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IDENTIFICACIÓN DE GRUPOS FUNCIONALES DE  
PLANTAS EN DIFERENTES ESTADIOS SUCESIONALES  
DEL BOSQUE TROPICAL CADUCIFOLIO:  
UNA HERRAMIENTA EN EL ESTUDIO DE LOS BOSQUES  
SECUNDARIOS

# TESIS

QUE PARA OBTENER EL GRADO ACADÉMICO DE

**DOCTORA EN CIENCIAS**

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Presente

Por medio de la presente me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día 26 de marzo del 2012, se acordó poner a su consideración el siguiente jurado para el examen de DOCTORA EN CIENCIAS de la alumna **ÁLVAREZ AÑORVE MARIANA YÓLOTL** con número de cuenta **94529157**, con la tesis titulada: **"Identificación de grupos funcionales de plantas en diferentes estadios sucesionales del bosque tropical caducifolio: una herramienta en el estudio de los bosques secundarios"**, bajo la dirección del **Dr. Mauricio R. Quesada Avendaño**.

Presidente: Dra. Guadalupe Judith Márquez Guzmán  
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El Comité Académico, aprobó que la integración del jurado se realizará a solicitud del alumno, **con cinco sinodales**, en apego a la nueva normatividad, acogiéndose al artículo **QUINTO TRANSITORIO**, con base en lo establecido en el Artículo 31 del Reglamento General de Estudios de Posgrado.

Sin otro particular, quedo de usted.

Atentamente  
"POR MI RAZA HABLARA EL ESPIRITU"  
Cd. Universitaria, D.F., a 14 de junio del 2012.

*M. del Coro Arizmendi*

Dra. María del Coro Arizmendi Arriaga  
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***“Por mi raza hablará el espíritu”***

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## RESUMEN

El Bosque tropical seco (BTS) es uno de los ecosistemas tropicales más ampliamente distribuidos y amenazados del mundo. Debido a la alta intensidad de actividades humanas asociadas a este bosque, actualmente la mayoría de su área se encuentra conformada por un mosaico de bosques secundarios en diferentes estadios de sucesión. Resulta imprescindible, por tanto, conocer la dinámica sucesional y de regeneración natural de estos ecosistemas ya que esto sentaría las bases científicas para su manejo y conservación. A pesar de la alta diversidad, el alto grado de endemismos y la gran variedad de servicios ambientales que prestan los BTS, los estudios sobre su dinámica sucesional son relativamente recientes y aún insuficientes; la comunidad científica tradicionalmente ha prestado más atención a los bosques tropicales lluviosos. En general, se ha reportado que la recuperación estructural del BTS es relativamente rápida, mientras que parámetros como la riqueza y composición de especies experimentan una recuperación más lenta. La recuperación funcional, sin embargo, no se ha evaluado hasta el momento y existe muy poca información sobre los mecanismos funcionales que subyacen a la dinámica sucesional y al ensamblaje de comunidades de estos sistemas tropicales.

En esta tesis abordamos el estudio de la sucesión del BTS desde una perspectiva funcional. Para ello, evaluamos el desempeño funcional de comunidades arbóreas a lo largo de un gradiente sucesional en el BTS de Chamela-Cuixmala (Jalisco, México). Específicamente evaluamos caracteres funcionales de la vegetación relacionados con la adquisición y uso de recursos (luz, agua, nutrientes), en las especies arbóreas más abundantes de nueve sitios correspondientes a 3 estadios sucesionales del BTS (temprano, intermedio y tardío). Estos caracteres funcionales influyen procesos y propiedades emergentes de los ecosistemas, afectando directamente el funcionamiento de los mismos. El presente estudio comprendió: 1) la identificación de los procesos determinando el ensamblaje de las comunidades sucesionales, 2) la caracterización del sistema sucesional desde una perspectiva ecosistémica (grupos funcionales) y 3) la aplicación de la información generada en herramientas que nos permitirían estudiar estos ecosistemas a una escala de paisaje (reflectancia espectral de la vegetación).

Primeramente, mediante el estudio de la estructura filogenética y de la distribución de valores de los diferentes caracteres funcionales evaluados, determinamos que el ensamblaje

de las diferentes comunidades sucesionales del BTS estaba dirigido por procesos de nicho más que por procesos neutrales (capítulo 1). La fuerza de los procesos influenciando el ensamblaje cambió a lo largo de la sucesión. En los estadios tempranos e intermedios predomina la acción de filtros ambientales que solo permiten la ocurrencia de especies con alta capacidad de dispersión de calor y con altas tasas fotosintéticas. En estos estadios, sin embargo, también se detectaron procesos de partición de nicho (límites a la similaridad) actuando en sentido contrario pero con menor intensidad que los filtros ambientales. En el estadio tardío no se encontró evidencia de procesos de nicho que estuviesen estructurando las comunidades arbóreas; esto podría ser una consecuencia de que los límites a la similaridad aumentan en intensidad a lo largo de la sucesión, anulando, en los estadios avanzados, la evidencia (pero no necesariamente la acción) de los filtros ambientales. La acción de estos procesos se refleja nítidamente en la forma en que la diversidad funcional, el desempeño funcional y la abundancia de las especies cambian a lo largo del gradiente sucesional.

En segundo término, en aras de abordar el estudio funcional de la sucesión desde una perspectiva ecosistémica, se realizó una revisión bibliográfica sobre los grupos funcionales de plantas en sistemas sucesionales tropicales y sobre nuevas tecnologías que nos permitieran detectarlos (capítulo 2). De esta forma determinamos que: 1) hasta el momento, no se conocían los grupos funcionales de los sistemas sucesionales del BTS, 2) nuevas técnicas de percepción remota hiperespectral, capaces de medir la reflectancia espectral de la vegetación a lo largo del espectro electromagnético, podían ser utilizadas para distinguir diferentes tipos de vegetación en los sistemas naturales y 3) la relación existente entre los caracteres funcionales de la vegetación y la reflectancia espectral de la misma, podría resultarnos de utilidad para discriminar los diferentes estadios sucesionales del BTS.

Con base en esta información, caracterizamos nuestro gradiente sucesional (capítulo 3) desde una perspectiva funcional que nos permitiera: 1) evaluar la “regeneración funcional” en el BTS, 2) identificar a los grupos funcionales de plantas de este sistema y 3) explorar el potencial de índices espectrales relacionadas con el desempeño funcional de las plantas, para discriminar, en el largo plazo, los diferentes estadios sucesionales del BTS. Encontramos que la regeneración integral del BTS es más lenta de lo que se infiere a partir de estudios que no evalúan el componente funcional. Se identificaron, asimismo, dos

grupos funcionales, uno de especies “pioneras” compuesto mayormente por individuos asociados a los estadios tempranos e intermedios, y otro, asociado a estrategias de sucesión tardía, compuesto mayormente por individuos asociados al estadio de sucesión avanzada. Los grupos funcionales difieren principalmente en su capacidad fotosintética, su capacidad de disipación de calor y su capacidad de fotoprotección, capacidades todas que disminuyen desde los estadios tempranos hacia los tardíos. En este mismo sentido, un índice espectral asociado a la eficiencia fotosintética y a la capacidad de fotoprotección de la hoja, resultó útil para discriminar las hojas pertenecientes a los estadios tardíos, de las hojas provenientes de los otros estadios.

Finalmente, en aras de contribuir a la aplicación de la tecnología de percepción remota en el estudio de las comunidades de plantas tropicales, analizamos detalladamente la relación de la reflectancia espectral, con características, anatómicas, bioquímicas y funcionales a nivel foliar; posteriormente, evaluamos la variación de los datos espectrales en los diferentes estadios sucesionales y finalmente identificamos los datos espectrales más adecuados para clasificar/discriminar los diferentes estadios sucesionales (capítulo 4). Cinco índices espectrales de la vegetación estuvieron correlacionados significativamente a la mayoría de los caracteres funcionales que cambian a lo largo de la sucesión. El estadio intermedio mostró una mayor variación en los datos espectrales que los estadios temprano y tardío. Esto coincide con la hipótesis de perturbación intermedia que implica una mayor diversidad funcional en los estadios intermedios de la sucesión. Estos resultados y datos previos sobre el comportamiento de los caracteres funcionales en este sistema de estudio, sugieren que algunos procesos de nicho podrían explicar en parte el comportamiento de los datos espectrales. Los estadios temprano e intermedio, que son funcionalmente similares, fueron también similares desde el punto de vista espectral. Así, la discriminación más precisa (86% de precisión), se logró entre los estadios temprano y tardío usando dos índices espectrales altamente correlacionados con los caracteres funcionales que varían a lo largo del gradiente sucesional. Nuestros resultados sugieren que los índices espectrales son potencialmente útiles para inferir no solo el estado funcional y sucesional de la vegetación tropical, sino también los procesos ecológicos determinando dicho status. Esto haría posible el advenimiento de técnicas más simples, rápidas y, en el largo plazo, escalables desde el punto de vista espacial para monitorear la dinámica de los bosques tropicales.

## ABSTRACT

The seasonally dry tropical forest (SDTF), is one of the most widely distributed and endangered ecosystems of the world. As a consequence of the high intensity of human activities, most of the SDTFs are constituted by a mosaic of secondary forest under different stages of succession. Hence, it is necessary to study the successional and natural regeneration dynamics of this ecosystem, generating information that would constitute a scientific basis for its management and conservation. Despite the high diversity, the high number of endemisms and the great variety of environmental services that SDTF provides, studies on its successional dynamics are relatively recent and still insufficient; the scientific community has traditionally paid more attention to tropical rain forests. In general, it has been reported that SDTF structural recovery is relatively quickly, whereas parameters such as species richness and composition are recovered more slowly. The SDTF functional recovery, however, has not been evaluated until now and we have little information about the functional mechanisms underlying the successional dynamics and community assembly of these tropical systems.

In this thesis, we studied SDTF succession from a functional perspective. Specifically, we assessed the functional performance of tree communities along a successional gradient in the Chamela-Cuixmala SDTF (Jalisco, Mexico). We evaluated plant functional traits related to the acquisition and use of resources (light, water, nutrients) in the most abundant tree species occurring in nine plots correspondent to three SDTF successional stages (early, intermediate and late). These plant functional traits influence processes and emergent properties of ecosystems, affecting their functioning directly. This study included: 1) the identification of processes determining the assembly of successional communities, 2) the characterization of the successional systems from an ecosystemic perspective (functional groups) and 3) the application of this information in the exploration of tools allowing us to study these systems at a landscape level (vegetation spectral reflectance).

First of all, by analyzing the phylogenetic structure and the distribution of the functional traits values in the different communities, we determined that the assembly of SDTF

successional communities was influenced by niche processes more than by neutral processes (chapter 1). The strength of niche processes changed along succession. In early and intermediate stages predominated the action of environmental filters selecting for species with high heat dispersion capabilities and high photosynthetic rates. In these stages, however, we also detected evidence of niche partitioning processes (limits to similarity) acting in the opposite direction and with less intensity than environmental filters. In the late successional stage there was no evidence of niche processes structuring tree communities. This could be a consequence of the increasing intensity in the strength of niche partitioning processes along succession that would preclude the evidence (but not necessarily the action) of environmental filtering. The effects of niche processes were clearly reflected in the way that functional diversity, functional performance and species abundance changed along the successional gradient.

Secondly, in order to study the SDTF succession from an ecosystemic perspective, we searched in the literature for information about plant functional groups in tropical successional systems and about new technologies allowing us to detect them (chapter 2). We found that: 1) there was no information about the plant functional groups of SDTF successional systems, 2) new techniques of hyperspectral remote sensing, which measure the vegetation spectral reflectance along the electromagnetic spectra, could be useful to distinguish different types of vegetation in natural systems and 3) as plant functional traits could be “tracked” through plant spectral reflectance, we could use spectral reflectance data to discriminate the different SDTF successional stages.

Based on this information, we characterized our successional gradient (chapter 3) from a functional perspective allowing us: 1) to evaluate the SDTF “functional recovery”, 2) to identify the plant functional groups of a SDTF successional system, 3) to explore the potential of spectral indices related to plant functional performance to discriminate, in the long term, the different successional stages of SDTF. We found that an integral recovery of the SDTF is slower than the inferred from studies that do not evaluate the functional component. We identified two functional groups, one “pioneer” group mainly constituted by individuals from early and intermediate successional stages, and a “late successional”

group mainly constituted by individuals from the late successional stage. These functional groups essentially differ from each other in their photosynthetic capacity, their heat dissipation capacity and their photoprotection capacity. These capabilities diminish from the early to the late successional stage. In this sense, an spectral index related to the photosynthetic efficiency and leaf photoprotection capacity, was useful to discriminate leaves from late successional stages from leaves of the other stages.

Finally, in order to contribute to the application of remote sensing technology in the study of tropical plant communities, we: 1) analyzed in detail the relationship of leaf spectral reflectance with leaf anatomy, biochemistry and functioning, 2) evaluated the variation of spectral data in the different successional stages and 3) identified the spectral data most useful to classify/discriminate SDTF successional stages (chapter 4). Five spectral vegetation indices showed significant correlations to most of the functional traits varying along succession. The intermediate successional stage showed a greater variation in their spectral data than the early and late successional stages. This coincides with the intermediate disturbance hypothesis which implies a greater functional diversity at intermediate successional stages. These results and previous reports on the behavior of leaf functional traits in this study system, suggest that some niche processes could explain in part the behavior of spectral data. The early and intermediate stages, which are functionally similar, were found to be spectrally similar as well. In this sense, the most accurate discrimination (86% of accuracy) was achieved between the early and late stages by using two spectral indices highly correlated to our plant functional traits varying along succession. These results suggest that spectral data have potential to infer not only the functional and successional status of tropical vegetation, but also the ecological processes influencing such status. This would make possible the upcoming of simpler, faster and, in the long term, spatially scalable techniques, in the study/monitoring of tropical forests dynamics.

# **INTRODUCCIÓN**

Los ecosistemas tropicales enfrentan actualmente una grave amenaza debido a que grandes proporciones de su área de distribución han sido alteradas por acciones humanas con la consecuente pérdida de biodiversidad y de procesos ecosistémicos (Bullock *et al.* 1995, Mass 1995, Trejo y Dirzo 2000, Quesada y Stoner 2004). El estudio ecológico de los sistemas que han sufrido dicha alteración se ha vuelto entonces de suma importancia tanto para conocer su valor como para entender los procesos de recuperación que operan en los mismos (Sánchez-Azofeifa *et al.* 2005, Chazdon *et al.* 2007).

Idealmente, este tipo de estudios deben ser capaces de identificar y caracterizar los distintos estadios sucesionales de los sistemas perturbados tanto en su estructura y composición como en sus procesos ecológicos, además de responder a cuestiones acerca de las principales vías de sucesión que están operando en cada sistema y de los mecanismos que subyacen al proceso de regeneración natural. Este conocimiento constituye, en sí mismo, una base científica para el manejo y conservación de los sistemas tropicales ya que, entre otras cosas, permite el desarrollo de métodos útiles en la identificación de los diferentes estadios sucesionales, facilitando así el estudio sistemático de los mismos.

El presente proyecto tiene como objetivo contribuir en este sentido mediante el estudio de los bosques secundarios del Bosque Tropical Seco (BTS). El BTS presenta una alta biodiversidad y gran número de endemismos (Ceballos 1995, Gentry 1995). Actualmente, este sistema se encuentra amenazado por altas tasas de pérdida, un bajo nivel de protección y una escasa atención de la comunidad científica (Money *et al.* 1995, Miles *et al.* 2006, Sánchez-Azofeifa *et al.* 2005).

El BTS es el ecosistema tropical más extenso del orbe, representando, aproximadamente, el 42 por ciento de los sistemas tropicales (Murphy y Lugo 1986). En el neotrópico, presenta una distribución que va desde México hasta el norte de Argentina y se caracteriza por una alta diversidad florística así como por albergar un número considerable de especies endémicas (Lott 1993, Gentry 1988, 1995, Trejo 1998). En el caso específico del BTS de la región Chamela-Cuixmala, Jalisco, donde se realizó este estudio, se registra una alta diversidad de especies y una gran heterogeneidad en la disponibilidad de recursos,



como agua, nutrimentos y luz debido a su marcada estacionalidad (Bullock 1986). El número de endemismos suele ser alto pues presenta más de 1100 especies de plantas y, de éstas, aproximadamente el 16% son endémicas (Lott 1993).

El conocimiento que se tiene acerca de los BTS en la actualidad, es relativamente escaso. Históricamente, la mayor parte de la atención científica y popular se ha centrado en la pérdida reciente y futura de los bosques tropicales lluviosos (Money *et al.* 1995). De hecho, en el periodo comprendido entre 1945 y el 2004, solamente el 14 por ciento de los artículos científicos publicados en relación a los bosques tropicales, versaban sobre los BTS (Sánchez-Azofeifa *et al.* 2005).

Aunado a esto, el estatus actual de conservación de este tipo de bosque es preocupante, ya que el 97% de su territorio presenta algún tipo de amenaza y solamente el 33% se encuentra bajo algún régimen de protección (Miles *et al.* 2006). Se estima que en 1991, el 78% del área original de este ecosistema ya había sido modificada (Houghton *et al.* 1991). Las principales amenazas que enfrentan estos bosques son: el cambio climático, la fragmentación del hábitat, la urbanización, la agricultura y la ganadería (Miles *et al.* 2006), siendo estas dos últimas las principales causas de pérdida en la región neotropical (Bullock *et al.* 1995, Mass 1995, Sánchez-Azofeifa 1997, Trejo y Dirzo 2000, Quesada y Stoner 2004, Portillo y Sánchez-Azofeifa 2010).

La dramática situación del BTS ha provocado que los estudios que incluyen bosques degradados y de crecimiento secundario se vuelvan cruciales, dado que dichos sitios están aumentando en área e importancia (Opler *et al.* 1980, Gillespie 1999). Así, los bosques secundarios de este ecosistema, quienes ocupan ya un área mayor que los conservados (Miles *et al.* 2006, Portillo y Sánchez-Azofeifa 2010), juegan ahora un papel clave en su conservación. El estudio del proceso sucesional resulta entonces prioritario para conocer la dinámica actual de estos sistemas.

En los estudios existentes al respecto hasta este momento, se asume que la recuperación del BTS a través del proceso sucesional ocurre más rápidamente que en los bosques maduros (Ewel, 1977; Murphy y Lugo, 1986; Segura et al., 2003). Sin embargo, hay relativamente poca evidencia empírica acerca de esto (Quesada et al., 2009). En general, la literatura reporta una rápida recuperación de este ecosistema en términos de estructura (e.g. Ceccon et al., 2002; Chazdon 2003, Ruiz et al., 2005; Vieira y Scariot, 2006; Chazdon et al., 2011), pero parámetros como la riqueza y la composición de especies frecuentemente presentan una recuperación mas lenta que la estructural (area basal y biomasa) (Sheil, 2001; Ceccon et al., 2002; Pascarella et al., 2004; Ruiz et al., 2005; Toledo y Salick, 2006; Chazdon et al., 2007; Chazdon, 2008; Quesada et al., 2009). La recuperación del BTS en términos funcionales, en contraste, no se había evaluado ni comparado con la recuperación en términos de estructura o composición de especies. Existe, asimismo, muy poca información sobre los mecanismos funcionales que subyacen a la dinámica sucesional y al ensamblaje de comunidades de estos sistemas tropicales. Estas carencias con respecto a la teoría sucesional del BTS, hacen necesario el estudio de los patrones y procesos que subyacen al ensamblaje de comunidades de este ecosistema, así como la caracterización del cambio funcional de la vegetación (e.g. recuperación funcional) durante el proceso sucesional. Al mismo tiempo, desde una perspectiva ecosistémica, es necesario identificar los principales grupos funcionales de plantas propios del gradiente sucesional.

Por otra parte, debido a la rápida tasa de pérdida de los BTS y de los sistemas tropicales en general, se requiere desarrollar técnicas de estudio que nos permitan obtener información acerca de la dinámica de estos bosques de manera más rápida e incluso a grandes escalas. Los caracteres funcionales de la vegetación están correlacionados con las propiedades ópticas (e.g. reflectancia) de la misma. Así, ciertos caracteres funcionales pueden “rastrearse” mediante el uso de espectrómetros de reflectancia que lo mismo se encuentran a bordo de satélites que en aparatos portátiles que pueden ser llevados al campo para hacer mediciones *in situ* (i.e. Peñuelas et al. 1994, Gamon et al. 1995, Asner 1998). Esto significa que los datos espectrales correlacionados con los procesos funcionales que varían a lo largo de la sucesión podrían ser de utilidad para discriminar los diferentes estadios sucesionales de los sistemas tropicales (Alvarez-Añorve et al. 2008, 2012).

Adicionalmente, los procesos de nicho (e.g. filtros ambientales) que afectan la naturaleza (e.g. variación) de los datos funcionales, pueden afectar también el rango de variación de los datos espectrales, lo cual nos permitiría detectar estos procesos a través de las técnicas espectrales. La inferencia del status funcional y sucesional de la vegetación, así como de los procesos ecológicos que determinan dicho estatus haría posible el advenimiento de técnicas de estudio más rápidas, más fáciles e incluso escalables a nivel de paisaje. Esto podría ser un paso importante para el estudio de la dinámica de nuestros altamente diversos, pero gravemente amenazados, sistemas tropicales.

En esta tesis se aborda el estudio de la sucesión del BTS desde una perspectiva funcional. Para ello, valoramos el desempeño funcional de comunidades arbóreas a lo largo de un gradiente sucesional en el BTS de Chamela-Cuixmala (Jalisco, México). Específicamente, evaluamos caracteres funcionales de la vegetación relacionados con la adquisición y uso de recursos (luz, agua, CO<sub>2</sub>, nutrientes), en las especies arbóreas más abundantes de nueve sitios correspondientes a 3 estadios sucesionales del BTS (temprano, intermedio y tardío). Este tipo de caracteres funcionales influyen procesos y propiedades emergentes de los ecosistemas, afectando directamente el funcionamiento de los mismos. También evaluamos índices espectrales relacionados con el desempeño funcional de la vegetación. Brevemente, el estudio comprendió:

- a) La identificación de los procesos ecológicos que dirigen el ensamblaje de las comunidades sucesionales del BTS (**capítulo 1**).
- b) La búsqueda de métodos para caracterizar los sistemas tropicales sucesionales desde una perspectiva ecosistémica, tanto con datos funcionales, como con datos espectrales (**capítulo 2**).
- c) La caracterización de nuestro sistema sucesional per se desde una perspectiva ecosistémica (e.g. recuperación funcional y grupos funcionales, **capítulo 3**).
- d) La aplicación de la información generada en herramientas que faciliten el estudio de la dinámica de estos bosques tropicales (e.g. reflectancia espectral de la vegetación, **capítulo 4**).

Estudiar el proceso de regeneración natural de los BTS, así como el identificar y caracterizar los bosques secundarios de este sistema, es ya una tarea prioritaria. Para ello, se requiere desarrollar un método estandarizado que permita reconocer y comparar los diferentes estadios sucesionales. Esto nos permitirá, a su vez, entender el proceso de sucesión mediante el cual se recuperan estos bosques.

