning contributes more to β-diversity than dispersal limitation. Previous studies (Bell, 2005; Laliberté *et al.*, 2009;

Borcard *et al.*, 2011) have also found that, as the spatial scale increases, there is an increase in environmental heterogeneity and a concomitant decrease in β-diversity (increase in among-site species similarity), resulting in an increase in the importance of environmental factors (niche partitioning) relative to the decay in species similarity with increasing spatial distance (dispersal limitation).

In this study we interpreted environmental variables (soil properties, topography, and landscape metrics) as a proxy for niche partitioning, and the spatial structure (PCNMs) as a proxy for dispersal limitation. We are aware of the limitations and possible biases of both approaches; in the case of niche partitioning we focused on the differential use of the habitat, but we did not evaluate the biotic interactions that may ultimately be responsible for such partitioning. In the case of dispersal limitation and in agreement with other studies (Chust *et al.*, 2006; Jones *et al.*, 2008), our indirect measure of dispersal limitation (PCNMs), does not constitute a formal test of the neutral theory, since we did not assess factors such as ecological and competitive equivalence among species, or rates of speciation and immigration in the meta-community. Moreover, spatial patterns interpreted as evidence of neutral process could be simply due to unmeasured environmental variables (such as water availability), while variation attributed exclusively to environmental variables could coincidentally result from neutral processes (Anderson *et al.*, 2010). Despite these limitations of our approach and that of previous studies (Tuomisto & Ruokolainen, 2006; Soininen *et al.*, 2007; Jones *et al.*, 2008), we believe that our study contributes to our understanding of the relative influence of environmental vs. spatial drivers of β-diversity in tropical forests across different spatial scales.

Variation partitioning resulted in a great deal of unexplained variation at both spatial grains. This result is not unusual; for example, Cottenie (2005) found that 58% of total variation in 158 studies was explained neither by the environment nor by spatial variables. In our study, the unexplained variation (70-79%) could be partly attributed to environmental factors that were not evaluated, such as water availability, which is a key factor influencing β-diversity of woody species in dry forests in Chamela, Mexico (Balvanera *et al.*, 2002), and in the Yucatán Peninsula (Trejo, 1998). However, we believe that our results are sufficiently robust because water availability has been shown to be correlated with pH (Hájek *et al.*, 2011). Alternatively, the unexplained variation in species composition may be partly a result of a dispersal effect, but without presenting the pattern of decay in similarity with increasing distance, as reported by Nekola & White (1999).

To conclude, our results clearly show that the magnitude of β-diversity decreases with spatial scale (grain size) and successional age class –as long as total extent is kept constant. Our results also show that both environmental factors (local soil conditions, as well as landscape

structure), and spatial structure contribute to woody plant β-diversity in our TDF landscape, but their relative importance is scale-dependent. At the local scale (grain size), both the environment (mainly soil conditions) and spatial structure strongly affected β-diversity, while at the landscape grain, environmental factors (variation in soil conditions, as well as landscape configuration) played a more prominent role. These results therefore suggest that both niche partitioning and dispersal limitation affect β-diversity at the local grain size, while niche partitioning prevails at the landscape grain.

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Capítulo 3

Assessing the importance of niche partitioning and dispersal limitation on β diversity of woody plants: the importance of dispersal syndrome and growth form [2]

3.1 INTRODUCTION

Uncovering the mechanisms underlying β-diversity is a central goal for community ecology and biogeography (Tuomisto *et al.*, 1995, 2003b; Tuomisto, 2010). Different theories have been proposed that attempt to explain β-diversity, and many of our ideas about spatial variation in species composition are based on the observation that species differ in their environmental requirements (Grubb, 1977; Poorter, 2007).

The niche theory proposes that most of the differentiation in species composition among plant communities is related to particular adaptations of species to the environment (Hutchinson, 1957; Leibold, 1995, 2008). Therefore, species abundance may be taken as an indicator of how suitable environmental conditions are for species to grow and reproduce. In this sense, traits such as growth form, would be important to understand the mechanisms assembling plant communities, because they represent different strategies of resource partitioning (Grubb, 1977). For example, lianas have more plastic growth responses than trees, and are thus more able to grow quickly in sunlit conditions even when they are shade-tolerant.

In contrast to niche theory, the neutral theory (Hubbell, 1979, 2001, 2005) suggests that all species are competitively equal and able to grow equally well under a wide range of environmental conditions. This assumption of ecological equivalence or ecological symmetry is fundamental for the neutral theory, but it is also one of the main causes of controversy. Species obviously differ from each other in life history traits. According to the neutral theory, dispersal limitation or recruitment limitation – the limited capacity of plants to effectively disperse their seeds and establish seedlings away from parent individuals, which causes the spatial location of an individual to be constrained by the location of its parent, is the main factor determining plant community composition. Therefore, dispersal syndrome would be an important trait to take into account in order to understand the mechanisms affecting β-diversity. As a result, sites located closer together should be more similar

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[2] Jorge Omar López-Martínez, Lucía Sanaphre-Villanueva, José Luis Hernández-Stefanoni, J. Alberto Gallardo-Cruz, Jorge A. Meave, Juan Manuel Dupuy. Sometido a Journal of Ecology.

in composition than those lying far apart (Hubbell, 2001; Condit *et al.*, 2002) regardless of their environmental conditions (Primack & Miao, 1992). However, some authors have suggested that both niche partitioning and dispersal limitation are influential and complementary drivers in the maintenance of spatial variation in species composition (Gravel *et al.*, 2006; Leibold & McPeek, 2006).

Other factors may also influence β-diversity patterns, for example previous studies have shown that the magnitude of β diversity is influenced by secondary succession (López-Martínez *et al.* 2013), soil variation (Toumisto *et al.*, 1995, 2003a, 2003b; Paoli *et al.*, 2006), fragmentation (Fahrig 2003), and elevation (Gallardo-Cruz *et al.*, 2009). All of these factors produce changes in community patterns by modifying the local environment as well as resource availability and distribution (Motzkin *et al.*, 1999), hence creating opportunities for the establishment of new species and reducing populations of those that are already established (see reviews by Guariguata & Ostertag, 2001; Chazdon *et al.* 2007; Quesada *et al.*, 2009).

Additionally, species with specific traits may be favoured over others at different successional stages, and different ecological strategies are dominant at different moments of vegetation development (Chazdon *et al.*, 2010; Lebrija-Trejos *et al.*, 2010; Alvarez-Añorve *et al.*, 2012). For instance, in Neotropical lowland forests Opler *et al.* (1980) found that plants of early successional stages had primarily anemochorous seeds, while plants with zoochorous dispersion were dominant in old-growth forests. Similarity, Chazdon *et al.* (2003) found that the relative abundance of tree species with explosive dispersal was higher in early secondary forests, while animal dispersal was more common in old-growth forests. Moreover, it has been proposed that pioneer species exhibit long-distance seed dispersal patterns. This idea is based on the observation that appropriate microsites for establishment of these species (i. e. gaps with high light availability) have been rare over evolutionary time (Finegan, 1996; Dalling *et al.*, 2002). Accordingly, species with long-distance dispersal should be able to locate most of the appropriate habitats in a landscape, and such dispersal may compensate for low persistence rates at any given site (Nekola & White, 1999; Qian *et al.*, 2005). Therefore, spatial variation in species composition (i.e. β-diversity) is expected to be lowest for species with the longest dispersal distance. Nekola & White (1999) showed that β-diversity was higher for zoochorous species than for anemochorous species in Appalachian spruce-fir forests. On the other hand, species with fleshy fruits presented lower β-diversity than species with dry fruits in subtropical forests of Guangdong province, China. These contradictory results may be influenced by the fact that in the Appalachian Mountains plants are mostly dispersed by animals, whereas in Guangdong province, plants are dispersed both by animals and by

wind (Bin *et al.*, 2010). Thus ecosystem type seems to influence dispersal syndromes, which in turn may affect β-diversity patterns.