## REFERENCIAS

- Asner G.P. 1998. Biophysical and biochemical sources of variability in canopy reflectance. *Remote Sensing of Environment* 64(3): 234–253.
- Bullock S.H, Mooney H. A and E. Medina. 1995. Seasonally dry tropical forests. Cambridge University Press, Cambridge, UK.
- Bullock SH. 1986. Climate of Chamela, Jalisco, and trends in the south coastal region of Mexico. *Arch Met Geoph Biocl.* B36: 297-316.
- Ceballos, G. 1995. Vertebrate diversity, ecology, and conservation in neotropical dry forest. In: Bullock, S. H., H. A. Mooney and E. Medina, (Eds), Seasonally dry tropical forest. Cambridge University Press, Cambridge, pp. 195-214.
- Ceccon E, Omstea I, Vázquez-Yanes C and J. Campo-Alves. 2002. Vegetation and soil properties in two tropical dry forests of differing regeneration status in Yucatán. *Agrociencia* 36: 621-631.
- Chazdon R, S. Letcher, M. Van Breugel, M. Martinez-Ramos, F. Bongers and B. Finegan. 2007. Rates of change in tree communities of secondary Neotropical forests following major disturbances. *Philosophical Transactions of the Royal Society of London* 362: 273–289.
- Chazdon R. 2003. Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics* 6: 51–71
- Chazdon R. 2008. Chance and Determinism in Tropical Forest Succession. In W, Carson. and F, Schnitzer [eds.], *Tropical Forest Community Ecology*, 384-408. Wiley-Blackwell. Sussex, UK.
- Chazdon R. L, C. A. Harvey, M. Martinez-Ramos, P. Balvanera, K. E. Stoner, J. E. Schondube, L. D. Avila-Cabadilla and M. Flores-Hidalgo. 2011. Seasonally dry tropical forest biodiversity and conservation value in agricultural landscapes of Mesoamerica. In R. Dirzo, H. S. Young, H. A. Mooney and G. Ceballos [eds], *Seasonally Dry Tropical Forests*, 195-220. Island Press, Washington, D.C., USA.
- Ewel, J. 1977. Differences between wet and dry successional tropical ecosystems. *Geo-Eco-Trop* 1: 103–117.
- Gamon J, Field C.B, Goulden M, Griffin K, Hartley A, Joel G, Peñuelas J and R. Valentini. 1995. Relationships between NDVI, canopy structure, and photosynthesis in three Californian vegetation types. *Ecological applications* 5(1): 28-41
- Gentry AH. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* 75: 1-34.
- Gentry AH. 1995. Diversity and floristic composition of neotropical dry forests. In: Bullock SH, Mooney HA & Medina E (Eds.). *Seasonally Dry Tropical Forests*. Cambridge University Press. Cambridge pp. 146-194.
- Gillespie T. 1999. Life history characteristics and rarity of woody plants in tropical dry forest fragments of Central America. *Journal of Tropical Ecology* 15:637–649.
- Houghton RA, Lefkowitz DS & Skole DL. 1991. Changes in the landscape of Latin America between 1859 and 1985. I. Progressive loss of forest. *Forest Ecology and Management* 38: 143-172

- Lott E. J. 1993. Annotated checklist of the vascular flora of the Chamela Bay Region, Jalisco, Mexico. *Occasional Papers of the California Academy of Sciences* 148: 1–60.
- Maass JM. 1995. Conversión of tropical dry forest to pasture and agriculture. In: Bullock SH, Mooney HA & Medina E (Eds). *Seasonally dry tropical forest*. Cambridge University Press, Cambridge. pp. 399-342.
- Miles L, Newton A.C, DeFries R, Ravilious C, May I, Blyth S, Kapos V and J. E. Gordon. 2006. A global overview of the conservation status of tropical dry forests. *Journal of Biogeography* 33:491–505.
- Mooney H, Bullock S and E. Medina. 1995. Introduction. In: Bullock, S. H., H. A. Mooney, E. Medina, (Eds.), *Seasonally dry tropical forest*. Cambridge University Press, Cambridge, pp. 1-8.
- Murphy P. G, and A. E. Lugo. 1986. Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* 17: 67–88.
- Opler P, Baker H y Frankie G. 1980. Plant reproductive characteristics during secondary succession in Neotropical lowland forest ecosystems. *Biotropica* 12(Supplement):40–46.
- Pascarella J, Aide T and J. Zimmerman. 2004. Short-term response of secondary forests to hurricane disturbance in Puerto Rico, USA. *Forest Ecology and Management* 199: 379–393.
- Peñuelas J, Gamon J, Fredeen A. L, Merino J and C. B. Field. 1994. Reflectance indices associated with physiological changes in nitrogen- and water-limited sun flower leaves. *Remote Sensing of Environment* 48:135–146.
- Portillo C and Sánchez-Azofeifa GA. 2010. Extent and conservation of tropical dry forests in the Americas. *Biological Conservation* 143(1): 144–155
- Quesada M and K. E. Stoner. 2004. Threats to the conservation of tropical dry forest in Costa Rica. Pages 266-280 in: Frankie, G. W., A. Mata, and S. B. Vinson, editors. *Biodiversity Conservation in Costa Rica: Learning the Lessons in a Seasonal Dry Forest*. University of California Press. Berkeley, California.
- Quesada M, G. A. Sanchez-Azofeifa, M. Alvarez-Añorve, K. Stoner, L. Avila-Cabadilla, J. Calvo-Alvarado, A. Castillo, M. Espiritu-Santo, M. Fagundes, G. W. Fernandes, J. A. Gamon, M. Lopezaraiza-Mikel, D. Lawrence, P. Morellato, J. Powers, F. Neves, V. Rosas-Guerrero, R. Sayago, G. Sanchez-Montoya. 2009. Succession and management of tropical dry forests in the Americas: Review and new perspectives. *Forest Ecology and Management*, 258: 1014–1024.
- Ruiz J, Fandino M.C and R. L. Chazdon. 2005. Vegetation structure, composition, and species richness across a 56-year chronosequence of dry tropical forest on Providencia island, Colombia. *Biotropica* 37: 520–530.
- Sanchez-Azofeifa G. A, M. Quesada, J. P. Rodríguez, J. M. Nassar, K. E. Stoner, A. Castillo, T. Garvin, E. L. Zent, J. C. Calvo-Alvarado, M. E. Kalacska, L. Fajardo, J. A. Gamon, and P. Cuevas. 2005. Research Priorities for Neotropical Dry Forest. *Biotropica* 37 (4): 477-485.
- Segura G, Balvanera P, Durán E and A. Pérez. 2003. Tree community structure and stem mortality along a water availability gradient in a Mexican tropical dry forest. *Plant Ecology* 169:259–271.
- Sheil D. 2001. Long-term observations of rain forest succession, tree diversity and responses to disturbance. *Plant Ecology* 155: 183–199.

- Toledo M and J. Salick. 2006. Secondary Succession and Indigenous Management in Semideciduous Forest Fallows of the Amazon Basin. *Biotropica* 38: 161–170.
- Trejo I and R. Dirzo. 2000. Deforestation of seasonally dry tropical forest: a national and local analysis in Mexico. *Biological Conservation* 94(2): 133-142.
- Trejo I. 1998. Distribución y diversidad de selvas bajas de México: Relaciones con el clima y el suelo. *Ph.D. thesis*. Facultad de Ciencias, UNAM. México, DF.
- Vieira D.L.M and A. Scariot. 2006. Principles of natural regeneration of tropical dry forests for restoration. *Restoration Ecology* 14: 11–20.

# **CAPÍTULO 1**

**El ensamblaje de comunidades del bosque tropical seco está dirigido por procesos de nicho: la sucesión tropical desde una perspectiva funcional y filogenética.**



**Community assembly of tropical dry forest is driven by niche processes: the tropical forest succession from a functional and phylogenetic perspective.**

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## ABSTRACT

Tropical ecosystems are highly endangered by anthropogenic disturbance and climatic change. To understand the causes and consequences of tropical communities structure will allow us to understand their response to disturbance as well as their natural regeneration. In this study we evaluate the phylogenetic structure and the processes influencing such structure in a seasonally dry tropical forest (SDTF), one of the most widespread and endangered tropical systems in the world. We also assessed how processes influencing community structure do reflect in functional diversity and species abundance. For this purpose we evaluated a set of fundamental leaf functional traits in the most abundant tree species of a SDTF successional gradient. First, we found evidence of niche processes influencing the assembly of SDTF communities. The intensity of these processes changed along succession. In early and intermediate successional stages (ES and IS) predominates the action of environmental filtering favoring the occurrence of species with high heat dissipation capacity and high photosynthetic potential. Species in these stages were phylogenetically clustered. However, we also detected the simultaneous occurrence of limiting similarity in ES and IS. In the late successional stage (LS) we did not find evidence of phylogenetic structure nor the action of niche processes. This could be a consequence of the increasing intensity of niche forces such as limiting similarity toward LS. As limiting similarity acts in an opposite direction to environmental filtering, this would nullify the evidence of niche processes (but not necessarily their action) in the assembly of LS communities. Successional changes in species functional performance, functional diversity and species abundance/dominance, reflected adequately the described changes in the intensity of niche forces along succession. These results allowed us to understand how SDTF tropical communities assemble and how they respond to forces of change.

## INTRODUCTION

Different hypotheses have been proposed to explain the assemblage of plant communities. From niche-based assembly rules (e.g., MacArthur and Levins 1967, Diamond 1975) to neutral assembly with dispersal limitation (e.g., Hubbell 1979, Bell 2001, Hubbell 2001), these hypotheses discuss the existence and nature of “rules” explaining how assemblages are selected from a larger species pool and how species coexist (Ricklefs 2004). Today, ecologists are reexamining these issues using alternative approaches such as functional community ecology (e.g., Losos 1996, Webb et al. 2002) and phylogenetic community ecology (McGill et al. 2006).

As a direct link may exist between the evolutionary relatedness of organisms in a community, the functional traits they possess, and the ecological processes that determine their distribution and abundance (Ricklefs et al. 1987, Kraft et al. 2007), many communities may exhibit nonrandom patterns of evolutionary relatedness among constituent species (Webb et al. 2002), a phenomenon we refer to as phylogenetic community structure. Tests of phylogenetic community structure have attempted to quantify the relative importance of neutral vs niche forces (Kembel & Hubbell 2006; Kelly et al. 2008; Jabot & Chave 2009) to resolve the long-standing controversy about the roles of neutral vs. niche-related processes in community assembly (Cavender–Bares et al. 2009). Neutral processes would determine a random community structure whereas under niche processes the phylogenetic distance between species can be greater or smaller than expected by chance (Cavender-Bares et al. 2009).

Explicit tests connecting phylogenetic community structure to community assembly processes (i.e. environmental filtering, limits to similarity, etc) are rare (Vamosi et al. 2008, Kraft et al. 2007). As processes structuring communities can be revealed through functional traits analysis (Cavender-Bares et al. 2009), a combined functional-phylogenetic approach can be useful to identify the niche axes on which species segregate within communities. This is a necessary but infrequent approach that has rarely been applied in species rich ecosystems such as tropical forests (but see Swenson and Enquist 2009). Tropical ecosystems are facing high rates of degradation (Sanchez-Azofeifa et al. 2005, Wright and Muller-Landau 2006), therefore, an integral comprehension of tropical communities

assembly is urgent to decode the processes underlying their natural regeneration as well as to understand and predict their response to anthropogenic disturbance and climatic change.

For plants, in particular, functional traits influence processes and emergent properties of ecosystems (Grime 2006). Hence, plant functional traits are an important mechanistic link by which phylogenetic history influences ecological processes (Cavender–Bares et al. 2009). The change from undisturbed to disturbed vegetation modifies the balance of forces determining the structure and dynamics of the community (Dinnage 2009). This change is also associated with parallel shifts in a set of traits that are deeply embedded in the core physiology of plants (Grime 2006). Consequently, disturbance affects the structure and dynamics of the community as well as the functioning of the ecosystem (Grime 2006). After disturbance, as succession occurs, the balance of the forces is gradually restored. Then, ecological succession is community assembly in action (Lebrija-Trejos et al. 2010).

In this study, we assess the assembly of tropical communities by evaluating the occurrence and role of niche processes from a phylogenetic and functional perspective in a tropical dry forest successional gradient. Seasonally dry tropical forest (SDTF) is one of the most widely spread and endangered ecosystems in the world (Murphy and Lugo, 1986; Bullock et al., 1995; Quesada and Stoner, 2004; Sanchez-Azofeifa et al., 2005; Quesada et al., 2009). Despite its high biodiversity and proportion of endemisms, the research on their natural regeneration is relatively recent. Consequently, there is not a generalized view of ecological and evolutionary processes underlying its secondary succession and community's assembly (but see Vieira and Scariot 2006, Chazdon et al. 2007, Lebrija-Trejos et al. 2011).

Our specific goals were: 1) to evaluate if there is evidence of niche processes in the spatial phylogenetic structure of SDTF tree communities along a successional gradient, 2) to evaluate if there is evidence of niche processes in the distribution of the functional traits values assessed in these communities, 3) to evaluate the effect of community assembly processes in the functional diversity of these communities and 4) to depict how factors influencing community assembly are reflected on species functional performance and abundance. This information will allow us to establish the existence of niche processes in SDTF successional communities, to discern the mechanistic basis for such structuration, to

know how community assembly processes do reflect in communities species abundance, and, ultimately, to explore the impact of disturbance on the structure and dynamics of tropical plant communities.

Previous studies on SDTFs dynamics and community assembly have found that: i) mechanisms that depart from strict neutrality could regulate a large proportion of mature SDTF communities (Kelly et al. 2008), ii) early successional communities may be influenced by niche processes such as environmental filtering (Lebrija-Trejos et al. 2010, Alvarez-Añorve et al. 2012) and iii) forces structuring communities may change along the successional process (Alvarez-Añorve et al. 2012). In this study, we proposed as our first hypothesis that tree SDTFs successional communities will be phylogenetically structured and their structure will change along succession, if more closely related species are more ecologically/functionally similar. Because high temperature high radiation and low water availability are important environmental constraints in SDTFs early successional stages (Lebrija-Trejos et al. 2010, Alvarez-Añorve et al. 2012), species could be filtered according to their physiological tolerances to these factors (environmental filtering). Species bearing similar traits enhancing heat dissipation and photoprotection will be favored (Alvarez-Añorve et al. 2012) and therefore co-occurring species could be phylogenetically clustered (i.e. close relatives will occur together more than expected by chance alone). As succession progress by adding more species to the system and thus reducing space and resources, the impact of interspecific competition could increase. This would favor functional differences among co-occurring species (i.e. overdispersion of functional traits) resulting in phylogenetic overdispersion (co-occurring species will be less related than expected) of intermediate and late successional communities. In fact, in SDTFs, competitive exclusion appears to be enhanced at intermediate stages of succession (Bongers et al. 2009). Our second hypothesis, *sensu* Cornwell and Ackerly (2009), is that, if habitat filtering is occurring in early successional plots, the values of functional traits related to light and water use, will be restricted to those values allowing for greater heat dissipation and, consequently, the distribution of these values will show a high kurtosis. In contrast, if interspecific competition is causing niche (and traits) differentiation (i.e. limits to similarity) in more advanced successional stages, the values of functional traits related to light acquisition and water use will show a more even spacing, hence, the distribution of

these values will show a smaller kurtosis. Our third hypothesis is that functional richness and functional evenness will tend to increase toward late succession as a result of the addition of species and interspecific competition. Finally, we hypothesize that changes on the balance of forces affecting community assembly along succession will be reflected in species functional performance and abundance. Hence, species able to deal with high irradiance and high temperature will be abundant in early stages as they will be selected by environmental filtering; these species will decrease their abundance toward intermediate and late stages as interspecific competition become stronger.

## **MATERIAL & METHODS**

### **Study region and sampling sites**

The study was conducted in and surrounding the Chamela-Cuixmala Biosphere Reserve (CCBR), located in the central western coast of Mexico in the state of Jalisco (19°22' - 19°35'N, 104°56' - 105°03'W). The CCBR has an extension of 13,200 ha and is covered by a well preserved SDTF (Lott 2002) and some small areas of riparian forest, among other vegetation types (Lott 2002). In this region, the precipitation regime follows a markedly seasonal pattern as most of the rainfall occurs during June-October. Average annual precipitation is  $763 \pm 258$  (SD) mm and average annual temperature is 24.6°C (<http://www.ibiologia.unam.mx/ebchamela/index.html>). The seasonality is tightly related to plant phenology (Borchert, 1994), to above- and below-ground productivity (Martínez-Yrizar et al., 1996) and to nutrient cycling (Jaramillo and Sanford, 1995).

We selected nine sampling sites representing a SDTF successional gradient (chronosequence) of three successional stages. Each set of sites have different ages of abandonment: 3 early stage (ES) plots (5 – 7 years old), 3 intermediate stage (IS) plots (13 – 15 years old) and 3 late stage (LS) plots (at least 50 years old, located in the CCBR). Early and intermediate plots consisted of a quadrat of 120 \* 90 m embedded within a matrix of similar vegetation and were distributed around the reserve in order to generate a research design reasonably balanced. Features such as slope (ranging from 15°-30°) and aspect (S, SW and SE) were homogenized as much as possible to control topographical effects. Distance from the mature forest (in the case of early and intermediate plots) was

equal or higher than 1000 m. For more detailed information about the chronosequence see Alvarez-Añorve et al. (2012).

The land use history of each secondary forest plot was similar. First, forest was removed through slash and burn. Second, lands were subsequently used for maize and bean production during approximately two years. Finally, lands were converted into cattle pastures, being burned approximately every two years. For more detailed information about the land use history of sampling sites, including aspect photographs, see Avila-Cabadilla et al. (2009).

### **Vegetation sampling and species selection**

A vegetation census of all woody individuals above 2.5 cm DBH (diameter at breast height) were conducted in a 50 m \* 20 m (0.1 ha) subplot at every plot. We focused on plots of relatively small size falling in the ‘Darwin- Hutchinson zone 1’ described by Vamosi et al. (2008). Studies falling in this zone are extremely rare in the community assembly literature, but they are the most directly relevant to the competitive structuring of local communities (Vamosi et al. 2008). A total of 200 species corresponding to 48 families were found. Primary dominant families included the Leguminosae, Euphorbiaceae and Rubiaceae.

As the logic underlying community assembly rules is based on interactions among individuals that are cumulative in their effects (Vamosi et al. 2008), we focused in the most abundant tree species. Most abundant species are the most likely to interact with other species and, therefore, they are the ones influencing most niche processes occurring at the community level. Besides, these species are likely to represent a successful strategy in their correspondent environment. In order to include >70% of biomass of each plot in our study, we analyzed 31 species corresponding to 22 genera and 14 families (table 1). Of these 31 species, seven occur in all three stages (“shared”) and 24 in just one given stage (“exclusives”). Additionally, we considered the species abundance in all functional and phylogenetic analysis. Studies considering abundance are necessary because presence/absence data are very sensitive to the chance and perhaps temporary occurrence of a single individual in a habitat or competitive situation that is actually unsuitable (Vamosi et al 2008).

## Traits selection and measurements

Provided that different leaf traits/processes can be optimal in different regeneration scenarios (Grubb, 1977), we evaluated the following leaf traits and processes: 1) processes related to CO<sub>2</sub> acquisition and use: net photosynthesis ( $A_{\max}$ ) (Evans, 1989), 2) traits/processes related to water use and conservation: leaf water content (LWC, the difference between leaf fresh and dry mass per unit area), transpiration (E) and water use efficiency (WUE, the ratio of  $A_{\max}$  to E) (Reich et al., 2003), 3) traits related to light acquisition and/or heat load regulation: specific leaf area (SLA, leaf area per dry mass) and leaf density (LD, leaf dry mass/ (leaf area \* leaf thickness), leaf mass per area (LMA, Wright *et al.*, 2004) and 4) traits related to nutrient conservation or use: leaf thickness (LT) and leaf fresh mass per unit area (LFM) (Roderick et al. 1999; Garnier et al., 2001; Sims and Gamon, 2002). Several of these traits reflect plant responses in more than one function and can be used as indicators of different survival mechanisms, including physical protection, resistance to drought stress, competitive ability, etc (Wright et al., 2004).

Leaf collection and measurement were conducted in the rainy season during three years, 2006 to 2008, following standard methods (Cornelissen et al. 2003). At least five adult individuals were selected per species in each plot. To reach the crown, we used a 4 m long portable ladder and climbed trees when necessary to collect only sunlit leaves. Per individual, we collected 15 - 25 fully expanded, sun exposed, mature leaves without herbivore damage. We collected 9000 leaves of 450 individuals in total. Leaves were immediately placed in sealed plastic bags containing moistened paper towels and transported to the laboratory in a cooler. For more details on leaf traits measurement see Alvarez-Añorve et al. (2012).

Gas exchange measurements ( $A_{\max}$  and E) were evaluated in an average of four adult trees per species in each plot. We selected 3 - 5 sun exposed, mature and healthy leaves per tree. To reach the crown, we used a portable 4 m long ladder which allowed us to measure the top leaves of trees six meters height or less, and the outer lateral (but totally sun exposed) leaves of taller trees. We measured a total of 800 leaves from 240 individuals. All measurements were recorded between 0900 and 1200 hours local time in days with no clouds and similar climatic conditions. We used a portable gas exchange system (LI-COR



6400, LI-COR, Nebraska, USA) to measure the photosynthetic rates of selected plants. For more details about photosynthesis measurements see Alvarez-Añorve et al. (2012).

### **Data analysis**

The variables that were not normally distributed were log-transformed to allow for parametric statistical analyses. To incorporate the variation per plot and because the unit of analysis is the species level, individuals were averaged per species and per plot. We use the abbreviation MSP (mean per species per plot) to name these averages in the rest of the text. Every MSP represents an average of at least four individuals. Except when another program is specified, all statistical analysis were performed in R (v.2.12.1, R Development Core Team, 2011).

### **Spatial phylogenetic structure**

In order to make comparable analyses for the phylogenetic and functional approaches, we used the same method to test the occurrence of niche processes in phylogenetic and functional data.

To evaluate the potential influence of niche processes in the phylogenetic structure or SDTF tree communities along the successional gradient, we tested the spatial phylogenetic structure of each successional stage. We first built a phylogenetic tree (Phylocom, Webb et al. 2008) utilizing: 1) the megatree R20091110, incorporated into the data repository of Phylomatic (<http://svn.phylodiversity.net/tot/megatrees/>, Accessed 2011 Jun 03), and 2) an age file base on Wikstrom et al. (2001). Based on the phylogenetic tree we constructed a matrix of phylogenetic distances among species, which was used as input in non-metric multidimensional scaling ordination (NMDS), for mapping the degree of phylogenetic relationship among species. The scores of each species in the NMDS first ordination axis, were then used as a variable for evaluating the spatial phylogenetic structure of plant communities. The distribution of these new variable for each successional stage (considering only the subset of species from a given stage), was characterized through null model testing of the following parameters (sensu Cornwell and Ackerly 2009): 1) range and variance of the species phylogenetic distances, as evidence of environmental filtering (for more information see S1); 2) kurtosis and standard deviation of nearest

neighbors phylogenetic distances, as evidence of limiting similarity (table S1). We calculated the standard deviation of the nearest neighbor distances following three steps: 1) we ranked the species with respect to their NMDS axis 1 score, 2) we calculated the “nearest neighbor phylogenetic distances” as the difference in distance between every pair of adjacent species in the ranked list, and 3) we calculated the standard deviation of these “nearest neighbor phylogenetic distances”.

The null model tests evaluating significant deviation ( $\alpha = 0.05$ ) of each parameter from random expectation, were carried out based on 10000 randomizations. On each randomization, we selected a set of species from the entire species pool (all surveyed species), preserving the number of species found on each successional stage. All species were equally likely to be selected. Finally, for each successional stage, we compared the observed value of each parameter to their corresponding expected value generated through the null model. The p-value was calculated as the proportion of simulated values higher or equal and lower or equal than the observed value. It was also reported the standardized effect size index (SES) of Gotelli and McCabe (2002), where  $SES = \text{observed index} - \text{mean}(\text{simulated indices}) / \text{standard deviation}(\text{simulated indices})$ . The SES is derived from meta-analysis (Gurevitch et al. (1992) and is useful for comparing results from different matrices and algorithms (Gotelli and McCabe 2002).

### **Functional traits distribution**

To evaluate if there is evidence of niche processes in the functional traits values of SDTF tree communities along a successional gradient, for each successional stage, we characterized the distribution of functional traits values through null model testing of the following parameters: 1) mean, 2) range and variance as evidence of environmental filtering, and 3) kurtosis and standard deviation of nearest neighbor functional distances, as evidence of limiting similarity. We calculated the standard deviation of the nearest neighbor functional distances following three steps: 1) we ranked the species with respect to their mean trait values, 2) we calculated the “nearest neighbor functional distance” as the difference in trait values between every pair of adjacent species in the ranked list, and 3) we calculated the standard deviation of these “nearest neighbor functional distance”. For

interpretation of these parameters see table S1. Null models tests were performed as described in the “spatial phylogenetic structure” section.

### **Functional diversity**

Functional diversity changes along succession were evaluated using the set of 3 indexes proposed by Villeger et al. (2008): 1) functional richness, 2) functional evenness and 3) functional divergence. These indices directly measure the species distribution in a multivariate functional trait space, representing separate primary components of functional diversity (Mason et al. 2005). Functional richness corresponds to the amount of space filled by the community in the functional trait space, and it is calculated as the volume of the minimum convex hull, as proposed by Cornwell et al. (2006). The functional evenness index quantifies the regularity with which the functional space is filled by species, weighted by their abundance (Villeger et al. 2008); it is calculated defining the minimum spanning tree linking all the species in the functional trait space. The values of this index are constrained between 0 and 1; low values occur when distances among species are less regular and there is a low evenness in species abundance. Finally, functional divergence represents how species abundance is spread within the volume of functional space. This index quantifies how species diverge in their distances, weighted by their abundance, from the center of gravity in the functional space. This index is also constrained between 0 and 1; high values occur when abundant species are distant from the center of gravity relative to rare species. The index approach to 0 for the opposite case. For information on the characteristics of these indices see S2.

We estimated the functional diversity indices per successional stage. For this purpose we used two matrices, an abundance matrix (successional stage\*species) containing the relative abundance per species in each successional stage, and a trait matrix containing traits values for each species (species\*trait). Traits were standardized (mean 0 and variance 1) in order to guarantee equal weights for each trait and to avoid any influence of measurement units on calculations.

In order to evaluate significant deviations ( $\alpha = 0.05$ ) of indices from random expectations, we performed null model tests (Gotelli and Graves 1996) based on 10000 randomizations of the abundance matrix. On each randomization, the frequency of

occurrence for each species and the species richness of each successional stage were preserved, avoiding in this way to spuriously find a significant result (Wilson 1995, Mason et al. 2007). Finally, we compared the observed index value against the expected frequency distribution generated by the null model. The p-value and SES were calculated as described in the “spatial phylogenetic structure section”.

### **Species functional performance and abundance.**

Pearson correlations between the different functional traits were determined. Relationships between traits related to photosynthetic efficiency were evaluated at the leaf level through regression analyses in the different successional stages. The slopes of the regression lines were compared through analysis of covariance (ANCOVA) in which the nominal variable was the successional stage.

We evaluated changes in abundance of key plant groups along succession and also tested for phylogenetic signal in the changes of species abundance among successional stages, employing the randomization test suggested by Blomberg et al. (2003). Based on results from Alvarez-Añorve et al (2012) indicating that, in functional terms, early and intermediate successional stages (ES and IS respectively) are similar to each other but different from the late stage (LS), we measured the changes in the species abundance in two ways: 1) as the percentage of change between the early and the late successional stage, and 2) as the percentage of change between the early–intermediate stages (pooled together) and the late successional stage. A positive percentage of change indicates an increase in abundance toward the late successional stage, while a negative percentage indicates the opposite. We then calculated the standardized phylogenetically independent contrasts (PIC, Garland et al. 1992) for the two variables and the variance of these new set of values (variance of contrasts). For more details of Bloomberg’s test see S3.

## **RESULTS**

### **Spatial phylogenetic structure**

The parameters characterizing the distribution of species phylogenetic distances in the ES showed significant and marginally significant deviation from the null models. Specifically,

we observed a significantly lower variance, a significantly higher kurtosis and a tendency toward a narrower range in this stage (table 2). Only two axes were considered in the NMDS ordination because additional dimensions did not substantially diminish the stress. The stress value reached was 10.98.

### **Functional traits distribution**

**Mean:** ES was characterized by a higher E and  $A_{\max}$  and a lower WUE than expected. IS showed a lower SLA and a higher LD and LFM than expected. LS, on the contrary, showed a higher SLA and a lower LT, LFM,  $A_{\max}$  and E than expected

**Range and variance:** We detected significant and marginally significant deviations from the null model expectation for the range of several functional traits correspondent to ES and IS (table 3). Traits presenting a range lower than expected were: LWC (ES), WUE (ES and IS), E (IS), LFM (ES) and  $A_{\max}$  (ES and IS). Traits presenting a lower variance than expected were WUE and E, both in the IS. We also observed a marginally significant lower variance in WUE for the ES. This result shows evidence of environmental filtering in early and intermediate successional stages.

**Kurtosis:** We observed deviations from null model expectation in the kurtosis of distributions from ES and IS (table 3). Kurtosis was higher than expected (leptokurtic distribution) for LT (IS) and it was lower than expected (platykurtic distribution) for LFM (IS), LWC (ES), LFM (ES) and  $A_{\max}$  (ES). Additionally, we detected a kurtosis marginally significantly lower than expected for LWC, LFM and  $A_{\max}$  in the ES. A platykurtic distribution results from the absence of highly frequent traits values; most traits values appear in low frequency. This kind of distribution suggests limits to similarity in the functional traits. A leptokurtic distribution, on the contrary, results from the occurrence of highly frequent values and suggests that environmental filtering is occurring in functional traits (Cornwell & Ackerly 2009).

**Nearest neighbor distances standard deviation:** All the significant and marginally significant deviations from null model expectation were observed in the ES (for LWC, WUE and LFM) and IS (for WUE, SLA, LMA, LT and LFM, table 3). The standard deviation was lower than expected for LWC (ES), WUE (ES and IS), and LFM (ES and IS). As a low standard deviation indicates that traits values tend to be evenly spaced, this

suggests the existence of limits to similarity between species (Cornwell & Ackerly 2009) in these three cases.

### **Functional diversity**

The values of functional richness (FRic) for each successional stage were: 0.008 (LS), 0.001 (IS), and 0.000 (ES). These values were not significantly different from the null model expectation (fig. 1). On the other hand, all functional evenness (FEve) values (0.65 in LS, 0.54 in IS and 0.40 in ES) were significantly lower than expected (fig. 1). Finally, functional divergence values were significantly different from the null model expectation (fig. 1). Two values were significantly higher than expected: 0.81 (LS) and 0.84 (ES), and the third one was significantly lower than expected: 0.60 (IS).

### **Species functional performance and abundance.**

$A_{\max}$  is positively related to E ( $r=0.8$   $p=8.68 \times 10^{-12}$ ) which, in turn, is negatively related to WUE ( $r=-0.76$   $p=2.8 \times 10^{-10}$ ). However, when compared among different successional stages through ANCOVA, the slope of the regression line between  $A_{\max}$  and E (fig. 2) was significantly different ( $F(1,790) = 32.91$ ,  $p < 0.0001$ ) in ES and IS (slope value 2.52 and 2.6 respectively) versus LS (slope value 1.81). This indicates that trees of ES and IS can maintain a greater photosynthetic rate at a given transpiration rate than trees from LS and implies a greater photosynthetic water-use efficiency in ES and IS. In the same sense, the  $A_{\max}$  of trees from LS may have been limited by air temperature ( $r=-0.25$ ,  $r=0.58$  and  $r=0.38$  for LS, ES and IS respectively).  $A_{\max}$  is also negatively related to SLA ( $r=-0.47$   $p=0.001$ ) indicating a strategy for increasing Narea and photosynthetic capacity per unit leaf area at drier sites (ES). LT is positively related to LFM and WC ( $r=0.5$   $p=3.67 \times 10^{-8}$  and  $r=0.54$   $p=2.65 \times 10^{-9}$  respectively) but negatively related to SLA and LD ( $r=-0.38$   $p=0.001$  and  $r=-0.52$   $p=7.62 \times 10^{-9}$  respectively), suggesting that thickness of leaves is more related to the presence of water than to dry mass.

Most conspicuous changes in species abundance occurred in the legumes. Legume trees constituted the 80% of the individuals in ES and the 34% and 39% of the individuals in the IS and LS respectively. However, we found no evidence of phylogenetic signal in the changes of species abundance along succession (fig. S4), neither between the ES and LS

( $K= 0.12$ , observed PIC variance = 139.43, SES= -0.30) nor between the ES-IS (pooled together) and the LS ( $K= 0.13$ , observed PIC variance = 306.55, SES= -0.39).

## **DISCUSSION**

Today, that niches exist is hardly an issue (Engelbrecht et al. 2007). The larger question is to what extent they can or cannot be ignored in explaining community structure (Mason et al. 2008). Some recent evidence indicates the possibility of niche processes involved in the assembly of species in tropical plant communities (i.e. Silvertown 2004, Kelly and Bowler 2002, Kelly et al. 2008, Kraft et al. 2007 and 2008, Kelly 2008, Swenson and Enquist 2009, Letcher et al. 2010). However, we have no information on how tropical vegetation disturbance can change the balance of forces acting on a local community or how it affects the structure and dynamics of the community and consequently the functioning of these ecosystems. With the increasing rate of global change, basic understanding of the causes and consequences of tropical communities structure has never been more important (Cavender-Bares et al. 2009). In SDTFs in particular, this is the first study evaluating the role of neutral vs niche processes in the framework of succession and also the first study assessing community assembly from a combined functional-phylogenetic approach.

### **Spatial phylogenetic structure**

The lower range and variance as well as the higher kurtosis that we found in species phylogenetic distances (i.e. phylogenetic clustering) of the ES can be caused by environmental filtering. Thus, environmental filtering would be the predominating force on initial SDTF community assembly.

According to Webb et al. (2002), at local spatial scales, the underlying cause of phylogenetic clustering can be environmental filtering on shared physiological tolerances (trait conservatism). On the other hand, phylogenetic overdispersion could result either from competition causing overdispersion of conserved traits or environmental filtering on ecologically important convergent traits. We expected that, as succession progress, the gaining in number of individuals would necessary lead to a decrease in the resource availability. If species share limiting resources, competitive exclusion should limit the

coexistence of functionally (and phylogenetically) similar species (limits to similarity). This would lead community structure to the opposite pattern: phylogenetic overdispersion (Cavender-Bares et al. 2004, Dinnage 2009), evidenced in a lower kurtosis and an even distribution of phylogenetic distances (i.e. a low standard deviation of nearest neighbor phylogenetic distances) which is indicative of limits to similarity. Nevertheless, contrary to our hypothesis, we did not find evidence of limits to similarity (or any other process) in the distribution of species phylogenetic distances of the more advanced successional stages. The lack of clear phylogenetic patterns in IS and LS, however, might result from species interactions and environmental filtering operating in opposing directions in these successional stages (Cavender-Bares et al. 2006, 2009). The lack of phylogenetic community structure to provide support for neutral processes, has proved challenging because of the difficulty in ruling out contrasting niche-based processes that operate at different spatial, temporal or phylogenetic scales (Cavender-Bares et al. 2009).

### **Functional traits distribution**

We found that distributions of trait values within our plant communities were strongly nonrandom; this suggests an important role for species traits in determining community structure. Specifically, we found evidence of environmental filtering in ES and IS for traits related to evaporative cooling (WUE, E), water use (WC, LFM) and photosynthetic capacity ( $A_{\max}$ ). Environmental filtering in these communities would be favoring a combination of traits that allow for evaporative cooling at the time that enhance photosynthetic potential. Species lacking this combination would be excluded from these communities. This produces a reduction in the range of associated species traits in these stages (Pockman and Sperry 2000).

We also found evidence for niche partitioning in ES and IS. The ES communities showed a more even spacing than expected by chance as well as a more platykurtic distribution for traits related to nutrient, water and light use (WUE, WC, LFM and  $A_{\max}$ ). This suggests a wider arrangement of strategies toward the earlier, hotter and drier end of the gradient (i.e. early succession) providing further evidence for the idea that assembly processes generate communities with a wide array of regeneration strategies (Rees and Westoby 1997). These arrangements can also be the result of microsite variability within plots



that result in a dispersion of successful regeneration strategies. A wider arrange of strategies toward the dry end of gradients has also been found for other ecosystems (see Cornwell and Ackerly 2009). On the other hand, as we previously detected environmental filtering in these traits, a restricted range and an even spacing of coexisting species are occurring simultaneously for the same trait. This also occurs in IS communities were WUE also showed a more platykurtic distribution and a more even spacing than expected by random. The phylogenetic clustering observed in ES, however, indicates that environmental filtering is a greater force in the assembly of these communities. In fact, in this stage, five traits showed evidence of environmental filtering while just three showed evidence of niche partitioning.

It is important to note that habitat filtering and limiting similarity, both occur in this system, and can be seen as distinct steps in the assembly process that affects the distribution of functional strategies within communities. This means that within the limits imposed by environmental filtering, individuals are partitioning the niche as a result of interspecific competition or other kind of species interactions. As early successional species have previously been identified as a functional group (Alvarez-Añorve et al. 2012), this finding also constitutes an ultimate test of niche processes occurring at the finest scale (species) even within sets of species that are assumed to be functionally equivalent. This contributes to the development of theory for the assembly of functional groups, answering the plea of Hubbell (2005), as well as his question: Does a limiting niche similarity for species in functional groups exist? The answer is yes. In this case, assumed functional equivalence within the functional group is an effect of a restricted range in trait values caused by environmental filtering, whereas at the interior of the group, niche partitioning imposes limits to similarity. Then, at the interior of functional groups, there is no functional equivalence but (slightly) different functional responses.

Late successional communities, in contrast to younger communities, do not show evidence of environmental filtering or niche partitioning for most of the traits. However, analyses of traits dispersion that produce a random result do not necessarily imply that there is no functional mechanism of coexistence in the community analyzed. In fact, it could be the exact opposite where the extent of traits dispersion is simultaneously being influenced by abiotic filters and limits to similarity (Swenson and Enquist 2009). Then, more than

neutral processes, it is possible that environmental filtering and niche partitioning are contributing with similar force to community assembly in this stage. Indeed, in these communities, the mean for five traits were strongly nonrandom. In the same sense, other niche processes have already been described for the assembly of mature SDTFs communities (Kelly and Bowler 2002, Kelly et al. 2008).

### **Functional diversity**

Processes of environmental filtering and limits to similarity were reflected in functional diversity indices. Communities where environmental filtering predominates (ES and IS), restricting the range of functional traits values, tended to occupy a smaller volume in the functional space (i.e lower functional richness). These communities also showed a higher proportion of abundance concentrated within a narrow part of the functional traits gradient (lower functional evenness), which indicates that some species are tightly packed along the functional axis. However, within the small functional space/range occupied by these species, more abundant species appear to be distant from the center of gravity relative to rare species (higher functional divergence).

In contrast, the LS communities, not dominated by environmental filtering processes (i.e. traits values were not so restricted), tended to occupy a greater volume in the functional space (higher functional richness). As an indication that the limits to similarity could be stronger in these communities, they showed more regularity in the functional distances among species (higher functional evenness) than younger communities. However, their functional evenness values are still lower than expected by chance indicating that, in the whole system, abundance is not evenly distributed among species and there is no regularity in the way that species “fill” the functional space. In the same sense, most abundant species here probably have extreme functional trait values that place them distant from the center of gravity relative to rare species (higher functional divergence).

Only the IS communities showed significantly lower values of functional divergence, although still far from zero (0.6), indicating that, in the functional traits space, highly abundant species are closer to the center of gravity in comparison to the other successional stages. This suggests that interspecific competition plays a stronger role in the IS communities.

### **Species functional performance and abundance.**

Change in plant functional performance from ES to LS, clearly respond to changes in radiation, temperature and water availability along succession (Alvarez-Añorve et al. 2012). This constitutes also evidence that deterministic processes are driving the communities dynamics and functional performance in this system.

Correlations among traits show the action of environmental filters in ES and IS. The negative relation between  $A_{\max}$  and SLA clearly implies a strategy for maximizing photosynthesis at high temperatures and low water availability, through a more efficient evaporative cooling and a greater reduction of water loss toward the drier sites (ES). The steeper slope of the regression line between  $A_{\max}$  and E in ES and IS with respect to LS (fig. 2), indicates a higher photosynthetic efficiency in ES and IS (higher  $A_{\max}$  at the same transpiration rate and stomatal conductance of the LS plants). Lower photosynthetic rates of LS plants can be partially explained by lower light availability and limitation of  $A_{\max}$  by temperature as the relation between  $A_{\max}$  and air temperature was negative in this stage. Although plants in LS typically receive lower radiation loads, factors such as lower transpiration rates, higher leaf sizes and the resulting increase in the boundary layer in this stage, could lead to  $A_{\max}$  limitation by lower capabilities of evaporative cooling. Plants with this strategy can not occur in earlier successional stages. Therefore, functional differences among the successional stages appear to be mainly driven by the response of plants to changes in radiation, temperature and water availability along succession.

According to these findings, in the ES we should expect certain dominance of groups presenting traits related to the avoidance of the pervasive effects of high radiation (i.e. heat dissipation) and to the optimization of water use, such as smaller leaves, low SLA, lower boundary layer resistance, high leaf nitrogen concentrations and consequently, high photosynthetic potential. These traits in particular, are present in legumes that constitute the 80% of the individuals in ESS and the 34% and 39% of the individuals in the IS and LS respectively. The small leaflets of the legumes have a lower boundary layer resistance, which allows for better convective cooling of leaves (Parkhurst & Loucks 1972). Legumes often exhibit heliotropism (leaf movements), which can assist in optimizing radiation receipt and photosynthetic rates (Ehleringer & Forseth 1980; Gamon & Pearcy 1989). In fact, compound-leaved species are also able to drop individual leaflets, rather than whole

leaves, thus allowing plants to fine-tune leaf area during drought stress (Poorter & Markesteijn 2008). Being N fixers, these species are able to deal with the low nutrient and water availabilities characteristics of degraded soils and they are favored in colonization processes of disturbed sites. Besides, being functionally different from the rest, they experience a reduced competition for soil nitrogen (González-Iturbe *et al.* 2002). This could explain their clear dominance in ES. However, legume growth is often limited under conditions of reduced light and P availabilities (Fargione *et al.* 2003) which can explain the reduction of their dominance toward LS. Interestingly, the IS, although functionally similar to the ES (Alvarez-Añorve *et al.* 2012), shows also a decrease in legume dominance as well. This can be a consequence of the soil fertilization by legumes that eventually allow the establishment of more species.

Despite the marked changes in legumes abundance along the successional gradient, we found no evidence for phylogenetic signal in the changes of species abundance. This can be due to the method used to evaluate phylogenetic signal. Bloomberg's K only works on dycotomic trees, thus, polytomic trees must be "forced" into a dycotomic pattern reducing the statistical power of the analysis. Other studies have also suggested that this metric may be a poor indicator of phylogenetic conservatism (Revell *et al.* 2008, Swenson and Enquist 2009). Methods such as the NMDS we used to map phylogenetic distances among species, are probably more realistic as they use the phylogenetic distance matrix directly, hence, distance estimation is not affected by the occurrence of polytomies.

## CONCLUSIONS

The assembly of tropical dry forest successional communities is influenced by niche processes. The strength of these processes changed along ecological succession. In early and intermediate stages predominated the action of environmental filters selecting for species with high heat dispersion capabilities and high photosynthetic rates. In these stages, however, we also detected evidence of niche partitioning processes (limits to similarity) acting with less intensity than environmental filters. In the late successional stage there was no evidence of niche processes structuring tree communities. This could be a consequence of the increasing intensity in the strength of niche partitioning processes along succession

that would preclude the evidence (but not necessarily the action) of environmental filtering. The effects of niche processes were clearly reflected in the way that functional diversity, functional performance and species abundance changed along the successional gradient. These findings are especially important considering that neutral theory arose from tropical tree communities. This kind of studies contribute to discern the effects of disturbance on tropical ecosystems as well as to understand their natural regeneration processes.