Likewise, it has been shown that the predominance of certain plant growth forms and life strategies changes along secondary succession. In tropical wet forests, herbs, shrubs and lianas are dominant during the initial successional stages, and they are subsequently replaced by short- and long-lived pioneer trees; afterwards, these species are replaced by shade- tolerant trees (Chazdon, 2008). In Bolivian dry forests it has been reported that grasses are rare in old successional stages, while shrubs, lianas and bromeliads increase their abundance with successional age (Kennard, 2002).

β-diversity also varies with plant community type. For instance, Whittaker (1960) showed an increasing trend in β-diversity when moving from a tree-dominated community to a shrub- or herb-dominated one. However, β-diversity patterns among growth forms are not always consistent. For example, Nekola & White (1999) found β diversity values twice as high for herb assemblages compared to woody plants, while in a Chinese subtropical forest, herbs showed the highest β-diversity, while shrubs had the lowest (Bin *et al.*, 2010). Moreover, Davidar *et al.* (2007) reported that β-diversity of trees in three Indian tropical forests did not differ among forest strata or dispersal modes, suggesting that β-diversity is independent of these tree characteristics.

Several ecological theories have been advanced to explain the coexistence of a large number of species (Amarasekare, 2003, 2007), and the existences of trade-offs among traits is one of the major explanations that have been proposed (Ben-Hur *et al.*, 2012). Since the benefits of performing one ecological function well comes at cost of performing another function, these local trade-offs represent niche differentiation among species through complementarity in resource acquisition, such as nutrients, light, and water (Kneitel & Chase, 2004). Although local trade-offs are important for a differential use of resources, and for coping with environmental variability, there are also important trade-offs at the metacommunity level, such as the relative ability of species to compete and persist in patches and to colonize new ones (Kneitel & Chase, 2004). Thus, dispersal syndrome and growth form are important plant life-history traits and their study could shed light on the processes and mechanisms that influence plant community assembly (Grubb 1977, Amarasekare 2003, Ben-Hur *et al.*, 2012).

The objectives of this study were twofold. First, we compared the effects of environmental filters vs. dispersal limitation on β-diversity of species assemblages defined by dispersal syndrome and growth form. We used elevation, soil properties and forest stand age as indicators of environmental filters, whereas dispersal limitation was assessed in terms of the spatial autocorrelation of sampling sites. Second, we explored how species richness of dispersal syndromes and growth forms varied with forest stand age. We aimed at answering two main questions: (1) Does

β-diversity and species richness vary among seed dispersal syndromes and growth forms along secondary succession? (2) What are the relative roles of niche differentiation and dispersal limitation in driving β-diversity of different dispersal syndromes and growth forms?

We made three predictions based on the findings of previous studies and on the following arguments. Dispersal distance depends on the vector employed to disperse propagules (i.e. wind for anemochorous species, gravity or the plant itself for autochorous species, animals for zoochorous species), as well as on plant traits such as height of reproductive plants (Nekola & White, 1999; Muller-Landau *et al.*, 2008). β-diversity is expected to be inversely related to dispersal distance (Nekola & White, 1999; Quian, 2009). In turn, dispersal distance is expected to be greater for anemochorous and zoochorous species compared to autochorous ones (van der Pijl, 1982), as well as for trees and lianas compared to shrubs (Medina 2005). Therefore, our first prediction is that β-diversity would be greater for autochorus species, compared to zoochorus and anemochorus species; and for shrubs compared to trees and lianas (P1).

Since plant diversity and structural complexity generally increase during tropical forest succession (Finegan 1996, Guariguata & Ostertag, 2001; Chazdon, 2008; Lebrija-Trejos *et al.*, 2008; Dupuy *et al.*, 2012), we expected an increase in overall species richness (α-diversity) across growth forms and dispersal syndromes during succession, with a prevalence of shrub and anemochorous species in early successional ages, and of zoochory and tree species in more advanced successional ages (P2). Finally, plant traits can be viewed as evolving strategies that have developed in response to environmental filters (Grub, 1977; Howe & Smallwood, 1982; McGill *et al.*, 2006; Webb *et al.*, 2010). Moreover, greater dispersal distance may increase the chances of finding appropriate environmental conditions for establishment. Therefore, we predicted that environmental filters would be more strongly associated with β-diversity for trees and lianas compared to shrubs, as well as for anemochory and zoochory compared to autochory (P3).

3.2 METHODS

3.2.1 Study area

The study area (*ca.* 22 × 16 km) is located in the Yucatán Peninsula, México (20°01' - 20°16'N, 89°39' - 89°60'W) (Fig. 1). Climate is warm sub-humid, with summer rains (May – October) and a marked dry season (November – April). Mean annual temperature is ca. 26°C, and mean annual precipitation ranges from 1,000 to 1,200 mm. The landscape consists of Cenozoic (Eocene) limestone hills with moderate slopes (10-25°), which alternate with flat areas; elevation ranges from 60

to 180 m.a.s.l. (Flores and Espejel, 1994). Soil heterogeneity is strongly associated with topography; with shallow, rocky Lithosols and Rendzines dominating the hills, whilst deeper, clayey Luvisols and Cambisols prevail in flat areas (Bautista-Zúñiga *et al.*, 2003). The vegetation is classified as seasonally dry tropical forest (50-75% of the species shed their leaves during the dry season) composed of forest stands of different successional ages, i.e. time since abandonment after traditional slash-and-burn agriculture (Fig. 1). Canopy height ranges between 8 and 12 m, with a few prominent trees attaining 15 m in the oldest (60-70 yr-old) stands.

3.2.2 Vegetation and environmental data

A SPOT 5 satellite image (10 m spatial resolution) was acquired in January 2005 on which a supervised classification was conducted to obtain a map of vegetation classes. Six land-cover types were defined: (1) 3-8 yr-old secondary forest (vegetation class 1: VC1); (2) 9-15 yr-old secondary forest (vegetation class 2: VC2); (3) >15 yr-old secondary forest on flat areas (vegetation class 3: VC3); (4) >15 yr-old secondary forest on hills (vegetation class 4: VC4), (5) agricultural fields; (6) urban areas and roads (Dupuy *et al.* 2012).

Field data were collected during the rainy seasons (May – September) of 2008 and 2009 through a hierarchical design. First, we randomly selected 23 sampling landscapes (SL) of 1 Km^2 encompassing the whole range of forest fragmentation in the area study. Then, three plots were randomly located for each of the four vegetation classes (VC1-VC4) within each SL (276 sampling sites in total). Each sampling site was located using a GPS unit and consisted of a circular 200m^2-plot where all woody plants ≥ 5 cm in DHB were recorded and concentric 50m^2-subplot where all woody plants ≥1cm in DHB were recorded. Stand age of each site was determined through interviews with local residents who had lived in the area for >40 yr. Of the total number of sampling sites, 53 belonged to VC1, 75 to VC2, 86 to VC3, and 62 to VC4.

To characterize local soil conditions three 10 cm-deep soil samples (*ca* 400 g each) were taken at the centre, northern and southern limits of each sampling plot and subsequently pooled to obtain a single compound sample. These samples were then sent to the Laboratory of Water, Soils and Plants of Colegio de Postgraduados (Tabasco, Mexico) for the following physical-chemical analyses: pH in water (1:2 ratio), electric conductivity (EC; 1:5 extracts), cation exchange capacity (CEC; Olsen), soil organic matter (SOM, combustion or Walkley-Black), total nitrogen (N, Kjeldahl), available phosphorous (P, Bray), interchangeable potassium (K; with ammonium acetate), and soil texture (percent lime, clay and sand content, Bouyoucos). Finally, we recorded elevation and slope for each plot using a Digital Elevation

Model (DEM) from the Instituto Nacional de Estadística, Geografía e Informática (INEGI).

We categorized species according to growth form (shrubs, trees and lianas) and dispersal syndrome (authocory, anemocory and zoocory). The dispersal syndrome was assigned at the species level either based on information obtained from the herbarium at the Center of Scientific Research of Yucatan (CICY in Spanish) (http://www.cicy.mx/ofer-tec-herbario/herbario), or based on descriptions provided in Flora of Veracruz (http://www1.inecol.edu.mx/floraver/inicio.htm), Flora Mesoamericana (http://www.tropicos.org/Project/FM), Flora of Barro Colorado Island (http://biogeodb.stri.si.edu/bioinformatics/croat/home), Flora of Guatemala (http://archive.org/search.php?query=flora%20of%20guatemala), The Missouri Botanical Garden (http://www.mobot.org/mobot/fm/) or according to the expert opinion of regional parataxonomists.

3.2.3 Spatial data

We used a principal coordinate of neighbour matrices analysis (PCNM, (Borcard *et al.* 2004) using the R software with the 'spacemakeR' library (version 2.10.1, R Development Core Team) to generate a set of explanatory spatial variables (i.e. vectors) that represent the spatial structure of sampling sites. This analysis was performed separately for each dispersal syndrome and growth form. In each analysis we selected those PCNM vectors having positive and significant autocorrelation values (Moran's I; $P > 0.001$) (Borcard *et al.* 2004)). The selected vectors were used as predictors to partition the variation in β-diversity for each dispersal syndrome and plant growth form.

3.2.4 Data analysis

We examined the relative magnitude of variation in woody species composition by dispersal syndrome and growth form using Detrented Correspondance Analysis (DCA). The advantage of this method is that it indicates the variation in species composition in standard deviation units, which are directly comparable among datasets (Jongman *et al.*, 1987). To assess the differences in species composition of each dispersal syndrome and growth form among vegetation classes we used an analysis of similarity (ANOSIM) in PRIMER-E 6.1.12 (Clarke & Warwick, 1994).

We performed a variation partitioning analysis (Borcard *et al.* 1992) to evaluate the relative contribution of the abiotic environment (elevation and soil properties), stand age and spatial autocorrelation

among sampling sites on β-diversity for each dispersal syndrome and growth form. The total variation of each assemblage was dissected into five components: a pure abiotic environmental effect, a pure effect of spatial autocorrelation, a stand age effect, the combined variation explained by all components, as well as the unexplained variation. For this, we first transformed species abundance using Hellinger's transformation, which allows using species abundance data in redundancy analysis (RDA) (Legendre and Gallagher 2001) in CANOCO 4.0 (ter Braak & Smilauer, 1988), and down-weighted the most abundant species to reduce their influence on the analysis (Jones *et al.* 2008). We recorded the proportion of the variation (R^2) explained by all significant variables of each component (i.e. soil properties, stand age and PCNM vectors) using forward selection with unrestricted Monte-Carlo permutations.

Additionally, we evaluated differences in species richness (α-diversity) among dispersal syndromes, growth forms and vegetation classes using a generalized linear model (GLM) with a Poisson error distribution and a logarithmic link (Crawley, 2007; Zuur *et al.* 2009), in which dispersal syndrome and growth form were nested within stand age. The best explanatory model was selected using backward stepwise selection starting from a global model (Crawley, 2007). Post hoc comparisons among vegetation classes, growth forms and dispersal syndromes were performed using contrast tests. These analyses were carried out in R v. 2.13.0 (R Development Core Team 2011).

3.3 RESULTS

3.3.1 B diversity by dispersal syndrome, growth form and vegetation class

A total of 22,245 individuals belonging to 201 species and 52 families were recorded in 276 plots. By far the dominant growth form was trees with 120 species and 20038 individuals, representing 59.7% of the total species richness and as much as 90.1% of total abundance. Shrubs had 41 species (20.4%) and only 907 individuals (4%), while lianas had 39 species (19.4%) and 1300 individuals (5.8%). Zoochory was the most specious dispersal syndrome with 90 species (44.8%), but the least abundant syndrome: 6726 individuals (30.2%). Autochory represented 29.4% of species richness (59 species) and 35.7% of total abundance (7938 individuals), whereas anemochory represented 25.9% (52 species) and 34.1% of the total abundance (7583 individuals).

Spatial variation in floristic composition (β-diversity) was highest for shrubs (the first two DCA ordination axes represented 19.13 SD), lowest for trees (6.97 SD), and intermediate for lianas (12.83 SD). With

respect to dispersal syndrome, β-diversity was only slightly higher for the zoochorous guild (9.44 SD), than for the autochorous and anemochorous guilds (7.59 and 7.55 SD, respectively). The analysis of similarity (ANOSIM) revealed that tree species composition was similar among the youngest vegetation classes (VC1 and VC2), but differed among all other classes (Table 1). Shrubs differed in species composition among all vegetation classes, except for VC3 and VC4, which fell within the same range of successional age (16-70 years). In contrast, liana species composition did not differ among vegetation classes, except between VC1 and VC4. Dispersal syndromes generally differed among vegetation classes, except for the youngest ones: VC1 and VC2 (Table 1).

3.3.2 Species richness by dispersal syndrome and growth form across secondary succession

Species richness (α-diversity) differed among vegetation classes, as well as among dispersal syndromes and growth forms, and showed an increase with successional age with a peak in VC4 (> 15 yr-old forests on hills) (Fig 2). Zoochory was the dominant dispersal syndrome in all vegetation classes, except for VC1 (3-8 yr-old forests), and followed the same general pattern shown by overall species richness. Autochory dominated in VC1, and showed higher richness than anemochory in all vegetation classes, except for VC3 (> 15 yr-old forests on flat areas). Trees were clearly the dominant growth form, and showed the same general pattern of overall species richness, while shrubs and lianas had much lower and similar richness (Fig. 2).

3.3.3 Variation Partitioning

Abiotic environmental variables (elevation and soil properties), successional age and spatial autocorrelation among sampling sites all influenced β-diversity, but accounted for less than one third of the total variation, and their relative influence differed among growth forms and dispersal syndromes (Table 2). In terms of growth form, explanatory variables were more strongly associated with trees (29 % of total variation), compared to lianas (12.9%) and shrubs (10.3%). Moreover, the relative influence of explanatory variables varied considerably among growth forms. For trees, abiotic environmental variables accounted for most of the variation in β-diversity that was explained by the model (51%), while shrubs were more strongly influenced by the spatial structure of sampling sites (46.8 %), and lianas were similarly influenced by environmental variables and spatial structure (42% and 39.5%, respectively). Stand age accounted for around 12% of the variation in β-diversity of trees and shrubs, but had no significant influence on lianas. The single most important variable for trees was soil organic matter

(SOM; 74.5%), for shrubs it was cation exchange capacity (CEC; 76.5%) whereas for lianas it was pH (44.0%; Table 2).

Table 3.1 Results of ANOSIM comparisons of community composition among vegetation classes by life form and dispersal syndrome showing test statistics for global and pair-wise comparisons.