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## REFERENCES

- Alvarez-Añorve M, Quesada M, Sánchez-Azofeifa G.A, Avila-Cabadilla, L and J. Gamon. 2012. Functional regeneration and spectral reflectance of trees during succession in a highly diverse tropical dry forest ecosystem. *American Journal of Botany* 99(5): 816–826.
- Avila-Cabadilla L, Stoner K, Henry M and M. Alvarez-Añorve. 2009. Composition, structure and diversity of phyllostomid bat assemblages in different successional stages of a tropical dry forest. *Forest Ecology and Management*, 258: 986-996.
- Bell G. 2001. Neutral Macroecology. *Science*, 293: 2413-2418
- Blomberg, S. P., T. Garland, Jr., and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57:717–745.
- Bongers F, Poorter L, Hawthorne W and D. Sheil. 2009. The intermediate disturbance hypothesis applies to tropical forests, but disturbance contributes little to tree diversity. *Ecology letters* 12: 1-8.
- Borchert R. 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology* 75(5): 1437-1449.
- Bullock S.H, Mooney H. A and E. Medina. 1995. Seasonally dry tropical forests. Cambridge University Press, Cambridge, UK.
- Cavender-Bares J, Keen A and B. Miles. 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. *Ecology* 87(7): S109-S122.
- Cavender-Bares J, Kitajima K and F.A. Bazzaz. 2004. Multiple trait associations in relation to habitat differentiation among 17 Floridian oak species. *Ecological Monographs*, 74: 635–662.
- Cavender-Bares J, Kozak K, Fine P and S. Kembel. 2009. The merging of community ecology and phylogenetic biology. *Ecology letters* 12: 693-715
- Chazdon R, S. Letcher, M. Van Breugel, M. Martinez-Ramos, F. Bongers and B. Finegan. 2007. Rates of change in tree communities of secondary Neotropical forests following major disturbances. *Philosophical Transactions of the Royal Society of London* 362: 273–289.
- Cornelissen J.H.C, S. Lavorel, E. Garnier, S. Diaz, N. Buchmann, D.E. Gurvich, P.B. Reich, et al. 2003. A handbook of protocols for standardized and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335-380.
- Cornwell W. K and D. D. Ackerly. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs* 79(1): 109–126.
- Cornwell W. K, Schwilk D and D. D. Ackerly. 2006. A trait-based test for habitat filtering: convex hull volume. *Ecology* 87:1465–1471.
- Diamond J.M. 1975. Assembly of species communities. In: *Ecology and Evolution of Communities* (eds Cody, M.L. & Diamond, J.M.). Belknap Press of Harvard University Press, Cambridge, pp. 342–444.
- Dinnage R. 2009. Disturbance Alters the Phylogenetic Composition and Structure of Plant Communities in an Old Field System. *Plos One* 4(9): 1-9
- Ehleringer J and I. Forseth. 1980. Solar tracking by plants. *Science* 210: 1094-1098

- Engelbrecht B. M, Comita L. S, Condit R, Kursar T, Tyree M.T, Turner B.L and S. P. Hubbell. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* 447:80–82.
- Evans J. R. 1989. Photosynthesis and nitrogen relationships in leaves of C<sub>3</sub> plants. *Oecologia* 78: 9-19.
- Fargione J, Brown C.S. and D. Tilman. 2003. Community assembly and invasion: An experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences*. USA, 101, 8916–8920
- Gamon J. A and R.W. Pearcy. 1989. Leaf movement, stress avoidance and photosynthesis in *Vitis californica*. *Oecologia* 79: 475-481
- Garland T. Jr, Harvey P.H and A.R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology*. 41:18–32.
- Garnier E, Shipley B, Roumet C and G. Laurent. 2001. A standardized protocol for the determination of specific leaf area and leaf dry matter content. *Functional Ecology* 15:688–695.
- González-Iturbe J. A, Olmsted I and F. Tun-Dzul. 2002. Tropical dry forest recovery after long term Henequen (sisal, *Agave fourcroydes* Lem.) plantation in northern Yucatan, Mexico. *Forest Ecology and Management* 167: 67-82.
- Gotelli N.J and D.J. McCabe. 2002. Species co-occurrence: a meta-analysis of J. M. Diamond's assembly rules model. *Ecology* 83:2091–2096.
- Gotelli N.J and G.R. Graves. 1996. Null models in ecology. Smithsonian Institution, Washington, D.C.
- Grime J.P. 2006. Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. *Journal of Vegetation Science* 17: 255-260.
- Grubb P. J. 1977. Maintenance of species-richness in plant communities: importance of regeneration niche. *Biological Reviews of the Cambridge Philosophical Society* 52: 107–145.
- Gurevitch J, Morrow L, Wallace A and J. S. Walsh. 1992. A Meta-Analysis of Competition in Field Experiments. *The American Naturalist* 140(4): 539-572.
- Hubbell S. 1979. Tree dispersion, abundance and diversity in a tropical dry forest. *Science* 203: 1299–1309.
- Hubbell S. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton, NJ.
- Hubbell S. 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. *Ecology* 19: 166–172.
- Jabot F and J. Chave. 2009. Inferring the parameters of the neutral theory of biodiversity using phylogenetic information and implications for tropical forests. *Ecology Letters* 12: 239–248.
- Jaramillo V. J and R. L. Sanford. 1995. Nutrient cycling in tropical deciduous forests. Pages 346-361 in: Bullock, S. H., H. A. Mooney, and E. Medina, editors. Seasonally dry tropical forests. Cambridge University Press, Cambridge, UK.
- Kelly C.K and M.G. Bowler. 2002. Coexistence and relative abundance in forest tree species. *Nature* 417:437–440.
- Kelly C.K, Bowler M.G, Pybus O and P.H. Harvey. 2008. Phylogeny, niches, and relative abundance in natural communities. *Ecology*, 89, 962–970.

- Kembel S and S.P. Hubbell. 2006. The phylogenetic structure of a neotropical forest tree community. *Ecology* 87(7): S86–S99
- Kraft N.J, Cornwell W.K, Webb C.O and D.D Ackerly. 2007. Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *American Naturalist* 170, 271–283.
- Kraft N.J, Valencia R and D. Ackerly. 2008. Tree Community Assembly in an Amazonian Forest. *Science* 322: 580-582.
- Lebrija-Trejos E, Pérez-García E, Meave J.A, Bongers F and L. Poorter. 2010. Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology* 91(2): 386-398.
- Letcher S. 2010. Phylogenetic structure of angiosperm communities during tropical forest succession. *Proc. Biol. Sci.* 277(1678): 97–104.
- Losos J.B. 1996. Phylogenetic perspectives on community ecology. *Ecology*, 77, 1344–1354.
- Lott E.J. 2002. Lista anotada de las plantas vasculares de Chamela-Cuixmala. In: Noguera, F.N., Vega Rivera, J.H., García Alderete, A.N., Quesada Avendaño, M. (Eds.), *Historia Natural de Chamela*. Inst. Biol., Universidad Nacional Autónoma de Mexico, Mexico, pp. 99–136.
- Mac Arthur R and R Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* 101: 377–385.
- Martínez-Yrizar A, Maass M, Pérez-Jiménez A and J. Sarukhán. 1996. Net primary productivity of a tropical deciduous forest on the coast of Jalisco, Mex. *Journal of Tropical Ecology* 6: 433-444.
- Mason N, Lanoiselée C, Mouillot D, Irz, P and C. Argillier. 2007. Functional characters combined with null models reveal inconsistency in mechanisms of species turnover in lacustrine fish communities. *Oecologia* 153:441–452.
- Mason N, Lanoiselée C, Mouillot D, Wilson J.B and C. Argillier. 2008. Does niche overlap control relative abundance in French lacustrine fish communities? A new method incorporating functional traits. *Journal of Animal Ecology* 77(4): 661–669.
- Mason N, Mouillot D, Lee W and J. B. Wilson. 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111:112–118
- Maza-Villalobos A, Balvanera P and M. Martínez-Ramos. 2011. Early regeneration of Tropical Dry Forest from abandoned pastures: contrasting Chronosequence and Dynamic approaches. *Biotropica* DOI: 10.1111/j.1744-7429.2011.00755.x
- McGill B, Enquist B, Weiher E and M. Westoby. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* 21(4): 178-185
- Murphy P. G, and A. E. Lugo. 1986. Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* 17: 67–88.
- Parkhurst, D. F., and O. L. Loucks. 1972. Optimal leaf size in relation to environment. *Journal of Ecology*. 60: 505–537.
- Pockman W. T. and J. S. Sperry. 2000. Vulnerability to xylem cavitation and the distribution of Sonoran desert vegetation. *American Journal of Botany* 87:1287–1299.
- Poorter L and L. Markesteijn. 2008. Seedling Traits Determine Drought Tolerance of Tropical Tree Species. *Biotropica* 40(3): 321–331



- Quesada M and K. E. Stoner. 2004. Threats to the conservation of tropical dry forest in Costa Rica. Pages 266-280 in: Frankie, G. W., A. Mata, and S. B. Vinson, editors. *Biodiversity Conservation in Costa Rica: Learning the Lessons in a Seasonal Dry Forest*. University of California Press. Berkeley, California.
- Quesada M, G. A. Sanchez-Azofeifa, M. Alvarez-Añorve, K. Stoner, L. Avila-Cabadilla, J. Calvo-Alvarado, A. Castillo, M. Espiritu-Santo, M. Fagundes, G. W. Fernandes, J. A. Gamon, M. Lopezaraiza-Mikel, D. Lawrence, P. Morellato, J. Powers, F. Neves, V. Rosas-Guerrero, R. Sayago, G. Sanchez-Montoya. 2009. Succession and management of tropical dry forests in the Americas: Review and new perspectives. *Forest Ecology and Management*, 258: 1014–1024.
- R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Rees M and M. Westoby. 1997. Game-theoretical evolution of seed mass in multi-species ecological models. *Oikos* 78: 116–126.
- Reich P, Wright I, Cavender-Bares J, Craine J, Oleskyn J, Westoby M and M. Walters. 2003. The evolution of plant functional variations: traits, spectra and strategies. *International Journal of Plant Sciences* 164(3): S143-S164
- Revell L. J, Harmon L and D. C. Collar. 2008. Phylogenetic signal, evolutionary process, and rate. *Systematic Biology* 57:591–601.
- Ricklefs R. E. 2004. A comprehensive framework for global patterns in biodiversity. *Ecology Letters*: 1–15
- Ricklefs R.E. 1987. Community diversity: relative roles of local and regional processes. *Science*, 235, 167–171.
- Roderick M. L, Berry S. L, Noble I.R and G. D. Farquhar. 1999. A theoretical approach to linking the composition and morphology with the function of leaves. *Functional Ecology* 13: 683–695.
- Sanchez-Azofeifa G. A, M. Quesada, J. P. Rodríguez, J. M. Nassar, K. E. Stoner, A. Castillo, T. Garvin, E. L. Zent, J. C. Calvo-Alvarado, M. E. Kalacska, L. Fajardo, J. A. Gamon, and P. Cuevas. 2005. Research Priorities for Neotropical Dry Forest. *Biotropica* 37 (4): 477-485.
- Silvertown J. 2004. Plant coexistence and the niche. *Trends in Ecology and Evolution* 19: 605-611.
- Sims D and J. A. Gamon. 2002. Relationships between leaf pigment content and spectral reflectance across a wide range of species, leaf structures and developmental stages. *Remote Sensing of Environment* 81: 337– 354
- Swenson N.J and B. Enquist. 2009. Opposing assembly mechanisms in a Neotropical dry forest: implications for phylogenetic and functional community ecology. *Ecology*, 90,2161–2170.
- Vamosi S.M, Heard S.B, Vamosi J.C. and C.O. Webb. 2008. Emerging patterns in the comparative analysis of phylogenetic community structure. *Molecular Ecology*, 18, 572–592.
- Vieira D.L.M and A. Scariot. 2006. Principles of natural regeneration of tropical dry forests for restoration. *Restoration Ecology* 14: 11–20.
- Villéger S, Mason N, Mouillot D. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89(9) 2290–2301.

- Webb C.O, Ackerly D.D, McPeck M.A. and M.J. Donoghue. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, 33, 475–505.
- Webb C.O, Ackerly D.D and S.W. Kembel. 2008. Phylocom: software for the analysis of phylogenetic community structure and character evolution. *Bioinformatics* 24: 2098-2100.
- Wikstrom N, Savolainen V and M. Chase. 2001. Evolution of angiosperms: Calibrating the family tree. *Proceedings of the Royal Society of London, Series B - Biological Sciences* 268:2211–2220.
- Wilson J.B. 1995. Null models for assembly rules—the Jack-Horner effect is more insidious than the Narcissus effect. *Oikos* 72:139–144.
- Wright I. J, P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P. K. Groom, J. Gulias, K. Hikosaka, B. B. Lamont, T. Lee, W. Lee, C. Lusk, J. J. Midgley, M. Navas, U. Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V. I. Pyankov, C. Roumet, S. C. Thomas, M. G. Tjoelker, E. J. Veneklaas, and R. Villar. 2004. The worldwide leaf economics spectrum. *Nature* 428:821–827.

## TABLES

**Table 1.** Family, species and successional stage (S.S) in which species occur. “All” indicates when a species was evaluated in the three successional stages (early, intermediate and late)

Family	Species	Successional stage
Achatocarpaceae	<i>Achatocarpus gracilis</i> (H. Walt.)	All
Amaranthaceae	<i>Lagrezia monosperma</i> (Rose) Standl.	Late
Anacardiaceae	<i>Spondias purpurea</i> (L.)	All
Apocynaceae	<i>Stemmadenia donnell-smithii</i> (Rose) Woods.	Early
Boraginaceae	<i>Cordia alliodora</i> (Ruiz & Pav.) Oken	All
Ebenaceae	<i>Diospyros aequoris</i> (Standl.)	Late
Euphorbiaceae	<i>Croton niveus</i> (Jacq.)	Late
	<i>Croton pseudoniveus</i> (Lundell)	All
	<i>Croton suberosus</i> (H.B.K)	Late
	<i>Pyranhea mexicana</i> (Standl.)	Intermediate
Fabaceae	<i>Bauhinia subrotundifolia</i> (Cav.)	Early
	<i>Caesalpinia pulcherrima</i> (L.)	Late
	<i>Erythrina lanata</i> (Standl.)	Late
	<i>Lonchocarpus constrictus</i> (Pittier)	Intermediate
	<i>Lonchocarpus eriocarinalis</i> (Micheli)	All
	<i>Lonchocarpus mutans</i> (Sousa)	Late
	<i>Platymiscium lasiocarpum</i> (Sandwith)	Intermediate
	<i>Senna atomaria</i> (L.)	Early
Flacourtiaceae	<i>Casearia corymbosa</i> (H.B.K)	All
Polygonaceae	<i>Coccoloba liebmannii</i> (Lindau)	Early
	<i>Ruprechtia fusca</i> (Fernald)	All
Rubiaceae	<i>Randia thurberi</i> (S. Watson)	Late
Rutaceae	<i>Zanthoxylum fagara</i> (L.)	Intermediate
	<i>Zanthoxylum caribaeum</i> (Lam.)	Intermediate
Sapindaceae	<i>Thouinia paucidentata</i> (Radlk.)	Late

**Table 2.** Parameters characterizing the phylogenetic distances distribution for the most abundant species present on three SDTF successional stages.

S.S	Parameter			
	Range	Variance	Kurtosis	NDsd
E	<b>216.46</b> (-1.18)	<b>3680.93</b> (-2.09)	<b>5.52</b> (2.07)	20.88 (-0.78)
I	243.77 (-0.28)	6906.11 (0.14)	1.97 (-0.77)	12.82 (-0.77)
L	255.38 (1.13)	7539.90 (0.78)	2.11 (-0.44)	14.73 (-0.64)

*The parameter sdND is the standard deviation of the distribution of nearest neighbor functional distances for the set of community members. Successional stages (S.S) are: early (E), intermediate (I) and late (L). In bold and in bold and italic, respectively, are represented significant ( $p < 0.05$ ) and marginally significant deviations ( $0.05 \leq p < 0.1$ ) from the null expectation.*

**Table 3.** Parameters characterizing functional traits distribution for the set of species occurring on each successional stage.

Trait S.S	Parameter				
	Mean	Range	Variance	Kurtosis	NDsd
<b>LWC</b>					
E	-1.90 (0.87)	<b>0.41</b> (-1.76)	0.02 (-1.27)	<b>1.63</b> (-1.30)	<b>0.02</b> (-1.43)
I	-1.91 (0.81)	0.49 (-1.07)	0.02 (-0.97)	1.75 (-1.11)	0.03 (-1.09)
L	-1.94 (-0.54)	0.58 (-0.33)	0.02 (-0.58)	<b>2.98</b> (1.67)	0.04 (0.28)
<b>WUE</b>					
E	<b>0.70</b> (-2.10)	<b>0.31</b> (-1.43)	<b>0.01</b> (-1.36)	2.39 (-0.74)	<b>0.02</b> (-1.52)
I	0.76 (0.43)	<b>0.26</b> (-1.99)	<b>0.01</b> (-1.79)	2.59 (-0.50)	<b>0.02</b> (-1.48)
L	0.78 (1.23)	0.52 (0.71)	0.02 (0.38)	3.30 (0.10)	0.03 (0.12)
<b>E</b>					
E	<b>0.33</b> (1.97)	0.60 (-0.75)	0.03 (-0.92)	2.11 (-0.69)	0.05 (-0.88)
I	0.26 (0.45)	<b>0.46</b> (-1.39)	<b>0.02</b> (-1.39)	2.13 (-0.65)	0.06 (-0.60)
L	<b>0.17</b> (-1.71)	0.92 (0.29)	0.05 (0.04)	4.26 (0.85)	0.10 (0.53)
<b>SLA</b>					
E	2.20 (-0.45)	0.61 (0.55)	0.03 (0.00)	2.33 (0.33)	0.04 (-0.23)
I	<b>2.16</b> (-1.75)	0.61 (0.48)	0.04 (0.58)	2.41 (0.63)	<b>0.05</b> (1.97)
L	<b>2.27</b> (2.27)	0.62 (0.61)	0.03 (0.01)	2.43 (0.89)	0.03 (-0.07)
<b>LD</b>					
E	-1.42 (-0.16)	0.63 (-0.81)	0.04 (-0.61)	2.19 (-0.48)	0.04 (-0.72)
I	<b>-1.33</b> (2.32)	0.66 (-0.91)	0.04 (-0.46)	2.28 (-0.35)	0.04 (-0.77)
L	-1.44 (-1.03)	0.77 (0.24)	0.05 (0.57)	2.19 (-0.77)	0.04 (-0.62)
<b>LMA</b>					
E	-2.16 (0.53)	0.61 (0.39)	0.03 (-0.31)	2.71 (0.81)	0.04 (0.54)
I	<b>-2.12</b> (1.80)	0.61 (0.29)	0.03 (0.43)	2.64 (0.69)	<b>0.05</b> (1.97)
L	<b>-2.23</b> (-2.24)	0.63 (0.62)	0.03 (0.19)	2.38 (-0.01)	0.03 (0.00)
<b>LT</b>					
E	-0.73 (0.42)	0.65 (0.82)	0.03 (0.54)	3.18 (0.29)	0.06 (0.91)
I	-0.77 (-0.83)	0.65 (0.65)	0.02 (-0.67)	<b>4.53</b> (2.72)	<b>0.07 (1.92)</b>
L	<b>-0.77</b> (-1.29)	0.68 (0.71)	0.03 (0.85)	2.91 (-0.57)	0.04 (0.05)
<b>LFM</b>					
E	-1.70 (0.96)	<b>0.35</b> (-1.89)	0.01 (-1.22)	<b>1.81</b> (-1.45)	<b>0.02</b> (-1.96)
I	<b>-1.69</b> (1.52)	0.40 (-1.45)	0.02 (-0.60)	<b>2.01</b> (-1.25)	<b>0.02</b> (-1.56)
L	<b>-1.75</b> (-1.47)	0.54 (0.14)	0.02 (-0.28)	2.89 (0.39)	0.03 (-0.35)

Trait S.S	Parameter				
	Mean	Range	Variance	Kurtosis	NDsd
<i>A<sub>max</sub></i>					
E	<b>0.99</b> (1.63)	<b>0.38</b> (-2.29)	0.02 (-1.32)	<b><i>1.69</i></b> (-1.08)	0.05 (-0.06)
I	0.96 (0.74)	<b>0.40</b> (-1.94)	0.02 (-1.33)	1.80 (-0.87)	0.04 (-0.87)
L	<b>0.89</b> (-1.78)	0.55 (-0.02)	0.03 (-0.08)	2.24 (-0.18)	0.04 (0.48)

*The parameter sdND is the standard deviation of the distribution of neighbor functional distances for the set of community members. Successional stages (S.S) are: early (E), intermediate (I) and late (L). In bold and in bold and italic are represented, respectively, significant ( $p < 0.05$ ) and marginally significant ( $0.05 \leq p < 0.1$ ) deviations from the null expectation. The standardized effect size values are presented between parentheses. LWC: leaf water content, WUE: water use efficiency, E: transpiration rate, SLA: specific leaf area, LD: leaf density, LMA: leaf mass per area, LT: leaf thickness, LFM: leaf fresh mass, *A<sub>max</sub>*: net photosynthesis*

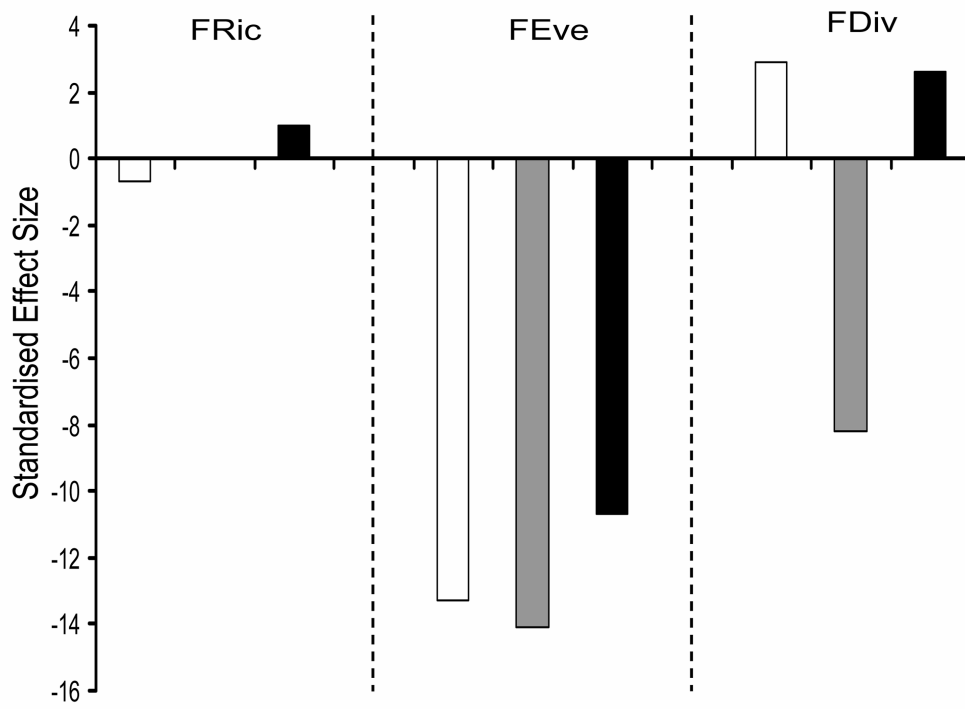


Figure 1.

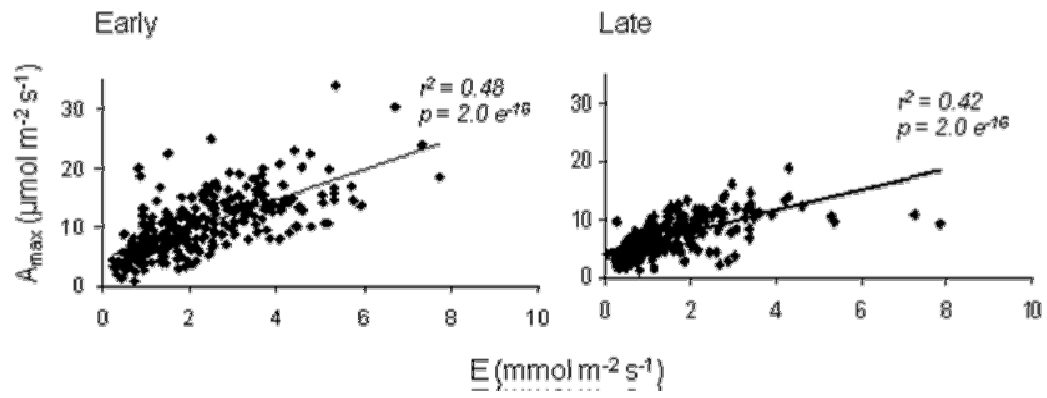


Figure 2.



## FIGURE LEGENDS

**Figure 1.** Standardized effect size of functional diversity indices on each successional stage. Functional diversity indexes are: functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv). Successional stages are: early (white bars), intermediate (gray bars) and late (black bars).

**Figure 2.** Relationship between the values of  $A_{\max}$  and E for individuals evaluated in the early and late successional stages. Every point represents a leaf. Correspondent  $r^2$  and p values are indicated.

## S1. Interpretation of distribution parameters.

**Table S1.** Possible outcomes from null model testing of environmental filtering and limiting similarity processes in community assembly.