		Life form						Dispersal syndrome					
		Trees		Shrubs		Vines		Anemochory		Autochory		Zoochory	
		r	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
All vegetation classes		0.28	< .01	0.11	< .01	0.014	0.17	0.18	< .01	0.24	< .01	0.18	< .01
Pairwise comparision	1 – 2	0.021	0.15	0.071	< .01	0.003	0.51	0.004	0.39	0.028	0.1	0.053	0.03
	1 – 3	0.29	< .01	0.21	< .01	0.031	0.24	0.241	< .01	0.128	< .01	0.212	< .01
	1 – 4	0.71	< .01	0.37	< .01	0.078	0.02	0.488	< .01	0.65	< .01	0.514	< .01
	2 – 3	0.16	< .01	0.05	0.011	0.009	0.18	0.129	< .01	0.113	< .01	0.055	< .01
	2 – 4	0.43	< .01	0.122	< .01	0.001	0.44	0.299	< .01	0.423	< .01	0.22	< .01
	3 – 4	0.24	< .01	0.016	0.12	0.006	0.34	0.053	< .01	0.25	< .01	0.229	< .01

Table 3.2 Variation partitioning of woody species composition according to life form and dispersal syndrome through partial Redundancy analysis (RDA). Values shown are percentage variation explained out of the total inertia by selected variables (vars.).Environ.: environmental; Space: spatial autocorrelation among sampling sites; SOM: soil organic matter; CEC:cation exchange

	Life form			Dispersal syndrome		
Group (%)	Trees	Shrubs	Lianas	Anemochory	Autochory	Zoochory
Total explained variation	29.2	10.3	12.9	27.4	31.2	20.4
Total unexplained variation	70.8	89.7	87.1	72.6	68.8	79.6
Types of variables (%)						
Environmental variables	51.0	36.2	42.1	48.8	59.0	47.6
Stand age	12.0	11.7		20.0	9.3	6.9
Space	27.7	46.8	39.5	24.2	22.4	40.2
Shared variation	9.3	5.3	18.5	7.0	9.3	5.4
Environmental variables						
SOM	74.5		18.0	61.9	82.1	81.4
pH	8.7		44.0	14.3	7.1	11.3
K	6.7	23.5		12.4	3.3	7.2
P					2.7	
Sand	6.0		24.0	11.4		
Clay	4.0					
CEC		76.5			2.7	
Elevation			14.0		2.2	

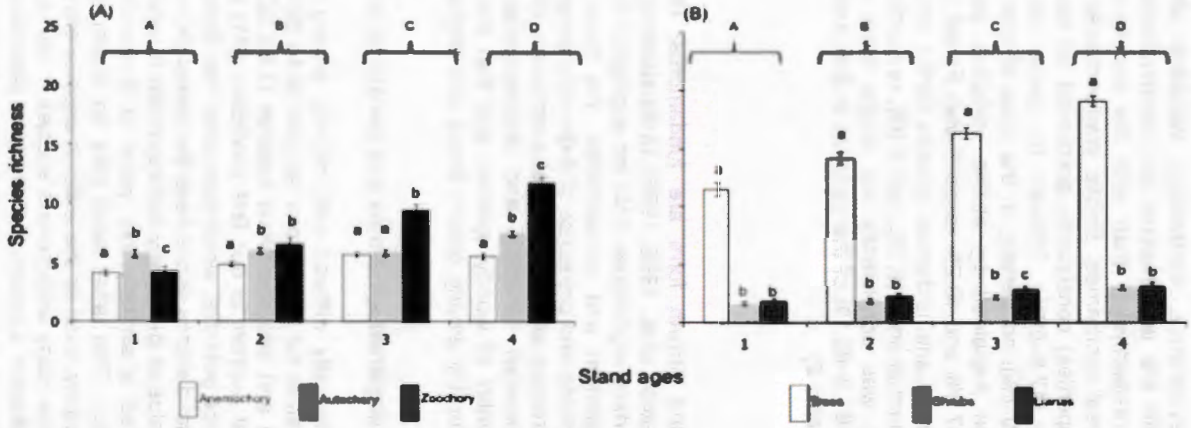

Figure 3.1 *Differences in species richness by dispersal syndrome and growth form among four vegetation classes, according to a nested variance analysis with generalized linear models. Different letters represent significant differences (P<0.001).*

Regarding dispersal syndromes, explanatory variables were more strongly associated with the autochorous and anemochorous guilds (31.2%, and 27.4%, respectively), than with the zoochorous guild (20.4%). Across dispersal syndromes, abiotic environmental variables (elevation and soil properties) consistently accounted for most of the variation in β-diversity (47.6–59%), followed by spatial structure of sampling sites (22.4–40.2%); conversely, in the case of zoochory, the percentage of variation explained by abiotic variables and spatial structure was similar (47.6% and 40.2% respectively). Forest stand age had a stronger influence on anemochorous species (20%), compared to autochorous and zoochorous ones (9.3%, and 6.9%, respectively). Soil organic matter (SOM) was consistently the single most important variable accounting for 61.9–82.1% of the variation in β-diversity across dispersal syndromes (Table 2).

3.4 DISCUSSION

Dispersal syndrome and growth form are fundamental life history attributes of plants (Westoby *et al.*, 1990, 1996). Understanding their role in β-diversity has important implications both for ecological theory and for biodiversity management and conservation. We found marked differences in the magnitude and correlates of β-diversity among growth forms and slighter differences among dispersal syndromes. Our results suggest that both dispersal limitation and environmental filtering contribute to the assembly of woody species, and that their relative influence varies considerably among growth forms and slightly among dispersal syndromes.

3.4.1 β-diversity by dispersal syndrome and growth form

The magnitude of β-diversity differed only slightly among dispersal syndromes and was greater for zoochorous species (9.44 SD) than for autochorous (7.59 SD) and anemochorous species (7.55 SD). These results give only partial support to our first prediction (P1) based on species dispersal distance potential, which postulates that those species with the longest dispersal distance would have the lowest β-diversity. As expected, the lowest value of β-diversity corresponded to anemochory. However, autochory had a similarly low value of β-diversity, which contradicts our prediction. This latter result may be related to factors other than dispersal capacity, such as the ability to coppice after frequent human disturbance, since many autochorous species in our study area, such as *Caesalpinia gaumeri, Lysiloma latisiliquum, Bahunia ungulata, Croton reflexifolius, Leucaena leucocephala* have a strong coppicing capacity and are among the most abundant species across successional age and topographic position. Coppicing allows plants to survive after disturbance (Swaine 1992, Miller & Kauffman, 1998), and uncouples

species composition from seed availability (Vieira & Scariot, 2006); this could help explain why species with low dispersal capacity can dominate throughout the landscape and across succession (Dupuy *et al.*, 2012), thereby reducing variation in species composition (i.e. β-diversity).

Contrary to our first prediction (P1), zoochory showed the highest value of β-diversity. This is likely the result of a highly variable dispersal range among zoochorous plant species depending on dispersers' motility, their body size, diet and home range, as well as on fruit traits and the availability of alternate food sources (Muller-Landau *et al.*, 2008). Furthermore, it has been found that few animal-dispersed seeds are brought into disturbed areas by frugivores, even when forest fragments are nearby, probably because of the scarcity of fruits, higher predation risk or the unfamiliar habitat that an open area represents for frugivores (Duncan & Chapman, 1999; van Breugel *et al.* 2006).Therefore, frequent disturbance, such as that produced by traditional shifting cultivation (as practiced in our study area) could reduce the dispersion of zoochorous species, thereby increasing the β diversity of this guild.