	Outcome		Evidence
	< Exp	> Exp	
<b><i>TDP</i></b>			
Range	X		EF, limiting the range of species trait values
Variance	X		EF, limiting the variation of species trait values
Kurtosis	X		LS, spreading species traits values distribution
NDsd	X		LS, tends to evenly space species trait values
<b><i>FDI</i></b>			
FRic	X		EF, limiting the volume of functional traits space filled by the species
FEve		X	LS, tends to evenly distribute species in the functional traits space
FDiv		X	LS, spreading the abundant species in the functional trait space
<b><i>PDP</i></b>			
Range	X		EF, limiting the range of species trait values
Variance	X		EF, limiting the variation of species trait values
Kurtosis	X		LS, spreading species traits values distribution
NDsd	X		LS, tends to evenly space species trait values

*Niche processes: environmental filtering (EF), and limiting similarity (LS). Outcomes: observed value is lower than expected at random (< Exp), and observed value is higher than expected at random (> Exp). Trait distribution parameters (TDP): the standard deviation of the distribution of neighbor functional distances for the set of community members (NDsd); the other parameters are as listed in the table. Functional diversity indexes (FDI): functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv). Phylogenetic distribution parameters (PDP): the standard deviation of the distribution of neighbor phylogenetic distances for the set of community members (NDsd); the other parameters are as listed in the table.*

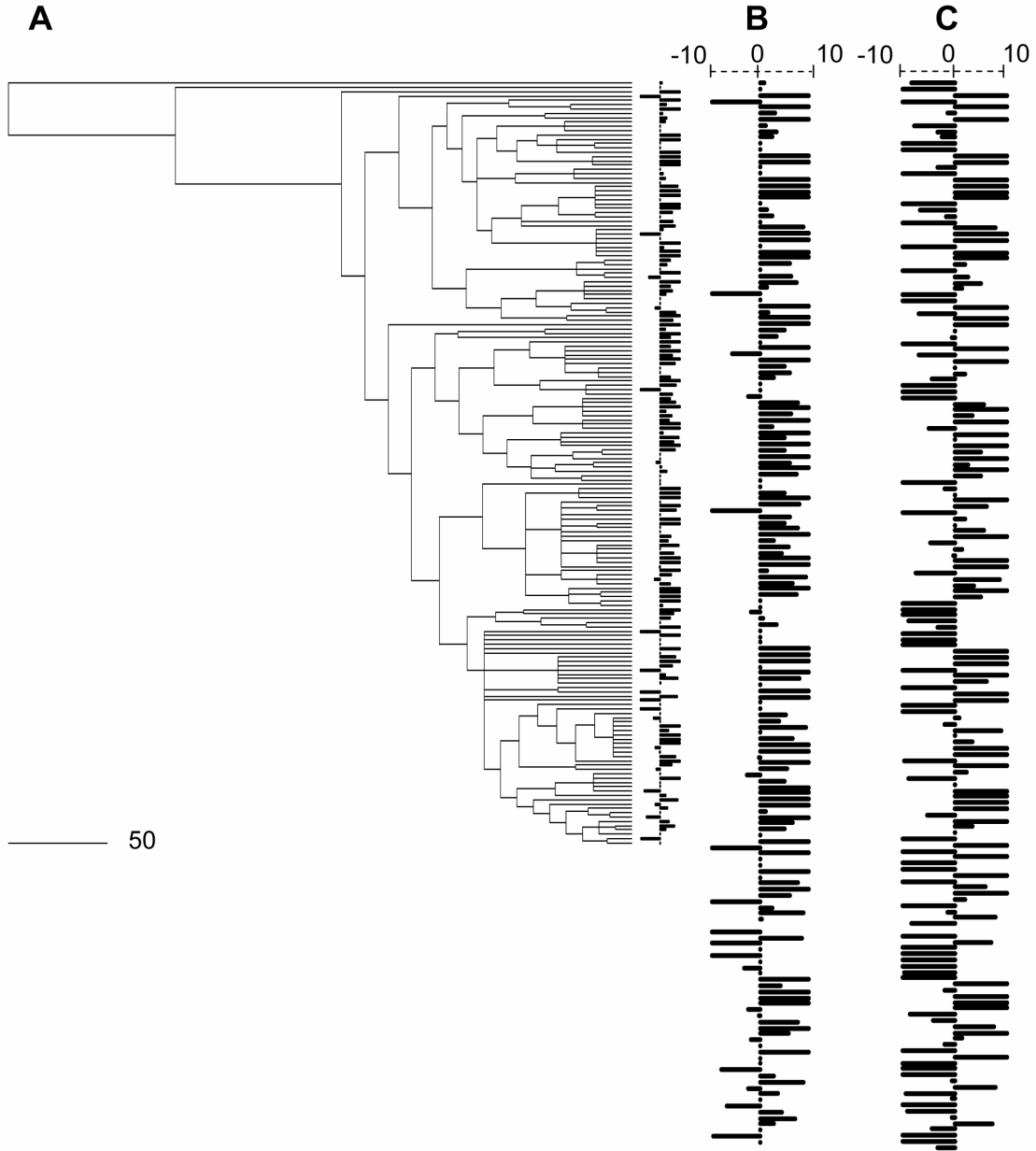
## **S2. Characteristics of the functional diversity indices of Villeger et al. (2008)**

This set of indexes present several advantages with respect to other estimations of functional diversity. First, they are designed to deal with several traits, which offer a more complete image of functional diversity in a community than single-trait indices. Second, they take into account the relative abundances of species, allowing to weight species contributions to functional diversity according to its abundance. Third, they provide a continuous measure of functional diversity that directly use quantitative values for functional traits; in this way, they deal properly with the continuous structure of functional differences between species. Finally, they are independent from species richness and from each other. The simultaneous analysis of the three indices increases the detail in the analysis of functional diversity variation; this allows for examining different possible hypothesis related to this variation. For example, the variations in the volume of functional traits space may indicate an increasing pressure of environmental filters (Cornwell et al. 2006), while a shift in the distribution of abundance may reveal a shift in the intensity of competitive interactions (Mason et al. 2008).

## **S3. Blomberg's test details**

The basic idea in the Blomberg's test is to assess whether a given phylogenetic tree better fits a set of tip data (i.e. our variables) in comparison to the fit obtained through the random permutation of the tip data, which destroys any phylogenetic signal that may have existed (Blomberg et al. 2003). In this sense, a lower variance of contrasts that expected by chance can be interpreted as an evidence of phylogenetic signal (the phylogenetic tree fit well the tip data), while a higher variance of contrasts can be interpreted as an evidence of "antesignal" (Blomberg et al. 2003). In this study we also reported the K statistic proposed by Blomberg et al. (2003), which indicates the strength of the phylogenetic signal. This statistic allows comparisons of different traits across different phylogenetic trees. A K statistic greater than 1 can be interpreted as an indicator of phylogenetic signal.

#### S4. Results of the Bloomberg's test



**Figure S4.** Representation of the phylogenetic tree (A) corresponding to species occurring in three successional stages of Chamela SDTF. Represented age of divergence was obtained from Wikstrom (2001) in million of years before present. At the right of the phylogenetic tree, for reference, we show the per-species percentage of change in abundance from early to late successional stages. This change can be better observed in B where bars are enlarged. In C, we show the per-species percentage of change in abundance from early and intermediate stages (pooled together) to late stages

## **CAPÍTULO 2**

**Percepción remota y grupos funcionales de plantas:  
Fisiología, Ecología y Espectroscopía en los sistemas tropicales.**

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# 2 Remote Sensing and Plant Functional Groups

## *Physiology, Ecology, and Spectroscopy in Tropical Systems*

*Mariana Alvarez-Añorve, Mauricio Quesada, and Erick de la Barrera*

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### 2.1 PLANT FUNCTIONAL GROUPS IN TROPICAL SYSTEMS

The term “functional groups” was proposed by Cummins [1] to classify species playing similar roles or performing analogous processes in the ecosystem. Plant functional types may describe groups of plants with common responses to certain

environmental influences [2,3] and have been applied to several ecosystem functions such as biochemical cycles, fire resistance, invasion resistance, acquisition and use of resources, defense against herbivory, pollination, and seed dispersal, among others [4].

In general, functional grouping of species allows us to simplify biodiversity into components capable of explaining patterns or processes in a certain system [5]. This concept has been useful to predict the types of responses of vegetation to environmental changes even without detailed information about each species [6]. Thus, functional groups are often used in global models of vegetation [7,8] and climatic change [9].

The most important approaches to plant functional groupings are based on the use of functional characteristics and have been used by ecologists for decades [10–14]. According to Reich et al. [6], there are four main kinds of functional groupings. The first one is based on categorical qualitative approaches that classify groups of plants based on certain characteristics such as life form and type of photosynthesis, among others. The second one groups species along a continuum of quantitative characteristics such as growth rate, specific leaf area, maximum photosynthetic capacity, etc. [15,16]. The third model is based on a combination of quantitative characteristics that may influence each other such as leaves, seeds, and tree height [17]. Finally, a fourth model groups plant species based on their responses to specific environmental factors; a good example of this is the classification of tropical plant species proposed by Mulkey, Wright, and Smith [18] on the basis of their shade tolerance or the C-S-R scheme of plant strategies proposed by Grime [10].

### 2.1.1 STUDIES ON FUNCTIONAL GROUPS

In general, the number of studies regarding functional groups has increased over the last two decades. An important number of these studies have focused on plant groups associated to successional stages after anthropogenic disturbance; another set of studies evaluated the response of predefined functional groups to global increments of CO<sub>2</sub> and temperature due to climate change; and a third group of studies evaluated the importance of functional diversity in synthetic or natural communities. Most of these studies, however, have been conducted in temperate regions rather than in tropical forests where biodiversity is higher and ecosystems are fragile [19]. The few studies in the tropics suggest that the quantity of plant functional groups is potentially very high and more complex [20]. Most of the studies in the tropics have been conducted in tropical rain forests with few in tropical dry and cloud forests [21–24]. Tropical systems other than tropical rain forests have been largely overlooked in the scientific literature [25].

In an extensive review, we surveyed the literature from different databases using a combination of the following keywords: “plant functional group,” “plant functional type,” and “tropical.” Searches were conducted in the Science Citation Index and Biological Abstracts databases as well as in the main editorials (Blackwell Science, Springer–Verlag, Elsevier) and scientific societies of the most important indexed journals of ecology, physiology, and conservation biology. In this revision we found a total of 50 studies that analyze plant functional groups in tropical systems. Fifty-four percent of the studies use data of tropical plants in combination with data

from other ecosystems to analyze three main aspects of functional groups related to (1) theoretical generalizations of ecological processes [2,6,26–30]; (2) performance of morphological and physiological characters and of their interrelationships [31–36], among others; and (3) the role of functional groups on the dynamics of communities and ecosystems [2,37–40]. The remaining 46% of these studies exclusively analyze tropical species to identify functional groups *de novo* or to evaluate the performance and consistency of functional groups previously defined for the tropics.

Ecophysiological characteristics are among the most used plant traits to classify functional groups. In tropical systems these traits have been mainly used for grouping plant species on the basis of (1) shade tolerance [41–43]; (2) maximum potential height [44–46]; (3) increment in diameter used as an indicator of growing rate [20,44,47–50]; (4) elements related to photosynthetic capacity [15,51]; and (5) water status and/or water use efficiency (i.e., water storage stems [21]), stomatal conductance [51], C isotopic composition ( $\delta^{13}\text{C}$ ) [52,53], or the difference between the air and leaf temperatures ( $\Delta T$ ) (i.e., indicator of heat dispersion capacity [23]).

Some other classifications including ecophysiological characteristics are based on species responses to different environmental factors such as plant response to abnormal patterns of drought and rain [22] or the response to changes in the landscape (i.e., structure of forest fragments [54]). Other studies have identified a combination of various other characteristics to define functional groups. These include reproductive traits, life forms and patterns of distribution in forests in different successional stages [55], demographic characteristics such as mortality rate [44], and, in the case of invasive species, the impact on native species [56]. In summary, we can classify the studies of functional groups of tropical plants in the following groups: (1) studies that characterized plant species associated to different successional stages, (2) studies that classify plants based on growth patterns, and (3) studies that classify plants based on water stress, water storage capacity, and heat dissipation.

The analysis of functional plants under succession has been emphasized due to the increasing importance of tropical secondary forests. There is increasing knowledge that recognizes different strategies of groups of plants specialized to regenerate in different successional stages; these studies have become crucial for the conservation of tropical systems [57,58]. Another set of studies emphasized the use of growth patterns to determine functional groups because growth rate is a trait that is correlated with ecophysiological characteristics of great importance for species performance [59]. Finally, some studies classify plants based on water use mechanisms because this resource plays a decisive role in species distribution and diversity gradients in tropical forests [60]. Water availability is an important determinant of species distribution in tropical dry forests [61].

As shown thus far in this review, most studies in tropical systems have analyzed single or a combination of a few ecophysiological characters for the discrimination of tropical functional groups. However, an analysis considering an assemblage of characteristics with ecological relevance that determine the establishment of species in a given habitat would be more realistic. Thus, we consider that a possible combination of plant traits should include plant growth rate, leaf longevity, specific leaf area, photosynthetic capacity, leaf water content, water use efficiency, and certain reproductive parameters. The use of this kind of assemblage would generate more



consistent information about a great number of species in order to detect tropical functional groups. The information generated in most studies until now did not consider a multivariate approach of both vegetative and reproductive parameters. Therefore, there is a lack of comprehensive analyses of functional groups in tropical systems—communities that are highly diverse and complex.

## 2.2 SOLAR IRRADIATION AND LEAF OPTICAL PROPERTIES

Solar electromagnetic radiation reaches the Earth's outer atmosphere with an energy of  $1366 \text{ W m}^{-2}$ . During its trajectory to the planet's surface, approximately 40% of the energy is attenuated, with an essentially absolute filtering of wavelengths below 200 nm and above 10,000 nm [62,63]. Considering that such radiation can be absorbed, transmitted, or reflected at different wavelengths, remote sensing takes advantage of the net reflected radiation by the various objects on the surface of the Earth, allowing for applications, for instance, in tropical ecology, as discussed later in this chapter. In the present section we will consider some of the factors that result in the range of reflected wavelengths registered by remote sensing satellites, with a special focus on leaf-level properties.

### 2.2.1 SOLAR IRRADIANCE AND RADIATION SOURCES

The wavelengths of the solar radiation reaching the outer layers of the atmosphere approximately range from 200 to 1600 nm, with most of the incident energy within the range of visible light [62,63]. Various components of the atmosphere attenuate such solar irradiance. For instance, the stratospheric ozone layer filters out wavelengths below 350 nm [64]. Water vapor, in turn, absorbs infrared radiation with major bands at 900, 1100, and above 1200 nm [63].  $\text{CO}_2$  has narrow absorption bands at 2700, 4300, and 15,000 nm [65]. In fact, the infrared absorption properties of water vapor and  $\text{CO}_2$  are widely utilized for the measurement of real-time gas exchange (i.e.,  $\text{CO}_2$  uptake and transpiration by plants).

In addition to the aforementioned solar irradiance attenuation by absorption, air and suspended particles further attenuate it by scattering, a phenomenon of special relevance for visible light. Indeed, when a light beam's trajectory is intercepted by an object, some of its energy is lost on impact and the rest is re-irradiated concentrically [66]. In fact, the sky's brightness and blue color during clear days are due to the scattering of light by air molecules—a phenomenon known as Rayleigh scattering—while larger particles, such as dust, further reduce the light's energy, as can be observed during red-sky sunsets due to Mie scattering [63,66].

In any case, six sources of radiation can reach an object (e.g., a leaf) on Earth's surface. First is direct solar irradiation or *sunlight*, for which most of its energy comes from visible light and whose range largely coincides with photosynthetically active radiation (wavelengths of 400–700 nm), with a special enrichment in yellow-orange (approximately 560–640 nm) wavelengths [62,63]. Due to scattering and absorption by the atmosphere, *skylight* also reaches the surface of the Earth during clear days, with energy of only 10% of that of direct solar irradiation with a peak wavelength near 400 nm [63,67]. Finally, visible *cloudlight*, with a peak around 500 nm, results

from the transmission through clouds of irradiance [67]. The optical properties of the objects encountered by direct sunlight, skylight, and cloudlight result in reflected long-wave radiation that also reaches objects such as leaves. Thus, the three remaining radiation sources can be identified as *reflected sunlight*, *reflected skylight*, and *reflected cloudlight*.

### 2.2.2 LEAF OPTICAL PROPERTIES

In the previous section we considered the six sources of radiation that can reach a leaf. Now we will discuss some leaf optical properties that result in the wavelength ranges, or bands, that are actually registered by remote sensors and some of their ecophysiological implications.

Pigments are highly conjugated biological molecules that absorb light at certain wavelengths. The most obvious pigment for studying plants is chlorophyll, which has absorption peaks in the blue and, especially, red regions of the visible spectrum, while light absorption of intermediate wavelengths is substantially reduced, especially in the green region. As a result, most of the red and blue radiation is absorbed by leaves, while most of the green light is reflected, conferring the familiar color to plants and vegetation in general. In this respect, remote sensors are able to detect a depletion in the red region that can be correlated with chlorophyll content (e.g., Castro-Esau, Sanchez-Azofeifa, and Caelli [68]). Higher chlorophyll contents, as suggested by remotely measured red-light depletion, can be indicators of higher canopy density or a more complex community structure. Another possibility is that such depletion indicates higher nitrogen content in the plant tissue. This is due to the fact that the most abundant protein in plants and on Earth is responsible for CO<sub>2</sub> fixation. Thus, chlorophyll content can be used as a proxy for determining protein and nitrogen content for plant tissue, as well as soil nitrogen levels [69,70].

While chlorophyll's maximum absorption occurs in the red region, accessory pigments absorb light of shorter wavelengths and, in consequence, of higher energy [63,70]. Of particular importance for tropical and subtropical forests, where the solar angle leads to higher irradiances than at higher latitudes, pigments that absorb in the blue-green region can be mentioned. In addition to funneling energy toward photosynthesis they also double as photoprotective pigments. First, as a result of photochemistry, a very reactive form of oxygen can result from an interaction with chlorophyll molecules. Carotenoids can quickly absorb the energy from such *free radicals*, thus preventing cellular damage. The second photoprotective function of carotenoids, specifically linked with the xanthophyll cycle, is nonphotochemical quenching. In this case, excited chlorophyll molecules can return to a basal state either by fluorescence (i.e., emitting light) or by transferring the excitation energy directly to other molecules. When exposed to high-light environments, a finite number of chlorophyll molecules become saturated, as illustrated by the numerous light response curves of net CO<sub>2</sub> uptake available in the literature, and such excess energy can inhibit or damage the photosynthetic machinery. In this respect, under high light the xanthophyll violaxanthin (absorption occurs in the blue region) is converted to zeaxanthin (absorption occurs in the green region), which in turn is converted back to violaxanthin when the light decreases [70].

Leaves also absorb infrared radiation, mainly from reflected light, which can increase their temperature. As a response, transpiration rates may also increase, taking advantage of the cooling effect resulting from evaporation. Nevertheless, because all objects with a temperature higher than absolute zero emit radiation, in addition to reflected radiation, leaves irradiate in the infrared [63]. The wavelength in which they maximally irradiate can be predicted, as a function of their surface temperature, by the Wien displacement law,  $\lambda_{\max} T = 3.67 \times 10^6 \text{ nm K}$ , on a photon basis, where  $\lambda_{\max}$  is the wavelength of maximum photon flux density, and  $T$  is the surface temperature of an object. For instance, the sun's surface temperature is 5800 K; according to Wien's displacement law, it maximally irradiates at 630 nm, while a leaf at 30°C would maximally irradiate at 35,631 nm. The relative importance of emitted vs. reflected infrared radiation in terms of the spectral signature of vegetation registered by remote sensors is not yet known. Yet, because infrared is absorbed by water, such bands can be utilized for assessing the water status of vegetation (e.g., Castro-Esau et al. [68] and Hunt, Rock, and Nobel [71]).

Plant anatomy also influences the optical properties of leaves. For instance, leaves from xeric environments may be more reflective of shorter wavelengths due to the higher contents of silicates in their leaves. In addition, some species present calcium oxalacetate crystals, which are believed to dissipate excess energy [63,72]. Also, the thickness of a leaf's mesophyll influences the amount of absorbed light as a consequence of the multiple layers of cells per leaf unit area [63,72]. Studies about the particular influences of cuticle composition, trichomes, and mesophyll thickness on leaf reflectance are recent and scarce, so further studies characterizing various functional groups may improve our understanding of the biological implications of remotely sensed spectra.

## 2.3 HYPERSPECTRAL DATA APPLICATIONS ON FUNCTIONAL GROUP DETECTION IN TROPICAL FORESTS: CASE STUDIES

Hyperspectral data are narrowband information on the reflectance of an object on Earth gathered by remote sensing analysis from in situ, airborne, or satellite sensors. This state-of-the-art technology allows for a detailed analysis of objects in the landscape from air and space; an example is provided by two hyperspectral satellites, Hyperion and Proba, now in orbit [73].

In hyperspectral imagery it is possible to subdivide the spectral range into over 200 intervals, each approximately 10–20 nm in width. If a radiance value is obtained for each interval, then a spectral curve of the wavelength intensity can be generated from the reflectance of each object in the landscape. The area covered by each hyperspectral image (and spatial resolution) varies by sensor; for example, Hyperion's ground coverage is 7.5 by 100 km with a resolution of 30 m per pixel [73]. Hyperspectral imaging is, then, a powerful and versatile means for continuous sampling of broad intervals of the spectrum.

The capability of hyperspectral sensors to detect numerous narrow bands can be applied to detect from space characteristic chemical and anatomical properties of vegetative and reproductive tissues of plants. A number of recent studies have indicated the advantages of using discrete narrowband data (i.e., hyperspectral data)

from specific portions of the spectrum, rather than broadband data (i.e., multispectral data), to obtain the most sensitive quantitative or qualitative information on vegetation or crop characteristics (i.e., references 74 through 77). For example, Thenkabail et al. [76] established the advantages of using narrowband Hyperion data over broadband IKONOS, ETM+, and ALI data in studying rainforest vegetation. When compared to broadband data from IKONOS, ETM+, and ALI sensors, Hyperion's narrow bands explained 36–83% more of the variability in biomass and increased by 45–52% land use/land cover (LULC) classification accuracies as verified by ground truthing. The overall accuracy in classifying nine rainforest LULC classes was 96% and was achieved by using 23 Hyperion wavebands. In comparison, the overall accuracies were only 48% for IKONOS (four bands), 42% for ETM+ (six nonthermal bands), and 51% for ALI (nine multispectral bands). Similarly, Lee et al. [78] and Kalacska et al. [79] indicated that the large number of narrow bands of hyperspectral data is an advantage for the estimation of structural and functional canopy characteristics.

Given the fact that 47% of the global forest cover is in the tropics [80], where the most biodiversity can be found, it is necessary to apply modern techniques to describe and study functional attributes of tropical plant communities using a large-scale landscape approach that can be corroborated with ground truth data at the species level. Thus, exploration of the role of hyperspectral remote sensing in the assessment and determination of functional traits in the tropics is an important task in order to evaluate current and future applications of these technologies in ecological sciences. At present, however, hyperspectral imaging techniques have been poorly applied in tropical zones, with only a few efforts to detect and study plant functional groups. In order to exemplify applications of hyperspectral remote sensing in this respect, in the following sections we will describe some case studies regarding identification of different kinds of vegetation based on functional attributes of species.