As expected, variation in floristic composition was greater for shrubs (the first two DCA ordination axes represented 19.13 SD) than for lianas and trees (12.83 SD and 6.97 SD, respectively). This result is partly in accordance with our first prediction (P1), and with other studies that have shown a positive influence of plant height on dispersal distance (Westoby *et al.*, 1990; Muller-Landau *et al.*, 2008), so that one may reasonably expect this variable to be inversely related to β-diversity. However, this does not explain why β diversity was almost twice as high for lianas as for trees.

The most important difference between these growth forms is their abundance and species richness which were both much lower for lianas than for trees. Lianas also showed a much lower ratio of individuals to species (33), compared to trees (167). The odds that two individuals taken at random belong to different species increases as this ratio decreases. Therefore, variation in species composition (β-diversity) should also increase as this ratio decreases, which could help explain why the magnitude of beta diversity was higher for lianas than for trees. In other words, the much lower abundance of lianas compared to trees may help explain why β-diversity was higher for lianas than for trees.

3.4.2 Species richness and composition by dispersal syndrome and growth form across secondary succession

As predicted (P2), overall species richness increased across dispersal syndromes and growth forms during secondary forest succession (Fig. 2). In terms of dispersal syndrome, we found only partial support for our second prediction. As predicted, zoochory dominated in late successional ages, and it also showed the highest α-diversity overall.

This result agrees with previous findings in other tropical dry forest ecosystms such as the Brazilian caatinga (Sobral and Machado 2001) and tropical dry forests in Ecuador (Jara-Guerrero *et al.* 2011), as well as in tropical wet forests in general (Armesto & Rozzi, 1989; Du *et al.*, 2009). Moreover, zoochory showed a clear increase in richness during secondary forest succession, as we initially predicted and as previously reported in tropical wet and dry forests (Armesto & Rozzi, 1989; Medina, 2005). For example, in early successional stands we recorded a small number of zoochorus species, such as the generalist species *Bursera simaruba* (L.) Sarg.. As succession advances, trophic complexity of the ecosystem increases, as well as richness of zoochorous species, which usually predominate in older stands, such as *Psidium sartorianum* (O. Berg) Nied., *Eugenia axillaris* (Sw.) Willd., *E. buxifolia* (Sw.) Willd and, *Neea psychotrioides* Don. Sm.

Contrary to our prediction P2, however, anemochory had the lowest species richness along forest succession, and showed a slight tendency to increase with successional age. Our study site is a semideciduous forest, a condition that could explain in part the low species richness of anemochory, since a considerable proportion of woody plants (25-50%) retain their leaves throughout the year. This phenological pattern could have a negative effect on the efficiency of anemochorous seed dispersal, since the advantage of this dispersal syndrome in dry forests is clearly associated with a higher wind circulation during the dry season both through the upper canopy and lower vegetation layers (Sobral and Machado 2001). The increase in anemochoruos species richness with successional age may result from the incorporation of new species belonging to the guild of long-lived pioneers species having wind-dispersed seeds, such as *Albizia tomentosa, Apoplanesia paniculata, Gyrocarpus americanus, Arrabidaea pubescens, Cydista potosina.*

In terms of growth form, we also found only partial support for our prediction (P2). Trees were the most specious growth form not only in late successional ages (as predicted), but also throughout succession (Fig. 2). Tree species richness also increased with successional age, as expected and as previously reported in tropical forests (Armesto & Rozzi, 1989; Medina, 2005; Butler *et al.*, 2007). Contrary to our prediction, shrubs did not dominate in the early phases of in succession in terms of absolute species richness; however, their relative richness was slightly higher in 3-8 yr-old forests (18.1%), compared to > 15 yr-old forests (16.2%). Overall relative richness of lianas (19.4%) was similar to that reported for other Neotropical forests –20% (Burnham, 2004). Absolute liana species richness increased slightly from early to more advanced successional age classes. This pattern has been reported in previous studies, such as Madeira *et al.* (2009) in Mata Seca, Brazil and Dewalt *et al.* (2000) in Barro Colorado, Panama. It has been observed that the increase in liana richness with successional age is related to the

increasing availability of large trees that can provide structural support (Clark & Clark, 1990; Nabe-Nielsen, 2001). The greater liana species richness found in more advanced successional ages compared to younger ones could thus be partly attributed to the presence of adequate support in older forest stands, combined with the relatively high light availability that characterizes tropical dry forests in general (Ceccon *et al.*, 2006; Lebrija-Trejos *et al.*, 2008).

Species composition of trees was similar between VC1 and VC2 (3-8 yr-old and 9-15 yr-old forests, respectively), although species richness differed. This may be attributed to the dominance of a group of pioneer species during the first 15 years of succession, which are subsequently replaced by shade-tolerant species, as has been reported in several studies both in wet and in dry tropical forests (Swaine & Hall, 1983; Finegan, 1996; Chazdon, 2008; Lebrija-Trejos *et al.*, 2010). All other pair-wise comparisons among vegetation classes differed in tree species composition, including VC3 and VC4 (> 15 yr-old forests on flat areas and on hills, respectively), which indicates that topographic position also contributes to tree β diversity –as well as to alpha diversity (Fig. 2b).

In contrast, species composition of shrubs differed among all vegetation classes except for VC3 and VC4, indicating that shrub β diversity varies with forest succession, but not with topographic position. Liana species composition did not differ significantly among vegetation classes (except between VC1 and VC4), suggesting that liana β diversity is relatively unaffected by forest succession and topographic position. This may be the result of the dominance across vegetation classes of three species of lianas that represent more than 50 % of their total abundance. Besides lianas tend to have deep roots and a highly efficient water-transport system, and they generally require high-light environments for successful establishment (Schnitzer & Bongers, 2002; Schnitzer, 2005). These characteristics could help explain why lianas seem to able to establish, grow and persist equally well under different topographic positions and successional age classes, since they may be able to cope with the major limiting factor in seasonally dry forests – water stress, and may not be limited by low light availability.

3.4.3 Variation partitioning (P3)

The proportion of the total variation in species composition accounted for by the explanatory variables, as well as the relative importance of explanatory variables varied markedly among growth forms and slightly among dispersal syndromes (Table 2). These results clearly indicate that β-diversity, as well as the factors that influence it depend on key plant attributes or functional groups, such as growth form and, to a lesser extent, dispersal syndrome. Our results supported partially our prediction

(P3), because environmental filters explained a larger percentage of β-diversity for trees and lianas than for shrubs. In fact, abiotic environmental variables contributed most to β diversity across growth forms and dispersal syndromes –except for shrubs. The dominant role of environmental factors in explaining β diversity of woody plants suggests that environmental filtering is a major driver of β diversity, as has been found in many studies (Tuomisto & Poulsen, 1996; Ruokolainen & Tuomisto, 2002; Tuomisto *et al.*, 2003a, 2003b; Paoli *et al.*, 2006) providing support for the niche partitioning theory.

Shrubs were the only guild for which the spatial structure of sampling sites explained a larger percentage of variation in species composition than environmental filters, suggesting that dispersal limitation plays a greater role on shrub β-diversity than environmental filters. This could be partly attributed to the relatively short stature of shrubs, which may impose important limits on their dispersal capacity, resulting in a strong spatial autocorrelation in species composition. Using the same data set and (local) spatial grain of this study, López-Martínez *et al.* (2012) found that environmental variables and spatial autocorrelation among sampling sites had a similar influence on overall β diversity of woody species. Our results clearly show that this general pattern masks major differences in the relative importance of environmental filters vs. dispersal limitation among growth forms.