### 2.3.1 DISCRIMINATION OF SUCCESSIONAL STAGES

The area covered by secondary forests has increased over the last decades worldwide, encouraging the interest in successional studies and the development of new techniques oriented to detect these habitats using remote sensing images (e.g., Landsat, SAR, MODIS, AVIRIS). Thus, studies in this respect could involve the detection and characterization of plant successional groups, which would be of crucial importance for conservation purposes [25].

In general, recent forest clearings are spectrally distinct as they have higher reflectance than mature forest in visible, near, and middle infrared wavebands used by satellite sensors. In forest succession, red reflection exhibits a slight decrease as increasing leaf area absorbs rising amounts of radiation in this range; meanwhile, near-infrared reflectance (NIR) increases as additional leaf layers are added to a canopy as a result of the increasing reflectance from the spongy mesophyll. Nevertheless, subsequent canopy maturation, characterized by the acquisition of more layers and complexity, reduces reflectance, given that shadowing traps incoming energy. Shadowing also depresses shortwave infrared reflectance (SWIR). Provided that the SWIR is influenced by water absorption, increasing canopy moisture content also leads to a decrease in SWIR through secondary forest succession. In fact, several

studies have indicated that SWIR bands contain most of the information relevant to plant regeneration [81].

At present, a few attempts have been made to discriminate tropical forest successional stages by using hyperspectral remote sensing. For example, Thenkabail et al. [76] used hyperspectral imaging in order to detect different types of LULC in several ecoregions of West Africa, including humid forests. Specifically, they classified primary forests without evidence of anthropogenic disturbance, degraded primary forest with some evidence of anthropogenic disturbance, young secondary forest between 9 and 15 years old, mature secondary forest between 15 and 40 years old, and mixed secondary forest with significant anthropogenic disturbance. They also attempted to identify LULC classes of agricultural lands recently abandoned with regrowth vegetation between 1 and 8 years old. Only seven to nine Hyperion bands were required to separate pristine vs. degraded primary forest, young vs. mature vs. mixed secondary forest, and fallows of 1–3, 3–5, or 5–8 years old. When all rain-forest vegetation was pooled, approximately 23 Hyperion bands were required to achieve adequate separability.

Indeed, examination of average reflectance spectra for the different vegetation types indicated that the Hyperion data provided many possibilities for separating vegetation categories using specific narrow bands throughout the 600- to 2350-nm spectral range. The most important wavebands were early mid-infrared (EMIR; 1300–1900 nm) bands followed by far near-infrared (FNIR; 1100–1300 nm), far mid-infrared (FMIR; 1900–2350 nm), and red (600–700 nm) wavebands. The results of this study showed that the two most frequently occurring wavebands sensitive to predicting forest biomass were centered at 682 and 1710 nm. Consequently, this study reaffirms the importance of using bands near 680 nm, as previously established by Thenkabail, Smith, and De Pauw [82], that are within a maximal absorption region for crops and vegetation. Some of the most important bands useful for detecting different vegetation types in this study were those related to leaf biochemical and physical traits such as content of water, chlorophyll, starch, lignin, cellulose, and proteins. Biophysical characteristics of vegetation such as biomass, vegetation growth, and leaf types were also important to obtain this segregation. Provided that most of these traits do differ among species in tropical forests [72], the potential use of hyperspectral remote sensing in the tropics to identify groups of species displaying different functional attributes associated to specific successional stages is clear.

### 2.3.2 DISCRIMINATION OF VEGETATION TYPES

Hyperspectral remote sensing has already shown important capabilities to differentiate vegetation types, especially when combined with data from other sensors such as radar that provide concurrent information about forest structure. An example for high-diversity mangrove systems is provided by Held et al. [83]. The study emphasizes the potential of hyperspectral scanners for identifying groups of species occurring under different grades of environmental stress. Provided that every group of species shares an assembly of physiological, anatomical, and ecological characteristics that allows survival under particular conditions, the differences among such groups

should be detected by hyperspectral sensors facilitating the discrimination of plant functional groups.

In mangrove ecosystems, gradients in salinity, tide action, and drainage often cause major differentiation in species composition and structure across a linear spatial arrangement from the water edge to inland. Thus, high-diversity mangrove systems can contain up to 30 different species, broadly segmented into “mangrove zones” [83]. In order to describe these ecosystems accurately and objectively in terms of their zonation, productivity, and diversity patterns, Held et al. [83] conducted an analysis combining high spatial (3-m pixels or less) and spectral resolutions by using SAR (synthetic aperture radar) and the airborne hyperspectral scanner CASI (compact airborne spectrographic imager).

Although SAR data separated the vegetation into its general structural groups quite well, it had difficulty discriminating any further detail; thus, the SAR-only analysis correctly classified 57.9% of the mangrove types. The CASI-only data, on the other hand, provided finer detail but exhibited considerable confusion between structurally different vegetation classes—specifically, between the sand-dune vegetation and mixed stands of the plant *Bruguiera* sp. The CASI-only analysis classified 71% of the mangrove types present in the subset. However, when the data from both sensors were considered together, the classification accuracy increased to 76%. There are only a few cases where mangrove types have been classified at this level of detail within an individual estuary. This study, therefore, showed that there is considerable scope in use of high-resolution hyperspectral data for detecting, mapping, and monitoring mangroves at the necessary level of detail for mangrove diversity, ecological, and even ecophysiological studies. This study also shows the potential of a combination of remote sensing techniques for increasing the level of accuracy in the detection of vegetation types.

### 2.3.3 LIFE FORM DISCRIMINATION

A specific case attempting to discriminate between species with different biochemical properties and ecological traits with hyperspectral data is the study of Castro-Esau et al. [68]. The objective of this study was to determine if it is possible to distinguish between lianas and supporting trees, at the leaf level, using hyperspectral reflectance measurements taken for two communities of tropical liana/tree species from a tropical dry forest (Parque Natural Metropolitano, Panama) and from a tropical wet forest (Fort Sherman, Panama). The study showed that lianas and trees from the tropical dry forest are distinguishable based on their spectral reflectance at the leaf level with the use of pattern recognition techniques. It is suggested that the chlorophyll concentration of liana leaves is lower than for tree leaves and that this difference is highly significant, resulting in an increase in reflectance at 550 nm as liana quantity/coverage increases.

Differing levels of water or nutrient stress (i.e., nitrogen) between lianas and trees could also have induced the differences observed in leaf reflectance between lianas and trees, and/or possibly differences in photosynthetic capacity between the two structural groups. Indeed, lianas typically were forming monolayers above tree crowns, favoring high light interception and low light transmission. Trees, in

contrast, favor greater light transmission [68]. According to the authors, further study is required to clarify the physiological mechanisms between the two groups and whether such differences are maintained throughout the year. It must be emphasized, however, that in this case hyperspectral data effectively reflected general physiological differences between species with different ecological traits. Information produced in this respect could be useful for mapping species or communities with applications in biodiversity assessment studies. Indeed, mapping of lianas would be helpful for carbon budgets' estimation, because carbon sequestration is impeded in areas where liana proliferation obstructs tree regeneration to the point, in some cases, that a net release of  $\text{CO}_2$  can be measured for some tropical forests [84,85].

### 2.3.4 DISCRIMINATION OF BIOPHYSICAL PROPERTIES

Hyperspectral remote sensing has proven to be useful in distinguishing biophysical properties of tropical forests, which usually differ among vegetation types. Kalacska et al. [79], for instance, examined forest structure and biodiversity of tropical dry forest from satellite imagery. They addressed the inference of neotropical dry forest biophysical characteristics (i.e., structure), biomass, and species richness directly from hyperspectral remote sensing imagery acquired over three seasons: wet, transition, and dry. They also examined six narrowband spectral vegetation indices that were sensitive to canopy characteristics in other ecosystems: normalized difference vegetation index (ND705), canopy normalized difference vegetation index (NDcanopy), single ratio (SR705), canopy single ratio (SRcanopy), modified single ratio (MSR), and canopy structure index (CSI). The results of this study showed that all canopy characteristics share similarities in shortwave infrared, except for biomass, which had important spectral regions in the visible, near infrared, and shortwave infrared. In addition, for species richness, the shortwave infrared was also heavily favored with the exception of one wavelength from the visible.

In contrast, for canopy height, basal area, and the Holdridge complexity index (HCI), none of the wavelengths were from the visible range, but instead all wavelengths were from the near infrared and shortwave infrared (743–2257 nm). Differences in canopy openness and structure among seasons were considered the most important factor in predicting biomass. According to the authors, low-canopy leaf area index (LAI) observed in the dry season exposed woody material, leaf litter, and soil with minimal to no contribution from green leaves, accounting then for the importance of the shortwave- and near-infrared regions. The intermediate stage had an important contribution of woody material and dry leaves, of less importance of the soil and green leaves; while in the late stage the green leaf was an important contribution to the spectral response in the visible region of the spectrum.

These studies provide new techniques to identify groups of species with functional differences by their particular biophysical properties, especially when such differences are reflected at the phenological level. In this sense, hyperspectral technology would allow for more accurate quantification of forest biophysical and biochemical attributes, which is essential for biodiversity assessment, land cover characterization, biomass modeling, and carbon flux estimation [86].

## 2.4 HYPERSPECTRAL REMOTE SENSING AND FUNCTIONAL GROUP STUDIES: PRESENT AND FUTURE APPROACHES

The capability of hyperspectral remote sensing to discriminate among plant functional groups has already been explored directly or indirectly, as mentioned in the previous section. However, such a discriminatory capability has several potential applications that have not been properly explored at present in the tropics: for example, differentiation of land vegetation/forest types, carbon flux estimates, description of ecosystem status, and assessment of vegetation functional changes, among others. Now we will briefly explain some of these potential applications in order to present a general view of future approaches for studies on tropical vegetation.

### 2.4.1 VEGETATION TYPE DISCRIMINATION ON TROPICAL LAND VEGETATION

Vegetation surveys in tropical forests are difficult and time consuming because plant species diversity is extremely high, their taxonomy is known only by a few specialists, and remote areas are logistically difficult to work in. As a result, it is difficult to collect field data that cover the area of interest sufficiently [87]. Remote sensing data are then an alternative technique that could be applied for separating vegetation types [88].

Provided that tree species composition is related to soil differences [89], spectral characteristics may behave similarly because they are mostly determined by the forest canopy. For example, Salovaara et al. [87] were able to separate floristically defined terra firma forest classes in Amazonia from Landsat ETM+ images with a reasonable accuracy. On the other hand, inundated and noninundated forests have been mapped and discriminated with high accuracy by Hess et al. [90]. Hyperspectral data, however, could help discern unique spectral patterns of different vegetation types and could be useful in extracting biophysical information such as biomass. These data will then be extremely useful for vegetation studies since they can contribute to tropical functional group differentiation. Indeed, hyperspectral remote sensing would be especially helpful for this purpose in complex tropical rain forests, where the distribution patterns of individual species are poorly known and a high level of accuracy is required. This type of datum could additionally offer valuable information for sustainable resource use and biodiversity conservation, where vegetation types can be used as surrogates for modeling the distributions of species and communities [91].

### 2.4.2 CARBON FLUX ESTIMATIONS

Globally, terrestrial vegetation sequesters some 100 Pg of carbon from the atmosphere each year for the production of organic matter through photosynthesis, half of which occurs in the tropics. The role of the various major forest ecosystems in the carbon cycle must therefore be assessed, particularly as carbon sinks that may be managed to reduce the atmospheric carbon load. Currently, attention is focused on tropical forests, which cover 7% of the Earth's land surface, playing a major but poorly understood role in the cycling of carbon [92].

Many studies have used remote sensing analysis to discriminate between mature tropical forest and nonforest areas [93] because monitoring of secondary forest



regrowth may be important in the carbon balance of the tropics. Tropical secondary forests that follow nonforested stages have the facility to decrease atmospheric carbon concentrations to some degree in relatively short periods of time [94]. Recent special attention to tropical secondary forests may then be attributed to their capacity to act as carbon sinks and their potential role to serve as regulators of climate change. A secondary forest may actually have higher net primary production than a mature forest and may rapidly sequester carbon from the atmosphere, converting it to biomass. The strength of this carbon sink and the size of the resulting carbon pool depend on a range of factors, such as species composition and, remarkably, on the age of the regenerating forest [95]. Thus, to understand the role of regenerating forests as carbon sinks, information about their age, species composition, location, and extent is required. The most feasible way to derive this information is through remote sensing [92].

In order to analyze the progress and future potential of research to monitor carbon sequestration, Castro-Esau, Sanchez-Azofeifa, and Rivard [96] reviewed the attempts for estimating secondary forest biomass from space-borne data in the neotropics. This review states that considerable progress has been made in classifying neotropical secondary forests according to age using Landsat TM data. Currently, most Landsat TM studies of secondary forests have separated few broad regrowth classes of fairly young age (usually up to 20 years old or less) and with varying degrees of accuracy. The majority of studies analyzed have involved multitemporal images of sites in the Brazilian Amazon. Foody et al. [92], for instance, investigated ability of Landsat TM data to identify different successional stages of tropical rain forest in Amazonia. A range of forest classes (11) varying in strength as carbon sinks was identified accurately from these data. Their results also indicated that the youngest age class may be more variable in composition and spectral response than the older forest. This could be a function of a range of successional pathways being followed.

These results demonstrated that it is possible to use image classifications to scale up point measurements of carbon flux between regenerating forest classes and atmosphere over large areas. Moreover, the dynamics of the forest succession was to some extent manifested in the remotely sensed data. Castro-Esau et al. [96] stated that, although much research is required, it is possible that accurate classification of secondary forests in tropical areas will necessitate the use of imagery with higher spectral resolution (i.e., hyperspectral data) from which unique spectral signatures (i.e., for certain common crops) might be determined for their distinction from secondary forests. Furthermore, the capability of hyperspectral remote sensing to discriminate the dominant species within a regenerating forest would refine carbon accounting models, increasing classification accuracy of regeneration stages. Hyperspectral remote sensing could then be used to classify regenerating tropical forest classes accurately and even to identify different successional pathways.

Hyperspectral data will also be especially useful in highly heterogeneous sites, where pixels with mixed classes would be abundant and an entire area of interest with secondary forests of varying ages might occupy only a few pixels [96]. However, we must consider that the use of only hyperspectral data could eventually fail when discriminating different secondary forests, especially when dealing with highly homogeneous areas. An example of such limitation is the study performed by

Lucas et al. [97], who made the first attempt at mapping tropical forest regeneration stages using only hyperspectral data in the Brazilian Amazon and failed to obtain an acceptable level of accuracy for further estimation of biomass and carbon accumulation rates. Thus, the combination of hyperspectral imagery with data from other sensors is recommended. The integration of Landsat TM data with selected Hyperion scenes, for instance, may be useful for the separation of secondary forests from land cover types that have appeared spectrally similar [96]. Nonetheless, the determination of secondary forest biomass content from remote sensing data with greater precision would provide a better understanding of the role of secondary forests in global biogeochemical cycles as well as of their potential for mitigating atmospheric carbon [96].

### 2.4.3 DIRECT DETECTION OF PLANT FUNCTIONAL TYPES

Hyperspectral data have directly been used to discriminate plant functional types in nontropical zones. Studies carried out by Schmidlein and Sassin [98] used hyperspectral remote sensing to analyze gradual floristic differences difficult to assess by conventional field surveys. They ranked species according to their functional responses and successfully modeled gradients in the appearance of plant functional response groups. These modeled gradients served to map species distributions. The results from this study indicate the potential of hyperspectral remote sensing and gradient analysis for mapping of continuous gradients in species assemblages. Of course, longer-term work with multitemporal data is needed to determine whether the approach can become a useful supplement to ground surveys. Such investigation must also be performed in the tropics in order to analyze functional diversity.

A specific attempt to discriminate tropical plant functional groups is currently being performed in a Mexican tropical dry forest by the authors. In order to identify and characterize secondary forest we are determining functional groups of plant species from different successional stages in the tropical dry forest of Chamela, a highly diverse tropical system located on the Pacific coast of Mexico. To define functional groups we decided to evaluate different morphological and physiological attributes highly involved in resource acquisition mechanisms, such as maximum photosynthesis, leaf dynamics, relative growth rate, and various leaf traits (specific leaf area, blade shape, thickness, water content, and chlorophyll content).

Preliminary results suggest that attributes such as water content, photosynthesis, specific leaf area, and chlorophyll content account for a substantial part of the functional differences observed among species from different successional stages, as well as among individuals of the same species growing in different stages. The phylogenetic origin of species appears to be an important factor for the variability of functional traits among evaluated stages. However, species growing in the different successional stages showed important differences in such traits, providing evidence of the response of certain functional traits to specific environmental factors associated with successional change. Variability of evaluated functional traits must be reflected at the spectral level, as demonstrated by Castro-Esau et al. [72]. Thus, by relating these attributes to the spectral reflectance of each species, we will be able to recognize the different types of secondary tropical dry forests (successional stages)

by hyperspectral remote sensing. This kind of information is crucial for the understanding of the natural regeneration process as well as to determine the area covered by secondary vegetation in the tropics.

#### **2.4.4 CHANGES IN FUNCTIONAL PROPERTIES OF ECOSYSTEMS**

As mentioned previously, remote sensing can provide accurate estimates of functional features of tropical forests. Studies assessing changes in functional properties of the tropics by using remote sensing have been performed with coarse-resolution imagery by Koltunov et al. [99]. Provided that changes in forest function can be expressed as changes in forest phenology, these changes can be detected via remote sensing. Koltunov et al. used MODIS imagery to show that removal of timber species during selective logging changes forest composition and structure. Imagery analysis showed changes sufficiently large in magnitude to alter biosphere–atmosphere exchange of CO<sub>2</sub>, water vapor, and energy in the logged regions of the Amazon basin. These changes could, in turn, alter a range of biogeochemical processes in the region and may have cascading effects on the regional climate system.

In the same sense, in order to understand canopy gap dynamics following selective logging, Asner et al. [100] used a spectral mixture analysis of the Landsat ETM data to estimate damage as well as to monitor intensity and canopy closure following timber harvests in eastern Amazon forests. They evaluated the impacts of different kinds of logging in terms of the canopy gap formations and showed that approximately one-half of the canopy opening caused by logging is closed within 1 year of regrowth following timber harvests. As stated by Asner et al., forest canopy damage monitored by remote sensing has several applications at the regional level—for example, to predict the location of fire-prone sites and respiration hotspots likely to result from coarse woody debris and damaged roots. Spatial and temporal dynamics of faunal species can also be linked to forest disturbance. Thus, an understanding of the components of canopy recovery will be important both for carbon balance as well as for other ecological and biogeochemical functions of the system [100]. These findings highlight the need for using higher resolution data to carry out a detailed analysis of the consequences of selective logging or other anthropogenic disturbances that may cause changes in the functional properties of tropical systems.

## **2.5 CONCLUSIONS**

The current conservation status of tropical forests demands systematic approaches to study functional diversity. Such approaches must focus on the discrimination of coherent (consistent) plant functional groups as representative as possible of the great diversity of these systems. Assemblages of ecophysiological characteristics are considered of great utility to characterize tropical functional groups. These characteristics are susceptible to being detected and analyzed with modern techniques such as hyperspectral remote sensing, which allows for studying vegetation at a landscape level. At present, the capability of hyperspectral remote sensing to detect anatomical, biochemical, and biophysical properties of vegetation has been applied to tropical forests to discriminate successional stages, structural characteristics, life

forms, and vegetation types, among others. Thus, the high accuracy and discriminatory capability of this technique on the detection of information of ecological relevance could be used for the discrimination of plant functional groups in the tropics. Such an approach would generate valuable knowledge about tropical functional diversity, would constitute a powerful tool for the study of forest dynamics, and would contribute to our understanding of the responses of tropical vegetation to human disturbance and climatic change.

## REFERENCES

1. Cummins, K.W., Structure and function of stream ecosystems, *Bioscience*, 24, 631, 1974.
2. Lavorel, S. and Garnier, E., Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail, *Functional Ecology*, 16, 545, 2002.
3. Lavorel, S., McIntyre, S., Landsberg, J., et al., Plant functional classifications: From general groups to specific groups based on response to disturbance, *Trends in Ecology and Evolution*, 12, 474, 1997.
4. Blondel, J., Guilds or functional groups: Does it matter? *Oikos*, 100, 223, 2003.
5. Naeem, S., Species redundancy and ecosystem reliability, *Conservation Biology*, 12, 39, 1998.
6. Reich, P.B., Wright, I.J., Cavender-Bares, J., et al., The evolution of plant functional variations: Traits, spectra and strategies, *International Journal of Plant Science*, 164, S143, 2003.
7. Cramer, W., Using plant functional types in a global vegetation model, in *Plant functional types: their relevance to ecosystem properties and global change*, T.M. Smith, H.H. Shugart, and F.I. Woodward, eds. Cambridge University Press, Cambridge, 1997, 271.
8. Leemans, R., The use of plant functional type classifications to model global land cover and simulate the interactions between the terrestrial biosphere and the atmosphere, in *Plant functional types*, T. Smith, H. Shugart, and F. Woodward, eds. Cambridge University Press, Cambridge, 1997, 289.
9. Bugmann, H., Functional types of trees in temperate and boreal forests: Classification and testing, *Journal of Vegetation Science*, 7, 359, 1996.
10. Grime, J.P., Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory, *American Naturalist*, 111, 1169, 1977.
11. Pearcy, R.W. and Ehleringer, J., Comparative ecophysiology of C3 and C4 plants, *Plant Cell and Environment*, 7, 1, 1984.
12. Garnier, E., Growth analysis of congeneric annual and perennial grass species, *Journal of Ecology*, 80, 665, 1992.
13. Craine, J.M., Tilman, D., Wedin, D., et al., Functional traits, productivity and effects on nitrogen cycling of 33 grassland species, *Functional Ecology*, 16, 563, 2002.
14. Ackerly, D.D. and Monson, R.K., Waking the sleeping giant: The evolutionary foundations of plant function, *International Journal of Plant Sciences*, 164(suppl), S1, 2003.
15. Ellis, A.R., Hubbell, S.P., and Potvin, C., In situ field measurements of photosynthetic rates of tropical tree species: A test of the functional group hypothesis, *Canadian Journal of Botany*, 78, 1336, 2000.
16. Foster, T.E. and Brooks, J.R., Functional groups based on leaf physiology: Are they spatially and temporally robust? *Oecologia*, 144, 337, 2005.
17. Westoby, M., A leaf-height-seed (Lhs) plant ecology strategy scheme, *Plant Soil*, 199, 213, 1998.