Dispersal syndromes showed more consistent patterns of variation partitioning of β-diversity than growth forms, and a clear predominance of environmental filters (Table 2). Contrary to our prediction (P3), the autochorous guild showed a slightly stronger association with environmental variables compared with the zoochorous and anemochorous guilds. Moreover, the lowest percentage of β diversity explained by spatial autocorrelation corresponded to the autochorous guild. As previously discussed, these unexpected results could be partly attributed to the dominance of tree species with strong coppicing capacity, belonging to different dispersal syndromes, predominantly autochory. In rural landscapes that have been subjected to recurrent slash and burn agriculture for over 2000 years (Rico-Gray y García-Franco, 1991), coppicing could offset dispersal limitation and enable species with short-distance seed dispersal to persist across the landscape.

The effects of forest succession on β-diversity varied among growth forms and dispersal syndromes. Stand age explained almost 12% of the total variation in species composition of trees and shrubs, but was unrelated to liana β diversity, possibly due to the capacity of lianas to establish, grow and persist equally well under different topographic positions and successional age classes, as discussed previously. Similarly, stand age explained less than 10% of variation in species composition of zoochorous and autochorous species, and 20% of the anemochorous β diversity. In this same study area, López-Martínez *et al.*

(2012) found that stand age explained only 3% of the total variation in species composition of all woody species. These contrasting results clearly illustrate the importance of considering different growth forms and dispersal syndromes when evaluating the ecological factors that influence β diversity.

Our variance partitioning analysis showed that soil variables explained more than 50% of the variation in tree species composition. This is consistent with previous findings in the same study area indicating that hills have a thinner soil layer with high rock and nutrient content, whereas flat areas have deeper soils with high clay content and that these characteristics have a major influence on woody species composition –which is dominated by trees (Dupuy *et al.*, 2012).

The most important environmental variable explaining β diversity differed among growth forms: soil organic matter for trees, cation exchange capacity for shrubs and pH for lianas. This result further suggests that growth forms are differentially limited by different soil variables, which is consistent with niche partitioning. Soil organic matter (SOM) was consistently the single most important factor influencing β diversity of dispersal syndromes, as well as of trees (Table 2). Soil organic matter has been shown to positively influence soil fertility, as well as the capacity of soils to hold water and incorporate nutrients (Swaine, 1992; Swaine, 1996; Guariguata & Ostertag 2001). Our results agree with those found in the Amazon by Tuomisto *et al.* (2003a) and Costa *et al.* (2005), and in Indonesia by Paoli *et al.* (2006), suggesting that soil nutrients strongly influence variation in plant species composition.

To conclude, our results clearly show that the magnitude of β-diversity varied markedly among growth forms and slightly among dispersal syndromes. They also showed that environmental filters are the most important factor explaining β-diversity, except for shrubs, for which dispersal limitation appears to be more important, possibly due to their low stature that may limit their dispersal capacity. Additionally,stand age clearly influenced α-diversity across growth forms and dispersal syndromes, but showed a relatively low influence on β-diversity, possibly due to the predominance of tree species with strong coppicing capacity across successional age as well as across the study landscape. Finally, our results clearly show that considering different plant traits can reveal important differences in β-diversity patterns and correlates that are not apparent when one considers overall woody plant diversity. Such differences are important to inform detailed conservation, restoration and management strategies needed to stem the relentless deforestation, degradation and fragmentation of tropical dry forests.

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Capítulo 4

Discusión general y conclusiones

4.1 DISCUSIÓN GENERAL

Esta tesis doctoral surge de una pregunta que ha sido estudiada por mucho tiempo, alrededor de la cual, sin embargo, hasta el día de hoy no existe un consenso general: ¿Cuáles son los factores que determinan la variación espacial en la composición (diversidad β) de especies leñosas? Para abordar esta controversial pregunta, la dividimos en dos tópicos principales. Por un lado, evaluamos la importancia relativa de los mecanismos que afectan a la diversidad β de las especies leñosas con respecto a la escala espacial (Capítulo 2). Por otro el lado analizamos la importancia relativa de los mecanismos que afectan a la diversidad β de acuerdo con el síndrome de dispersión y forma de crecimiento (Capítulo 3). En el Capítulo 1 se abordó el marco teórico y los conceptos básicos que le dan sustento a esta tesis y en el presente Capítulo se integran los principales resultados de la investigación doctoral.

4.1.1 Importancia de la escala (el grano espacial) en la diversidad β de especies leñosas

En este estudio observamos que la magnitud de la variación en la composición de especies está supeditada al tamaño de muestra utilizado (grano espacial). Es decir, granos más gruesos (unidades de muestra más grandes) presentaron una diversidad β menor en comparación con granos más finos (unidades de muestra de menor tamaño). Este resultado fue similar utilizando dos diferentes medidas de la magnitud de la diversidad β: un índice de disimilitud florística (DCA basado en el índice χ^2), el cual toma en cuenta la abundancia de cada especie y la medida tradicional de la diversidad β de Whittaker (1972), el cual se basa solamente en el número de especies. El patrón fue similar en ambos casos y se mantuvo, aún después de estandarizar esta última medida a un número comparable de individuos (por medio del procedimiento de rarefacción). Esto indica que la menor magnitud de la diversidad β en el tamaño de grano más grande no se debe solamente a la diferencia en el número de individuos entre las dos escalas. Por el contrario nuestros resultados sugieren que el aumentar el tamaño del grano de una escala local a una escala de paisaje se incrementa la diversidad α y por lo tanto, en un área con una diversidad γ constante,

hay una reducción en la diversidad β. Estos resultados concuerdan con la idea propuesta por Rosenzweig (1995) sobre la relación especie–área (P1 del Capítulo I) y nuestra hipótesis 1 (H1), así como con la manera tradicional de estimar la diversidad β a partir de la diversidad γ y α (Whittaker 1972).

Pocos estudios han evaluado la influencia del tamaño de muestra sobre la variación espacial en la riqueza de especies de una comunidad (Jones *et al.* 2008). Field y colaboradores (2009) hicieron un meta–análisis y encontraron que el tamaño del grano es un elemento determinante en la variación espacial de la riqueza de especies, aunque pobremente explorado, ya que sólo encontraron 16 artículos de 397 en los que se consideró la variación en el tamaño de grano. Nuestros resultados claramente mostraron que la magnitud de la diversidad β es dependiente de la escala; la diversidad β decreció conforme se incrementó la escala espacial (tamaño del grano), siempre y cuando la extensión total del sitio de estudio y, por lo tanto, la diversidad gamma (γ) permaneciera constante. Esto ocurrió no solamente en términos del número de especies (diversidades γ y α), sino también en términos de la variación en la composición (abundancia) de las especies (disimilitud florística). Este último resultado indica que el tamaño del grano afecta no solamente al número de especies muestreado, sino también a la composición de las especies (en términos de abundancia).

4.1.2 Segregación de los nichos vs capacidad de dispersión limitada

Como se ha mencionado, la variación en la composición de especies ha sido ampliamente abordada principalmente a la luz de dos hipótesis contrastantes, que son la teoría de la segregación de los nichos, cuyo principal mecanismo es el filtrado ambiental, y la teoría neutral, basada en capacidad de dispersión limitada. Ambas teorías han ido ganado apoyo de estudios empíricos (Condit *et al.*, 2002; Duivenvoorden *et al.*, 2002; Tuomisto *et al.*, 2003a; Gilbert y Lechowicz, 2004; Legendre *et al.*, 2009). En este estudio encontramos que ambos mecanismos afectan a la variación en la composición de especies, y su importancia relativa varía con la escala espacial, así como con la forma de crecimiento y el síndrome de dispersión, lo cual apoya el planteamiento de las hipótesis dos y tres.

A escala (tamaño de grano) local encontramos que tanto las variables ambientales (medida indirecta del filtrado ambiental) como la autocorrelación espacial (medida indirecta de la dispersión limitada) afectaron por igual a la diversidad β. Estos resultados concuerdan con lo encontrado por Tuomisto *et al.* (2003b) en la Amazonia, así como con la hipótesis del continuo de Gravel *et al.* (2006). Dicha hipótesis postula que existe un continuo entre la exclusión competitiva y la estocasticidad

desde las comunidades estructuradas por la segregación de los nichos hasta las comunidades neutrales. Sin embargo, a escala de paisaje encontramos que la contribución relativa del filtrado ambiental fue mayor a la de la limitación en la dispersión. Nuestros resultados apoyan hallazgos de estudios previos en los que se observó que a medida que aumenta algún componente de la escala espacial aumenta la heterogeneidad ambiental, lo cual conlleva un aumento en la importancia relativa del filtrado ambiental con respecto a la dispersión limitada (Bell, 2005; Jones *et al.*, 2008; Laliberté *et al.* 2009; Borcard *et al.*, 2011)

Por otro lado, se sabe que caracteres como la forma de crecimiento y el síndrome de dispersión son elementos que manifiestan procesos tanto ecológicos como evolutivos que afectan a la diversidad beta y que pueden ayudar a comprender los mecanismos que influyen en el ensamblaje de las comunidades vegetales (Howe y Smallwood, 1982; Levin *et al.*, 2003; Cavender-Bares *et al.*, 2009; Kooyman *et al.*, 2010). De acuerdo con este planteamiento, al analizar la diversidad β de especies leñosas para diferentes formas de crecimiento y síndromes de dispersión encontramos que el filtrado ambiental es el principal promotor y mantenedor de la diversidad β (excepto para los arbustos). Estos resultados apoyan el planteamiento teórico de la segregación de los nichos como un mecanismo que permite reducir la presión de competencia y promover la coexistencia de las especies a través de diferentes estrategias como la forma de crecimiento y el síndrome de dispersión.

Los arbustos fueron la única forma de crecimiento para la cual la autocorrelación espacial de los sitios de muestreo explicó un mayor porcentaje de la variación en la composición de especies, lo cual sugiere que la limitación en la dispersión es un mecanismo clave para entender la diversidad β en especies arbustivas. Este resultado puede atribuirse a la morfología de los arbustos, ya que generalmente éstos presentan una estatura relativamente baja que puede limitar su capacidad de dispersión, resultando en una fuerte autocorrelación espacial en la composición de especies.

Es importante destacar que la variación total explicada fue mayor cuando se analizó la diversidad β de especies leñosas para diferentes síndromes de dispersión y formas de crecimiento (Capítulo 3) que cuando el análisis se hizo para todas las especies leñosas juntas (Capítulo 2). Esto sugiere que estos caracteres (forma de crecimiento y síndrome de dispersión) proporcionan más información que la simple identidad de las especies. Además, la influencia relativa de los factores y mecanismos analizados varió entre las formas de crecimiento y, en menor medida, entre los síndromes de dispersión. Esto indica que la influencia relativa de los factores y procesos que determinan la diversidad β varía entre diferentes gremios, y que esta variación

quedaría enmascarada al considerar a todas las especies leñosas juntas.

Un porcentaje alto de la variación total no fue explicado ni a diferentes escalas espaciales ni considerando diferentes síndromes de dispersión y formas de crecimiento. Éste es un resultado común en estudios de diversidad β de especies vegetales (Chust *et al.*, 2004; Cottenie, 2005; Chust *et al.*, 2006; Jones *et al.*, 2008). El alto porcentaje de variación no explicado puede ser atribuido a variables ambientales no evaluadas en los modelos, tales como la disponibilidad de agua o la intensidad lumínica, las cuales se ha observado que son elementos importantes en los BTS (Balvanera *et al.*, 2002; Quesada *et al.*, 2009) y particularmente en la Península de Yucatán (Trejo, 1998), así como la capacidad de rebrote de las especies, la cual puede influir de manera importante en la variación en la composición de especies (Dupuy *et al.*, 2012).

Entre los principales factores del filtrado ambiental encontramos que la materia orgánica, el pH, el K, la capacidad de intercambio catiónico (CIC), y la topografía afectaron la variación en la composición de especies leñosas a escala local, así como para conjuntos de especies definidos por diferentes síndromes de dispersión y formas de crecimiento. La materia orgánica y el pH contribuyen fuertemente a la fertilidad del suelo, aumentando la capacidad de intercambio catiónico y favoreciendo la retención de agua y de nutrimentos (Guariguata y Ostertag, 2001). Nuestros resultados sugieren que la topografía promueve la variación en las condiciones del suelo entre los lomeríos y las zonas planas. Estos resultados concuerdan con estudios realizados en la Amazonía peruana (Tuomisto *et al.*, 1995, 2003a, 2003b; Costa *et al.*, 2005), en Indonesia (Paoli *et al.*, 2006), y en México (White y Hood, 2004; Gallardo-Cruz *et al.*, 2009; Hernández-Stefanoni *et al.*, 2011; Dupuy *et al.*, 2012), en los que se observó que los nutrimentos del suelo, la estructura del paisaje, la topografía, la pendiente y la elevación son factores que afectan la distribución, la abundancia y la composición de las especies leñosas, en coincidencia con nuestros resultados.

En este estudio se encontró una correlación positiva entre la diversidad β y la diversidad de parches (SHEI), así como, una correlación inversa con respecto al índice del parche más grande (LPI), siendo ambas medidas indicadoras de fragmentación. Diversos estudios han encontrado que niveles moderados de fragmentación promueven la variación en la composición a través del aislamiento geográfico y el efecto de borde; esto último genera cambios microclimáticos que favorecen la heterogeneidad ambiental y el establecimiento de diversas especies (Laurence *et al.*, 1998; Honnay *et al.*, 1999; Bascompte y Rodríguez, 2001; Laurence *et al.*, 2002). En resumen nuestros resultados indican que, en un paisaje poco fragmentado como el nuestro, la fragmentación contribuye (al menos hasta cierto punto) a

incrementar la variación espacial en la composición de especies leñosas.

Para concluir, se ha argumentado que resultados como los encontrados por nosotros pueden ser interpretados de dos maneras: (1) como el efecto de un entorno estructurado espacialmente, con influencia sobre la variación en la composición de especies leñosas, o (2) como un efecto neutral que actúa sobre la diversidad β en un entorno heterogéneo (Bell *et al.*, 2006). De acuerdo con Li *et al.* (2011) y tomando en cuenta la contribución relativa alta del filtrado ambiental en nuestros resultados, podemos inferir que la diversidad β a escala local, así como para diferentes formas de crecimiento y síndromes de dispersión (excepto para arbustos) es el resultado de un entorno ambiental estructurado espacialmente. Esto explicaría la variación compartida por ambos tipos de variables, la cual puede interpretarse como la interacción entre ambos mecanismos. A escala de paisaje podemos concluir que el principal mecanismo promotor de la diversidad β es la variación ambiental entre los sitios. Por otro lado, la capacidad de dispersión limitada (teoría neutral) parece ser el principal mecanismo que afecta la diversidad β de arbustos. Nuestros resultados sugieren que la segregación del nicho ecológico reduce la presión de competencia y promueve la coexistencia de especies (Macarthur y Levins, 1967; Tilman, 1994) y que la diversidad β de especies leñosas depende fuertemente de atributos clave de plantas o grupos funcionales, tales como el síndrome de dispersión y la forma de crecimiento.