18. Mulkey, S.S., Wright, S.J., and Smith, A.P., Comparative physiology and demography of three neotropical shrubs: Alternative shade-adaptive character syndromes, *Oecologia*, 96, 526, 1993.
19. Groombridge, B. et al., *Global biodiversity: Status of the Earth's living resources: a report*. Chapman & Hall, London, 1992.
20. Clark, D.B. and Clark, D.B., Assessing the growth of tropical rain forest trees: Issues for forest modeling and management, *Ecological Applications*, 9, 981, 1999.
21. Borchert, R., Soil and stem water storage determine phenology and distribution of tropical dry forest trees, *Ecology*, 75, 1437, 1994.
22. Borchert, R., Rivera, G., and Hagnauer, W., Modification of vegetative phenology in a tropical semideciduous forest by abnormal drought and rain, *Biotropica*, 34, 27, 2002.
23. Souza, G., Ribeiro, R., Santos, M., et al., Functional groups of forest succession as dissipative structures: An applied study, *Brazilian Journal of Biology*, 64, 3, 2004.
24. Velaquez-Rosas, N., Meave, J., and Vazquez-Santana, S., Elevational variation of leaf traits in montane rain forest tree species at La Chinantla, Southern Mexico, *Biotropica*, 34, 534, 2002.
25. Sanchez-Azofeifa, G.A., Quesada, M., Rodriguez, J., et al., Research priorities for neotropical dry forests, *Biotropica*, 37, 477, 2005.
26. Davis, A.J., Liu, W.C., Perner, J. et al., Reliability characteristics of natural functional group interaction webs, *Evolutionary Ecology Research*, 6, 1145, 2004.
27. Fonseca, C.R. and Ganade, G., Species functional redundancy, random extinctions and the stability of ecosystems, *The Journal of Ecology*, 89, 118, 2001.
28. Gillison, A.N. and Carpenter, G., A generic plant functional attribute set and grammar for dynamic vegetation description and analysis, *Functional Ecology*, 111, 1169, 1997.
29. Colassanti, R.L., Hunt, R., and Askew, A.P., A self-assembling model of resource dynamics and plant growth incorporating plant functional types, *Functional Ecology*, 15, 676, 2001.
30. Eviner, V.T. and Chapin, F.S., Functional matrix: A conceptual framework for predicting multiple plant effects on ecosystem processes, *Annual Review of Ecology and Systematics*, 34, 455, 2003.
31. Coomes, D.A. and Grubb, P.J., Colonization, tolerance, competition and seed-size variation within functional groups, *Trends in Ecology and Evolution*, 18, 283, 2003.
32. Reich, P.B., Ellsworth, D.S., and Walters, M.B., Leaf structure (specific leaf area) modulates photosynthesis-nitrogen relations: Evidence from within and across species and functional groups, *Functional Ecology*, 12, 948, 1998.
33. Reich, P.B., Walters, M.B., Ellsworth, D.S., et al., Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: A test across biomes and functional groups, *Oecologia*, 114, 471, 1998.
34. Wright, I.J., Clifford, H.T., Kidson, R., et al., A survey of seed and seedling characters in 1744 Australian dicotyledon species: Cross-species trait correlations and correlated trait-shifts within evolutionary lineages, *Biological Journal of the Linnean Society*, 69, 521, 2000.
35. Poorter, H. and Navas, M.L., Plant growth and competition at elevated CO<sub>2</sub>: On winners, losers and functional groups, *New Phytologist*, 157, 175, 2003.
36. Diaz, S., McIntyre, S., Lavorel, S., et al., Does hairiness matter in Harare? Resolving controversy in global comparisons of plant trait responses to ecosystem disturbance, *New Phytologist*, 154, 7, 2002.
37. Wardle, D.A., Bonner, K.I., and Barker, G.M., Stability of ecosystem properties in response to aboveground functional group richness and composition, *Oikos*, 89, 11, 2000.
38. Walker, B.H., Biodiversity and ecological redundancy, *Conservation Biology*, 6, 18, 1992.
39. Petchey, O.L. and Gaston, K.J., Extinction and the loss of functional diversity, *Proceedings of the Royal Society of London*, 269, 1721, 2002.

40. Petchey, O.L. and Gaston, K.J., Functional diversity (FD), species richness and community composition, *Proceedings of the Royal Society of London Series B-Biological Sciences, Ecology Letters*, 5, 402, 2002.
41. Shugart, H.H., Plant and ecosystem functional types, in *Plant functional types: their relevance to ecosystem properties and global change*. T.M. Smith, H.H. Shugart, and F.I. Woodward, eds. Cambridge University Press, Cambridge, 1997, 20.
42. Whitmore, T.C., Canopy gaps and the two major groups of forest trees, *Ecology*, 70, 536, 1989.
43. Slik, J.W.F., Assessing tropical lowland forest disturbance using plant morphological and ecological attributes, *Forest Ecology and Management*, 205, 241, 2005.
44. Condit, R., Hubbell, S.P., and Foster, R.B., Assessing the response of plant functional types to climatic change in tropical forests, *Journal of Vegetation Science*, 7, 405, 1996.
45. Denslow, J., Functional group diversity and responses to disturbances, in *Biodiversity and ecosystem processes in tropical forests*, G.H. Orians, R. Dirzo, and J.H. Cushman, eds. Springer, Berlin, 1996, 127.
46. Swaine, M.D. and Whitmore, T.C., On the definition of ecological species groups in tropical rain forests, *Vegetatio*, 75, 81, 1998.
47. Host, G.E. and Pregitzer, K.S., Ecological species groups for upland forest ecosystems of northwestern Lower Michigan, *Forest Ecology and Management*, 43, 87, 1991.
48. Kohler, P., Ditzer, T., and Huth, A., Concepts for the aggregation of tropical tree species into functional types and the application to Sabah's lowland rain forests, *Journal of Tropical Ecology*, 16, 591, 2000.
49. Vanclay, J., Aggregating tree species to develop diameter increment equations for tropical rain forest, *Forest Ecology and Management*, 42, 143, 1991.
50. Lieberman, D., Lieberman, M., Hartshorn, G., et al., Growth rates and age-size relationships of tropical wet forest trees in Costa Rica, *Journal of Tropical Ecology*, 1, 97, 1985.
51. Riddoch, I., Grace, J., Fasehun, F.E., et al., Photosynthesis and successional status of seedlings in a tropical semideciduous rain forest in Nigeria, *The Journal of Ecology*, 97, 39, 1991.
52. Bonal, D., Sabatier, D., Montpied, P., et al., Interspecific variability of delta C-13 among trees in rainforests of French Guiana: Functional groups and canopy integration, *Oecologia*, 124, 454, 2000.
53. Guehl, J.M., Domenach, A.M., Bureau, M., et al., Functional diversity in an Amazonian rainforest of French Guyana: A dual isotope approach (delta N-15 and delta C-13), *Oecologia*, 116, 316, 1998.
54. Metzger, J.P., Tree functional group richness and landscape structure in a Brazilian tropical fragmented landscape, *Ecological Applications*, 21, 1147, 2000.
55. Chazdon, R.L., Careaga, S., Webb, C., et al., Community and phylogenetic structure of reproductive traits of woody species in wet tropical forests, *Ecological Monographs*, 73, 331, 2003.
56. Horvitz, C.C., Pascarella, J.B., McMann, S., et al., Functional roles of invasive non indigenous plants in hurricane-affected subtropical hardwood forests, *Ecological Applications*, 8, 947, 1998.
57. Kalacska, M., Sanchez-Azofeifa, G.A., Calvo-Alvarado, J., et al., Species composition, similarity and diversity in three successional stages of a seasonally dry tropical forest, *Forest Ecology and Management*, 200, 227, 2004.
58. Sanchez-Azofeifa, G.A., Castro, K., Rivard, B., et al., Remote sensing research priorities in tropical dry forest environments, *Biotropica*, 35, 134, 2003.
59. Lambers, H. and Poorter, H., Inherent variation in growth rate between higher plants: A search for physiological causes and ecological consequences, *Advances in Ecological Research*, 23, 187, 1992.

60. Gentry, A.H., Changes in plant community diversity and floristic composition on environmental and geographical gradients, *Annals of the Missouri Botanical Garden*, 75, 1, 1988.
61. Murphy, P.G. and Lugo, A. E., Ecology of tropical dry forest, *Annual Review of Ecology and Systematics*, 17, 67, 1986.
62. Gliessman, S.R., Engles, E., and Krieger, R., *Agroecology: Ecological processes in sustainable agriculture*. Ann Arbor Press, Chelsea, MI, 1998.
63. Nobel, P.S., *Physicochemical and environmental plant physiology*, 3rd ed. Academic Press/Elsevier, New York, 2005.
64. Molina, L.T. and Molina, M.J., Absolute absorption cross sections of ozone in the 185- to 350-nm wavelength range, *Journal of Geophysical Research-Atmospheres*, 91, 14501, 1986.
65. Field, C.B., Ball, J.T., and Berry, J.A., Photosynthesis: Principles and field techniques, in *Plant physiological ecology: Field methods and instrumentation*, R.W. Pearcy, J. Ehleringer, H.A. Mooney, et al., eds. Chapman & Hall, London, 1989, 209.
66. Condon, E.U., Molecular optics, in *Handbook of physics*, E.U. Condon and H. Odishaw, eds. McGraw Hill, NY, 1958.
67. Gates, D.M., Keegan, H.J., Schleter, J.C., et al., Spectral properties of plants, *Applied Optics*, 4, 11, 1965.
68. Castro-Esau, K.L., Sanchez-Azofeifa, G.A., and Caelli, T., Discrimination of lianas and trees with leaf-level hyperspectral data, *Remote Sensing of Environment*, 90, 353, 2004.
69. Nobel, P.S. and De la Barrera, E., Nitrogen relations for net CO<sub>2</sub> uptake by the cultivated hemiepiphytic cactus, *Hylocereus undatus*, *Scientia Horticulturae*, 96, 281, 2002.
70. Taiz, L. and Zeiger, E., *Plant physiology*, 3rd ed. Sinauer Associates, Sunderland, MA, 2002.
71. Hunt, J.E.R., Rock, B.N., and Nobel, P.S., Measurement of leaf relative water content by infrared reflectance, *Remote Sensing of Environment*, 22, 429, 1987.
72. Castro-Esau, K.L., Sanchez-Azofeifa, G.A., Rivard, B., et al., Variability in leaf optical properties of Mesoamerican trees and the potential for species classification, *American Journal of Botany*, 93, 517, 2006.
73. Short, N. Hyperspectral imaging, in *Remote sensing tutorial*. 2003 [cited; available from <http://rst.gsfc.nasa.gov/Front/tofc.html>.NASA].
74. Blackburn, G.A., Relationships between spectral reflectance and pigment concentrations in stacks of deciduous broadleaves, *Remote Sensing of Environment*, 70, 224, 1999.
75. Elvidge, C.D. and Chen, Z.K., Comparison of broadband and narrowband red and near-infrared vegetation indices, *Remote Sensing of Environment*, 54, 38, 1995.
76. Thenkabail, P.S., Enclona, E.A., Ashton, M.S., et al., Hyperion, IKONOS, ALI, and ETM+ sensors in the study of African rainforests, *Remote Sensing of Environment*, 90, 23, 2004.
77. Thenkabail, P.S., Smith, R.B., and De Pauw, E., Hyperspectral vegetation indices and their relationships with agricultural crop characteristics, *Remote Sensing of Environment*, 71, 158, 2000.
78. Lee, K.S., Cohen, W.B., Kennedy, R.E., et al., Hyperspectral versus multispectral data for estimating leaf area index in four different biomes, *Remote Sensing of Environment*, 91, 508, 2004.
79. Kalacska, M., Sanchez-Azofeifa, G.A., Rivard, B., et al., Ecological fingerprinting of ecosystem succession: Estimating secondary tropical dry forest structure and diversity using imaging spectroscopy, *Remote Sensing of Environment*, 108, 82, 2007.
80. Food and Agricultural Organization (FAO), *Global forest resources assessment*. FAO of the United Nations, Rome, 2001.
81. Steininger, M., Satellite estimation of tropical secondary forest aboveground biomass: Data from Brazil and Bolivia, *International Journal of Remote Sensing*, 21, 1139, 2000.

82. Thenkabail, P.S., Smith, R.B., and De Pauw, E., Evaluation of narrowband and broadband vegetation indices for determining optimal hyperspectral wavebands for agricultural crop characterization, *Photogrammetric Engineering and Remote Sensing*, 68, 607, 2002.
83. Held, A., Ticehurst, C., Lyburner, L., et al., High resolution mapping of tropical mangrove ecosystems using hyperspectral and radar remote sensing, *International Journal of Remote Sensing*, 24, 2739, 2003.
84. Schnitzer, S.A. and Bongers, F., The ecology of lianas and their role in forests, *Trends in Ecology and Evolution*, 17, 223, 2002.
85. Korner, C., Slow in, rapid out-carbon flux studies and Kyoto targets, *Science*, 300, 1242, 2003.
86. Blackburn, G.A. and Milton, E.J., Seasonal variations in the spectral reflectance of deciduous tree canopies, *International Journal of Remote Sensing*, 16, 709, 1995.
87. Salovaara, K.J., Thessler, S., Malik, R.N., et al., Classification of Amazonian primary rain forest vegetation using Landsat ETM+ satellite imagery, *Remote Sensing of Environment*, 97, 39, 2005.
88. Achard, F., Eva, H., and Mayaux, P., Tropical forest mapping from coarse spatial resolution satellite data: Production and accuracy assessment issues, *International Journal of Remote Sensing*, 22, 2741, 2001.
89. Clark, D.B., Clark, D.A., and Read, J.M., Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest, *Journal of Ecology*, 86, 101, 1998.
90. Hess, L.L., Melack, J.M., Novo, E.M.L.M., et al., Dual-season mapping of wetland inundation and vegetation for the central Amazon basin, *Remote Sensing of Environment*, 87, 404, 2003.
91. Foody, G.M., Remote sensing of tropical forest environments: Towards the monitoring of environmental resources for sustainable development, *International Journal of Remote Sensing*, 24, 4035, 2003.
92. Foody, G.M., Palubinskas, G., Lucas, R.M., et al., Identifying terrestrial carbon sinks: Classification of successional stages in regenerating tropical forest from Landsat TM data, *Remote Sensing of Environment*, 55, 205, 1996.
93. Alves, D., Meira Filho, L., d'Alge, J., et al., The Amazonia information system, in ISPRS 17 in *ISPRS*, Washington, D.C., 1992.
94. Brown, S. and Lugo, A.E., Tropical secondary forests, *Journal of Tropical Ecology*, 6, 1, 1990.
95. Uhl, C., Buschbacher, R., and Serrao, E.A.S., Abandoned pastures in Eastern Amazonia. I. Patterns of plant succession, *Journal of Ecology*, 76, 663, 1988.
96. Castro-Esau, K., Sanchez-Azofeifa, G.A., and Rivard, B., Monitoring secondary tropical forests using space-borne data: Implications for Central America, *International Journal of Remote Sensing*, 24, 1853, 2003.
97. Lucas, R.M., Honzak, M., Curran, P.J., et al., Mapping the regional extent of tropical forest regeneration stages in the Brazilian legal Amazon using NOAA AVHRR data, *International Journal of Remote Sensing*, 21, 2855, 2000.
98. Schmidtlein, S. and Sassin, J., Mapping of continuous floristic gradients in grasslands using hyperspectral imagery, *Remote Sensing of Environment*, 92, 126, 2004.
99. Koltunov, A., Ustin, S.L., Ashner, G.P., et al., Selective logging changes forest phenology in the Brazilian Amazon, *Proceedings of the National Academy of Sciences*, in press.
100. Asner, G.P., Keller, M., Pereira, R., et al., Canopy damage and recovery after selective logging in Amazonia: Field and satellite studies, *Ecological Applications*, 14, S280, 2004.



## **CAPÍTULO 3**

**La regeneración funcional y la reflectancia espectral arbórea durante la sucesión en un bosque tropical seco altamente diverso.**

**FUNCTIONAL REGENERATION AND SPECTRAL REFLECTANCE  
OF TREES DURING SUCCESSION IN A HIGHLY DIVERSE  
TROPICAL DRY FOREST ECOSYSTEM<sup>1</sup>**

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- *Premise of the study:* The function of most ecosystems has been altered by human activities. To assess the recovery of plant communities, we must evaluate the recovery of plant functional traits. The seasonally dry tropical forest (SDTF), a highly threatened ecosystem, is assumed to recover relatively quickly from disturbance, but an integrated evaluation of recovery in floristic, structural, and functional terms has not been performed. In this study we aimed to (a) compare SDTF plant functional, floristic, and structural change along succession; (b) identify tree functional groups; and (c) explore the spectral properties of different successional stages.
- *Methods:* Across a SDTF successional gradient, we evaluated the change of species composition, vegetation structure, and leaf spectral reflectance and functional traits (related to water use, light acquisition, nutrient conservation, and CO<sub>2</sub> acquisition) of 25 abundant tree species.
- *Key results:* A complete recovery of SDTF takes longer than the time period inferred from floristic or structural data. Plant functional traits changed along succession from those that maximize photoprotection and heat dissipation in early succession, where temperature is an environmental constraint, to those that enhance light acquisition in late succession, where light may be limiting. A spectral indicator of plant photosynthetic performance (photochemical reflectance index) discriminated between early and late succession. This constitutes a foundation for further exploration of remote sensing technologies for studying tropical succession.
- *Conclusions:* A functional approach should be incorporated as a regular descriptor of forest succession because it provides a richer understanding of vegetation dynamics than is offered by either the floristic or structural approach alone.

**Key words:** functional groups; leaf reflectance; photochemical reflectance index (PRI); photosynthesis; plant functional traits; secondary tropical forests; successional stages discrimination.

Most ecosystems have been transformed by human activities that affect their functional performance and that alter the environmental services they provide (Turner et al., 1990; Steffen et al., 2005). However, many biotic communities eventually can recover most of their original properties if they have not

been severely damaged. Plant communities can recover from disturbance through ecological succession, a process that implies sequential changes in the community attributes (i.e., species richness, composition, and diversity) over time (Odum and Barrett, 2005; Chazdon et al., 2007). To assess the recovery of plant communities, an assessment of the changes in plant functional traits along succession is necessary. By using technologies that detect such changes in plant functional traits, we also can develop diagnostic tools for inferring the functional and successional status of different plant communities, facilitating the study of vegetation dynamics. This is especially important for the heavily transformed tropical systems, where functional recovery has been poorly explored.

Today large tracks of mature tropical forests are being supplanted by complex landscapes consisting of a matrix of agricultural fields and forest patches under different levels of succession (Quesada et al., 2009). Consequently, secondary forests can be considered the tropical forests of the future (Wright and Muller-Landau, 2006). Understanding the successional process underlying their natural regeneration has become critical for the development of tropical forest conservation strategies worldwide (Sanchez-Azofeifa et al., 2005).

Despite the high diversity present in seasonally dry tropical forests (SDTF), they are among the most threatened ecosystems of the world, and we need to fully understand their natural regeneration (Murphy and Lugo, 1986; Bullock et al., 1995;

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Quesada and Stoner, 2004; Sanchez-Azofeifa et al., 2005; Quesada et al., 2009). Although it is frequently assumed that SDTF are likely to recover more quickly to a mature state than are wet tropical forests (Ewel, 1977; Murphy and Lugo, 1986; Segura et al., 2003), little empirical evidence supports this assumption (Quesada et al., 2009). In general, literature reports a rapid structural recovery for these systems (i.e., Cecon et al., 2002; Chazdon, 2003; Ruiz et al., 2005; Vieira and Scariot, 2006; Chazdon et al., 2011), but parameters such as species richness and composition frequently lag behind the structural change (basal area [BA] and biomass) (Sheil, 2001; Cecon et al., 2002; Pascarella et al., 2004; Ruiz et al., 2005; Toledo and Salick, 2006; Chazdon et al., 2007; Chazdon, 2008; Quesada et al., 2009).

The SDTF “functional recovery,” however, has not been fully evaluated until now, as no study has simultaneously evaluated and compared SDTF succession in floristic, structural, and functional terms. The SDTF successional theory is then incomplete in relation to its functional component. To characterize this component, we need to describe the corresponding plant functional change (i.e., Lebrija-Trejos et al., 2010) and to identify the plant functional groups of these successional systems. Functional groups are sets of plants that exhibit similar responses to environmental conditions and have similar effects on dominant ecosystem processes (Gitay and Noble, 1997). Identification of these groups can provide an insight into how the ecosystem functions along succession (Diaz et al., 1999). In this context, it is necessary to develop techniques that enable us to obtain large-scale information on SDTF successional dynamics at the rapid pace imposed by the high rates of deforestation. Advanced techniques in remote sensing enable us to detect functional traits, allowing for determination of functional groups at the stand level (Alvarez-Añorve et al., 2008a; Asner and Martin, 2008; Ustin and Gamon, 2010). In the long term, the combination of sensors detecting functional traits and sensors detecting structural aspects of vegetation may provide innovative approaches to increase our understanding of physiological functional performance at regional scales (Asner and Martin, 2009; Ustin and Gamon, 2010). These regional-level studies could constitute a powerful tool for the study of SDTF dynamics (Sanchez-Azofeifa et al., 2005), but they also must be tied to a solid understanding of functional traits at finer scales (Alvarez-Añorve et al., 2008a).

In this study, we contribute to the understanding of SDTF dynamics along succession by functionally characterizing a highly diverse, endemic, and species-rich SDTF successional gradient. Specifically, we aim to (1) provide a preliminary evaluation of the SDTF functional recovery by comparing plant functional change with floristic and structural change along succession, (2) depict plant functional strategies by identifying plant functional groups, and (3) explore the use of remote sensing in the study of SDTF succession by using spectral reflectance data related to the plant functional traits most relevant to discriminating SDTF successional stages.

To characterize functional change and functional groups, we focused on adult trees and selected widely recognized hard and soft ecophysiological traits that are mainly related to radiation and water acquisition or use (Cornelissen et al., 2003), given that these two factors vary greatly with succession and often are negatively correlated across environmental gradients (Niinemets, 2001; Markesteijn and Poorter, 2009). Indeed, Lebrija-Trejos et al. (2010) found that from young to old forests sites of a dry tropical system, environmental gradients exist that

range from open canopy to closed canopy, hot to cool, and dry to moist. Studies regarding among-species variation along water availability and sun exposure gradients (Pillar, 1999; Cornwell and Ackerly, 2009), as well as comparisons between tree species of moist vs. dry tropical forests (Poorter and Markesteijn, 2008; Poorter, 2009), have identified some characteristic functional traits for species occurring in drier and more exposed habitats: as drought stress and light exposure increase, leaf size, leaf area ratio, specific leaf area (SLA), and mass-based leaf nitrogen content tend to decrease, whereas leaf thickness, area-based leaf nitrogen content ( $N_{area}$ ), and the incidence of compound leaves and modified leaf surfaces augmenting leaf reflectance (glaucous, trichomous), tend to increase. These trends probably reduce transpiration and water loss in environments where radiation loads and the water vapor pressure deficit are higher (Poorter, 2009); they also can enhance photosynthetic potential under such conditions (Eamus and Prior, 2001; Niinemets, 2001). If leaf morphological and physiological traits show repeatable trends with environmental conditions on global scales (Cavender-Bares et al., 2004; Wright et al., 2004), we expect that functional change from early to late successional stages of SDTFs occur in the same direction as the trends described previously.

We hypothesize the following. (1) Functional traits related to water and radiation use will probably lead the variation among different successional stages, as has been reported for similar environmental gradients. (2) Consequently, SDTF functional groups will reflect strategies to deal with the most important stresses associated with each successional stage. For example, trees from early succession are expected to increase photo-protective heat dissipation, evaporative cooling, and water conservation capacities as they experience stress by high light, high temperatures, and low water availability due to high evaporative demand. Trees from late succession, in contrast, would enhance light acquisition strategies, as light availability tends to decrease as succession progresses. (3) Because functional properties of vegetation are correlated with optical properties, spectral indices correlated to functional processes most sensitive to environmental change along succession (i.e., photosynthesis) will probably be useful to discriminate between the different successional stages of SDTF.