4.1.3 Sucesión y riqueza de especies

En esta investigación evaluamos la asociación entre la sucesión ecológica y la diversidad β a escala local (Capítulo 2), tanto para todas las especies como para diferentes síndromes de dispersión y formas de crecimiento (Capítulo 3). En términos generales, la edad sucesional contribuyó relativamente poco a explicar la variación en la composición de especies leñosas. Este resultado concuerda con los de estudios previos (Tabarelli *et al.*, 2008; Lôbo *et al.*, 2011) en los cuales se ha concluido que los bosques tropicales con disturbios humanos frecuentes presentan una tendencia hacia la homogeneización de su flora, debido a la dominancia de unas pocas especies adaptadas a los disturbios Algunos ejemplos de este grupo de especies en nuestra área de estudio son *Neomillspaughia emarginata, Mimosa bahamensis, Bursera simaruba, Caesalpinia gaumeri*, las cuales son predominantemente especies pioneras y con una gran capacidad de rebrote que les permite sobrevivir a los disturbios.

Por otro lado, encontramos que la diversidad β difirió entre las clases de vegetación, tanto para la comunidad de especies leñosas en conjunto, como para los diferentes síndromes de dispersión y formas de

crecimiento, excepto para las lianas, las cuales no mostraron diferencias en la diversidad β entre las clases de vegetación en general, pero sí presentaron un aumento en la riqueza de especies con la edad de sucesión. Estos resultados son contrarios a los reportados por Dewalt y colaboradores (2000) en Barro Colorado, Panamá y no coinciden con lo observado por Madeira *et al.* (2009) en Mata Seca, Brasil. El aumento en la riqueza de especies de lianas observado en este estudio puede estar asociado a la presencia de un soporte adecuado en las etapas de sucesión más maduras, combinado con una mayor disponibilidad de luz en general en los bosques tropicales secos, comparados con sus contrapartes húmedas (Ceccon *et al.*, 2006; Lebrija-Trejos 2009). Aunque en general, encontramos diferencias en la composición de especies entre las clases de vegetación, las clases CV1 y CV2 no difirieron. Esto podría deberse a la dominancia de un grupo de especies pioneras durante las dos primeras clases de edad (3 a 15 años de abandono), las cuales son reemplazadas subsecuentemente por especies tolerantes a la sombra, como se ha reportado frecuentemente en bosques tropicales secos y húmedos (Swaine y Hall, 1983; Finegan, 1996; Chazdon, 2003; Chazdon, 2008; Chazdon *et al.*, 2010; Lebrija-Trejos *et al.*, 2010). Es interesante que las clases CV3 y CV4 (> 15 años de edad en zonas planas y en cerros, respectivamente) también hayan diferido en la composición de especies en general; esto indica que la topografía es un elemento fundamental para entender la diversidad β. Estudios como el de White y Hood (2004) en la Península de Yucatán, encontraron un fuerte efecto de la topografía y los atributos del suelo sobre la abundancia de especies leñosas, mientras que Gallardo-Cruz *et al.* (2009) reportó una fuerte influencia de la pendiente y la elevación sobre la composición de especies leñosas en Oaxaca, México. Estos resultados ofrecen evidencias para inferir que las variaciones en los elementos del suelo entre las zonas altas y las zonas planas son un factor determinante de la variación en la composición de especies leñosas.

Por otro lado, encontramos que el patrón general de la riqueza de especies, tanto de los síndromes de dispersión, como de las formas de crecimiento, aumentó conforme aumentó la edad sucesional. Este resultado es consistente con los resultados de diversos estudios, tanto en bosques secos (Sobral y Machado, 2001; Jara-Guerrero *et al.*, 2011) como en bosques húmedos (Armesto y Rozzi, 1989; Du *et al.*, 2009). Este aumento en la riqueza puede deberse a un aumento en la complejidad estructural y micro-ambiental del sistema con la edad sucesional (Medina, 2005). Un ejemplo de lo anterior es el claro aumento del conjunto de especies zoócoras a través de la sucesión; en las primeras etapas de sucesión es común registrar un pequeño número de especies zoócoras, tal como *Bursera simaruba* (L.) Sarg. y conforme avanza el proceso de sucesión encontramos especies características de selvas maduras como *Psidium sartorianum* (O. Berg) Nied., *Eugenia*

axillaris (Sw.) Willd., *E. buxifolia* (Sw.) Willd and, *Neea psychotrioides* Don. Sm.

En resumen, nuestros resultados sugieren que la edad sucesional es un elemento relativamente poco determinante en la diversidad β de especies, quizás debido a la abundancia de ciertas especies muy dominantes, aunque sí es un elemento importante en la riqueza de especies. Esto podría deberse al alto porcentaje de similitud en la composición de especies leñosas independiente de la edad de sucesión. Se ha observado que la flora de las selvas tropicales es susceptible a los procesos de homogeneización como resultado a los disturbios antropogénicos, los cuales favorecen el establecimiento de especies pioneras de larga vida y con alta capacidad de rebrote, las cuales pueden colonizar las áreas perturbadas y permanecen hasta las edades más maduras (Lôbo *et al.*, 2011). Asimismo, sugerimos que, conforme aumenta la edad sucesional, se presenta un aumento en la complejidad estructural y micro-ambiental del sistema, lo cual favorece el incremento en la riqueza de especies en general, así como de diferentes síndromes de dispersión y formas de crecimiento.

4.2 CONCLUSIONES

A partir de la integración de los resultados de los diferentes componentes de esta tesis nos permitimos proponer las siguientes conclusiones:

1. La magnitud de la diversidad β disminuye conforme aumenta la escala espacial (tamaño del grano), siempre y cuando la extensión (y la diversidad γ) permanezcan constantes, lo cual apoya nuestra hipótesis uno (H1).

2. A escala local, la magnitud de la influencia en la diversidad β de la segregación de los nichos fue similar a la correspondiente a la capacidad de dispersión limitada; este resultado concuerda parcialmente con nuestra hipótesis dos (H2). Sugerimos que la diversidad β en esta selva es el resultado de un entorno estructurado espacialmente, con influencia sobre la variación en la composición de especies leñosas.

3. A escala de paisaje se observó que la diversidad β fue principalmente promovida por el filtrado ambiental, lo cual concuerda con lo planteado en la hipótesis dos (H2).

4. El filtrado ambiental también parece ser el principal promotor de la diversidad β de especies leñosas de diferentes formas de crecimiento y síndromes de dispersión, excepto para los

arbustos. Esto apoya parcialmente el planteamiento de nuestra hipótesis tres (H3) y resalta la importancia de la segregación de nichos en la estructuración de las comunidades vegetales.

5. La edad sucesional contribuyó relativamente poco a explicar la variación en la composición de especies leñosas; por el contrario, la heterogeneidad ambiental (incluyendo la topografía) parece ser más importante.

6. La riqueza de especies, tanto total, como por síndrome de dispersión o por forma de crecimiento, aumenta conforma aumenta la edad de sucesional; lo cual podría deberse a un aumento en la complejidad estructural con la edad sucesional.

7. La influencia relativa de los factores y mecanismos que afectan a la diversidad β varió entre los síndromes de dispersión y las formas de crecimiento evaluados. Esta variación quedaría enmascarada al considerar a todas las especies leñosas juntas.

8. Características funcionales, tales como el síndrome de dispersión y las formas de crecimiento explican un mayor porcentaje de la variación en la composición que cuando se analizan los datos de modo general. Esto nos sugiere la necesidad de tomar en cuenta los caracteres y grupos funcionales de plantas para estudiar la diversidad β.

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