## MATERIALS AND METHODS

**Study site**—The study was conducted in a SDTF of the Pacific coast of Mexico (state of Jalisco) in the Chamela-Cuixmala Biosphere Reserve (19°22′–19°35′N, 104°56′–105°03′W) and surroundings. Average annual temperature is 24.6°C, and average annual precipitation is 748 mm (<http://www.ibiologia.unam.mx/ebchamela/index.html>). Eighty percent of the annual rainfall occurs between July and October (García-Oliva et al., 1995). This seasonality is tightly related to plant phenology (Borchert, 1994), to above- and belowground productivity (Martínez-Yrizar et al., 1996), and to nutrient cycling (Jaramillo and Sanford, 1995). Variation in soil water availability is thought to be one of the most relevant sources of environmental heterogeneity for plant establishment and growth (Borchert, 1994). The predominant vegetation type is the seasonally dry tropical forest (Rzedowski, 1978). Lott (1993) reports 1120 species of vascular plants in the region. The most abundant family is the Leguminosae (14% of species).

**Chronosequence**—We used a set of study sites of different ages of abandonment, but with similar substrate and land use histories, which allowed inference of the successional process through time (see more details in Avila-Cabadilla et al., 2009). We selected nine 1.1-ha plots that were representative of the local mosaic of forests. These plots corresponded to three successional stages: early, intermediate, and late (5–7, 13–15, and >50 yr of abandonment, respectively).

Early-stage plots were characterized by a greater presence of shrubs and by the permanence of some nonnative grasses. Tallest woody plants averaged 5 m in height. The intermediate and late plots were dominated by trees. In both stages, tallest trees averaged 10 m in height (Avila-Cabadilla et al., 2009). We sampled three plots per successional stage to characterize seral stages. Early and intermediate plots consisted of a quadrat embedded within a matrix of similar vegetation and were distributed around the reserve to generate a research design reasonably balanced. Late forests plots were embedded in the reserve, and consequently, they have not suffered any kind of disturbance for at least 50 yr. Features such as slope (ranging from 15°–30°) and aspect (S, SW, and SE) were homogenized as much as possible to control topographical effects (Maza-Villalobos et al., 2011). Distance from the mature forest (in the case of early and intermediate plots) was equal to or higher than 1000 m. Plots differed in leaf area index or LAI (as measured by LAI-2000 Plant Canopy Analyzer LI-COR, Lincoln, Nebraska, USA, according to protocol in Alvarez-Añorve et al., 2008b); this parameter increased significantly from early to late successional stages ( $F_{(2,6)} = 13.75$ ,  $P = 4.7 \times 10^{-2}$ ). This is consistent with the decrease in vegetation canopy openness from early to late successional sites previously reported for this study system: 22.6–91.1% for early sites, 5.9–32% for intermediate sites, and 5.3–18.7% for late successional sites (Maza-Villalobos et al., 2011).

A vegetation census of all woody individuals above 2.5 cm DBH (diameter at breast height), as well as an assessment of vegetation structural traits such as LAI, stems density (SD), and BA, was conducted in a 50 × 20 m (0.1 ha) subplot at every plot. A total of 200 species corresponding to 48 families were found (Balvanera et al., personal communication). Primary dominant families included the Leguminosae, Euphorbiaceae, and Rubiaceae.

**Species**—We selected the most abundant tree species to include >70% of biomass of each plot in our study. We analyzed 25 tree species corresponding to 20 genera and 13 families (Table 1). Of these 25 species, seven occur in all three stages (“shared”) and 18 in just one given stage (“exclusives”).

**Functional traits**—Provided that different leaf traits/processes can be optimal in different regeneration opportunities (Grubb, 1977), we selected for

TABLE 1. Family, species, and the successional stage (SS) in which the species was evaluated (early, intermediate, late, or in all three stages).

Family	Species	SS
Achatocarpaceae	<i>Achatocarpus gracilis</i> (H. Walt.)	All
Amaranthaceae	<i>Lagrezia monosperma</i> (Rose) Standl.	Late
Anacardiaceae	<i>Spondias purpurea</i> (L.)	All
Apocynaceae	<i>Stemmadenia donnell-smithii</i> (Rose) Woods.	Early
Boraginaceae	<i>Cordia alliodora</i> (Ruiz and Pav.) Oken	All
Ebenaceae	<i>Diospyros aequoris</i> (Standl.)	Late
Euphorbiaceae	<i>Croton niveus</i> (Jacq.)	Late
	<i>Croton pseudoniveus</i> (Lundell)	All
	<i>Croton suberosus</i> (H.B.K.)	Late
	<i>Piranhea mexicana</i> (Standl.)	Intermediate
Fabaceae	<i>Bauhinia subrotundifolia</i> (Cav.)	Early
	<i>Caesalpinia caladenia</i> (Standl.)	Intermediate
	<i>Caesalpinia pulcherrima</i> (Swartz.)	Late
	<i>Erythrina lanata</i> (Rose)	Late
	<i>Lonchocarpus constrictus</i> (Pittier)	Intermediate
	<i>Lonchocarpus eriocarinalis</i> (Micheli)	All
	<i>Lonchocarpus mutans</i> (Sousa)	Late
	<i>Senna atomaria</i> (L.) Irwin and Barneby	Early
Flacourtiaceae	<i>Casearia corymbosa</i> (H.B.K.)	All
Polygonaceae	<i>Coccoloba liebmanni</i> (Lindau)	Early
	<i>Ruprechtia fusca</i> (Fernald)	All
Rubiaceae	<i>Randia thurberi</i> (S. Watson)	Late
Rutaceae	<i>Zanthoxylum fagara</i> (L.)	Intermediate
	<i>Zanthoxylum caribaeum</i> (Lam.)	Intermediate
Sapindaceae	<i>Thouinia paucidentata</i> (Radlk.)	Late

evaluation a set of fundamental leaf traits and processes that (a) strongly influence plant growth and survival, (b) reflect plant physiological responses to a changing environment, and (c) allow for discrimination regarding tropical successional stages (Swaine and Whitmore, 1988; Alvarez-Buylla and Martínez-Ramos, 1992; Westoby et al., 2002; Reich et al., 2003).

Specifically, we evaluated (1) processes related to CO<sub>2</sub> acquisition and use: net photosynthesis ( $A_{\max}$ ) (Evans, 1989); (2) traits/processes related to water use and conservation: leaf water content (LWC, the difference between leaf fresh and dry mass per unit area), transpiration (E), and water use efficiency (WUE, the ratio of  $A_{\max}$  to E) (Reich et al., 2003); (3) traits related to light acquisition and/or heat load regulation: specific leaf area (SLA, leaf area per dry mass) and leaf density [LD, leaf dry mass / (leaf area × leaf thickness)] (Wright et al., 2004); and (4) traits related to nutrient conservation or use: leaf thickness (LT) and leaf fresh mass per unit area (LFM) (Roderick et al., 1999; Garnier et al., 2001; Sims and Gamon, 2002). Several of these traits reflect plant responses in more than one function and can be used as indicators of different survival mechanisms, including physical protection, resistance to drought stress, competitive ability, etc. (Wright et al., 2004).

**Spectral reflectance data**—In addition to sampling the traits listed previously, the photochemical reflectance index (PRI, Gamon et al., 1992) was calculated from leaf reflectance measurements as  $(R_{531} - R_{570}) / (R_{531} + R_{570})$ , where R is the leaf reflectance at the wavelength indicated by the subscript. The PRI provides an indication of relative photosynthetic rates associated with different environmental conditions as it provides a measure of photoprotection and photosystem II (PSII) light use efficiency across species and functional types (Gamon et al., 1992, 1997). In the context of this study, where leaf reflectance was measured in the laboratory after a period in the dark, PRI provides a measure of pigment pool sizes, specifically the relative levels of chlorophyll and carotenoid pigments, which are indicators of photoprotection (Sims and Gamon, 2002; Styliński et al., 2002).

**Data collection**—Leaf collection and measurement were conducted during the rainy season of 3 yr, 2006 to 2008, following standard methods (Cornelissen et al., 2003). At least five adult individuals were selected per species in each plot. To reach the crown, we used a 4-m-long, portable ladder and climbed trees when necessary to collect only sunlit leaves. Per individual, we collected 15–25 fully expanded, sun exposed, mature leaves without herbivore damage. We collected 4800 leaves of 240 individuals in total. Leaves were immediately placed in sealed plastic bags containing moistened paper towels and were transported to the laboratory in a cooler. Maintaining leaf moisture prevents significant changes in leaf reflectance during transport (Foley et al., 2006). Once in the laboratory, we obtained the following measurements for each leaf: (1) spectral reflectance, (2) weight, (3) thickness, and (4) area. Leaf spectral reflectance was analyzed instantly with a VIS/NIR UNISPEC spectral analysis system (PP Systems, Amesbury Massachusetts, USA). Its spectral range is 350–1100 nm, with a sampling interval of 3.3 nm and a spectral resolution of <10 nm. A bifurcated fiber optic delivers light from an internal 7.0 W halogen lamp via one branch and receives reflected light via the other (Castro-Esau et al., 2006). To measure spectral reflectance of leaves, we used a leaf clip that holds the foreoptic at 60° and maintains a 2.3-mm-diameter field of view. Sample reflectance was measured by comparing leaf reflectance to reflectance of a white standard of Spectralon. Ten scans were averaged per recorded spectrum. We measured three different parts of the leaf to capture the potential variation of each leaf, and these three samples were expressed as a single average value for that leaf. Dark scans and white reference scans were performed frequently to detect instrument drift on the spectra. After these measurements were conducted, leaves were weighed to determine fresh mass. Leaf thickness was measured between the major veins by using a digital micrometer (Mitutoyo, Kawasaki, Japan). Leaf area was determined by photographing leaves at a fixed distance of 50 cm. Photographs were analyzed by means of pixel-counting software (Sigma Scan Pro 5; SPSS, 1999). Leaves then were oven dried for 48 h at 70°C and weighed again to determine dry mass.

Gas exchange measurements ( $A_{\max}$  and E) were evaluated in an average of four adult trees per species in each plot. Per tree, we selected 3–5 sun-exposed, mature, and healthy leaves. To reach the crown, we used a portable, 4-m-long ladder, which allowed us to measure the top leaves of trees up to 6 m tall and the outer, lateral (but totally sun-exposed) leaves of taller trees. We measured a total of 800 leaves from 240 individuals. All measurements were recorded between 0900 and 1200 h local time in days with no clouds and with similar climatic conditions. We used a portable gas-exchange system (LI-COR 6400, LI-COR, Nebraska, USA) to measure the photosynthetic rates of selected plants. Measurements were conducted under controlled conditions of light (1500  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) representative of the natural conditions of the system at the hours of optimal plant

photosynthetic performance for the rainy season (Parker et al., 2005). In general, tropical plants reach their maximum photosynthetic capacity between 1000 and 1500  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (Tinoco-Ojanguren and Pearcy, 1992; Ackerly and Bazzaz, 1995; Huante and Rincon, 1998). Reference  $\text{CO}_2$  concentration was set at 400 ppm. We averaged 3–5 sampling measurements per leaf to reduce natural variability and derive a consistent average for each leaf, increasing data reliability.

**Data analysis**—The variables that were not normally distributed were log-transformed to allow for parametric statistical analyses. To incorporate the variation per plot and because the unit of analysis is the species level, individuals were averaged per species and per plot. We use the abbreviation *MSP* (mean per species per plot) to name these averages in the rest of the text. Except when another program is specified, all statistical analyses were performed in R (v.2.12.1, R Development Core Team, 2010).

**Comparison of functionality, vegetation structure, and species composition**—To compare the change in functional traits vs. the change in structure and species composition along the successional gradient (objective 1), we evaluated whether the arrangements of plots from different successional stages in functional terms were similar to the arrangements based on structure and species composition through (1) a principal component analysis (PCA) of the functional traits, (2) a PCA of structural traits (BA, SD, species number, LAI), and (3) a nonmetric multidimensional scaling (NMDS) of the species composition based on a Bray-Curtis similarity matrix of the species. Nonmetric multidimensional scaling is the preferred method to analyze community data because it handles nonlinear species response of any shape (Oksanen, 1983). To compare the three successional stages (early, intermediate, and late) in functional, structural, and floristic terms, the new synthetic variables (axis) derived from these analyses were compared through an analysis of variance (ANOVA) with the scores of the main axis as the response variable and the successional stage as the independent variable. When *F* values revealed significant variation among successional stages, we used Tukey's means separation tests to determine how the stages differed from one another.

**Functional groups**—To determine the functional grouping of the *MSP* (i.e., the aggregation of species based on their functional traits, objective 2), we ran our database through hierarchical clustering analysis using Ward's method (Ward, 1963) on PC-Ord (v.4.01, Mc Cune and Mefford, 1999). To compare the functional groups, we conducted a multivariate ANOVA (MANOVA) in which the functional groups were the independent variable and the set of functional traits the response variable. Then we assessed the performance of functional traits using separate ANOVAs for each trait.

To evaluate whether functional grouping corresponded to phylogenetic aggregation, we constructed a hypothesized phylogenetic tree for our species using Phylomatic, version R20031202, software (Webb and Donoghue, 2005), a phylogenetic database and toolkit for the assembly of phylogenetic trees. We then tested for evidence of phylogenetic signal (i.e., closely related taxa being functionally more similar to one another than they are to distantly related taxa) using PICANTE (Kembel et al., 2010). PICANTE tests for evidence of greater resemblance among closely related lineages: the variance of standardized contrasts across the phylogenetic tree calculated from the actual trait values are compared with a distribution generated from 999 random assignments of the trait values across the tips of the given phylogeny. Polytomies were resolved to provide one contrast. Functional groups were characterized on the basis of the results obtained from all the analyses described here.

**Successional stage discrimination by spectral reflectance data**—From the leaf reflectance spectra, we calculated PRI values to assess whether it was possible to discriminate between successional stages by using a spectral index related to plant photosynthesis and photoprotection (objective 3). Successional stages were compared through ANOVA in which the successional stage was the independent variable and the index values the dependent variable. We used posteriori Tukey tests to perform multiple comparisons between successional stages.

## RESULTS

**Comparison of functionality, vegetation structure, and species composition**—The evaluation of succession in functional terms showed a different perspective from the structural and compositional analysis. The PCA of functional traits (Fig. 1A) showed a clear separation of plots from early and late succession (ES and LS,

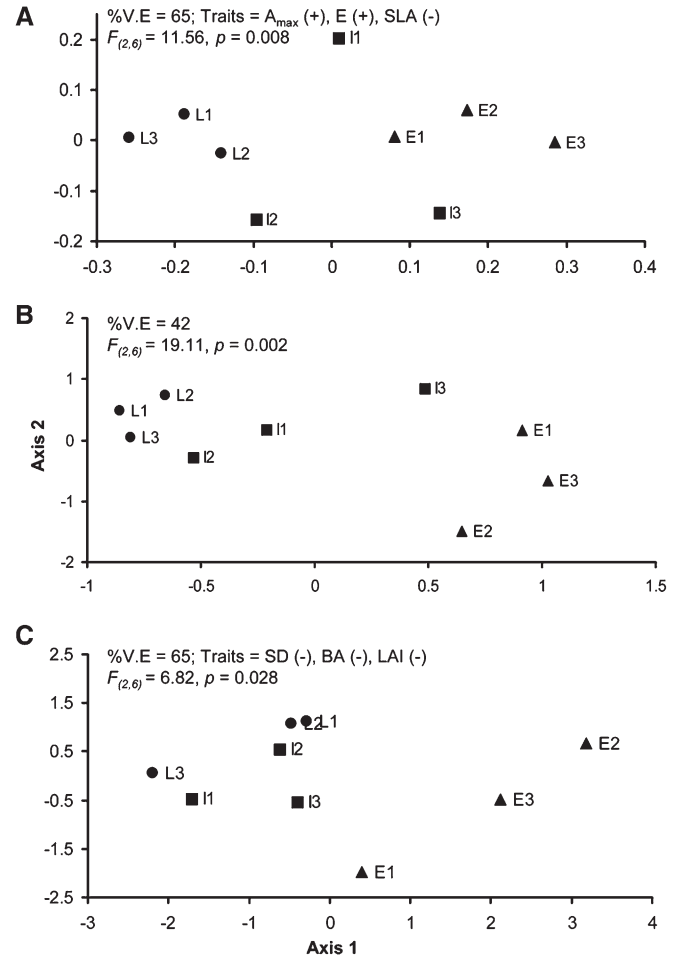


Fig. 1. Ordinations of nine plots from three seasonally dry tropical forest successional stages: (A) principal component analysis (PCA) of functional traits, (B) nonmetric multidimensional scaling in terms of species composition, and (C) PCA of structural traits. Triangles = early succession; squares = intermediate succession; circles = late succession. The following information related to axis 1 is provided: (1) percentage of variance associated with the axis (%V.E); (2) the three traits with the highest loadings (traits) and the relation of each (+ or -) to the axis (note that in B traits loadings are missing because the ordination is based on species, not in traits); and (3) the *F*, degrees of freedom, and *P* values from correspondent ANOVAs.  $A_{\max}$  = maximum net photosynthesis; E = transpiration rate; SLA = specific leaf area; BA = basal area; LAI = leaf area index.

respectively) along axis 1. The LS plots were located to the left side of axis 1, which is related to low levels of  $A_{\max}$  and E as well as to high levels of SLA. The ES and intermediate succession (IS) plots were located preferentially toward the right side of this axis, indicating opposite characteristics to the previous traits. In contrast, NMDS of species composition (stress = 6.19; Fig. 1B) showed a separation between ES and LS–IS plots along axis 1. The PCA of structural traits (Fig. 1C) also showed no clear separation of LS and IS plots along axis 1, whereas ES plots appear separated from the rest toward the right side of axis 1, with lower values of BA, SD, and LAI. According to ANOVA results, the variable (axis) explaining most of the variation in all ordinations was significantly different among successional stages (Fig. 1). With a floristic-structural approach, IS and LS appear to be similar but different from ES, whereas with a functional approach, ES and IS appear to be similar but different from LS (Table 2).

TABLE 2. Differences between successional stages according to post hoc Tukey mean separation test for the different comparisons performed through ANOVA. Successional stages (E = early; I = intermediate; L = late) that do not share a lowercase letter are statistically different from one another. The type of analysis and the ANOVA response variable are indicated. NMDS = nonmetric multidimensional scaling; PCA = principal component analysis.

Analysis	Response variable	Successional stage		
		E	I	L
NMDS of species composition	Axis 1	a	b	b
PCA of structural traits	Axis 1	a	b	b
PCA of functional traits.	Axis 1	a	a	b

**Functional groups**—We identified two functional groups (Fig. 2) significantly different from each other according to MANOVA ( $F_{1,55} = 55$ ,  $P = 9.51 \times 10^{-13}$ ). Group “A” is mainly composed (70%) of individuals from “exclusive” species of ES and IS as well as of individuals of “shared” species growing under such stages. The remnant (30%) corresponds to individuals growing in the LS plots. Group “B” is mainly composed (68%) of most of the “exclusive” species from LS as well as of individuals of shared species growing in this stage. The rest are individuals growing in the ES and IS plots. When the performance of functional traits was evaluated separately, five of them showed significant differences between groups A and B (Fig. 3). Group A includes trees with high  $A_{\max}$ , LD, and E and low SLA and WUE. Group B is characterized by the opposite. Considering the origin of most of the members of a given group and because the functional differences between groups A and B resemble the functional differences between ES–IS and LS, we consider that group A could mostly, but not completely, represent the ES and IS trees, and group B could mostly, but not completely, represent the LS trees. Means and standard errors of traits at the species level are provided in Appendix 1.

The lack of strong phylogenetic signal in our data (Table 3) indicates that functional grouping is not strongly influenced by evolutionary relationships among taxa. This conclusion should, however, be viewed with caution given that with the exception of the Fabaceae, the plant families were represented by four or fewer species. Functional grouping of species appears then to be largely determined by physiological responses to an environmental gradient along succession. Consequently, this functional classification revealed the phenotypic plasticity of certain species whose MSP values were classified in different functional groups when they belonged to different successional stages (e.g., *Achatocarpus gracilis*). There were also less-plastic species whose MSP values were always classified in the same group even when they grew in different successional stages.

**Successional stage discrimination by spectral reflectance data**—The PRI values showed significant differences among the successional stages ( $F_{2,237} = 9.76$ ,  $P = 0.01$ ), as can be inferred from the distribution of the values showed in Fig. 4. Differences occurred mainly between LS vs. ES and IS. Earlier stages exhibited lower PRI values, indicative of greater investment in photoprotective pigments (xanthophylls and carotenes) relative to chlorophyll. Thus, leaves from LS are functionally and spectrally different from leaves of earlier stages. This demonstrates that successional stages could be discriminated by using fundamental functional traits and spectral indices related to them.

## DISCUSSION

Provided that the functional performance of an ecosystem is tightly linked to plant functional traits performance, the assessment of an assembly of functional traits allowed us to characterize the response of SDTF communities to human disturbance. The functional performance of these communities along succession indicates that (1) the full recovery of these forests takes longer than previously thought, (2) plant functional strategies differ among successional communities, and (3) the functional differences of these successional communities are traceable through optical (spectral) indices. This suggests that in the future, we could apply novel remote sensing technology to the study of forest dynamics. In particular, “hyperspectral” remote sensing (with many narrow spectral bands) may be useful in characterizing changing functional traits during succession. However, more work is needed to develop appropriate operational remote sensing methods that facilitate the study of tropical vegetation at scales greater than individual forest stands.

**Comparison of functionality, vegetation structure, and species composition**—Our results show a clear difference between functional, floristic, and structural components of tropical dry forest communities under succession (Fig. 1). In terms of structure and species composition, IS is similar to LS, whereas ES is significantly different from both successional stages. In general, ES shows lower BA, SD, and LAI than IS and LS, which indicates that early successional plots show less vegetation density, less plant cover, and consequently more light availability. From these results it can be inferred that secondary forests 13–15 yr old (IS) have recovered the structural and floristic attributes of older forests. Several studies also have encountered a rapid structural recovery in SDTFs (i.e., Ceccon et al., 2002; Ruiz et al., 2005; Vieira and Scariot, 2006; Chazdon et al., 2007; Chazdon, 2008; Chazdon et al., 2011), reinforcing the idea that this ecosystem is likely to recover quickly to a mature state (Ewel, 1977; Murphy and Lugo, 1986; Segura et al., 2003). According to our results, however, IS is different from LS but similar to ES in functional terms, suggesting that the recovery of plant functional traits can be slower than the recovery of structural traits. Consequently, the evaluation of functionality in SDTF succession is necessary to understand the resilience of these tropical systems. Assessment of specific functional traits would indicate when a given ecosystem function returns to its original state (Guariguata and Ostertag, 2001). The accurate characterization of the functional status of secondary forests also is useful in terms of forest management for social (i.e., provision of environmental services) and conservation goals (i.e., quality of the habitat) (Quesada et al., 2009).

The functional differences encountered among successional stages indicate that SDTF species respond to the environmental heterogeneity associated with succession. Early and intermediate plots appear to be associated with high values of  $A_{\max}$  and E as well as with low values of SLA (Fig. 1A). This particular combination of traits generally occurs as a response to a particular combination of environmental conditions: low water availability, high light availability, and high temperature (Niinemets, 2001). Our ES plots, effectively, show high canopy openness (high light transmission) and low LAI as a consequence of their low vegetation density and plant cover. Low vegetation cover and BA have been proved to determine high

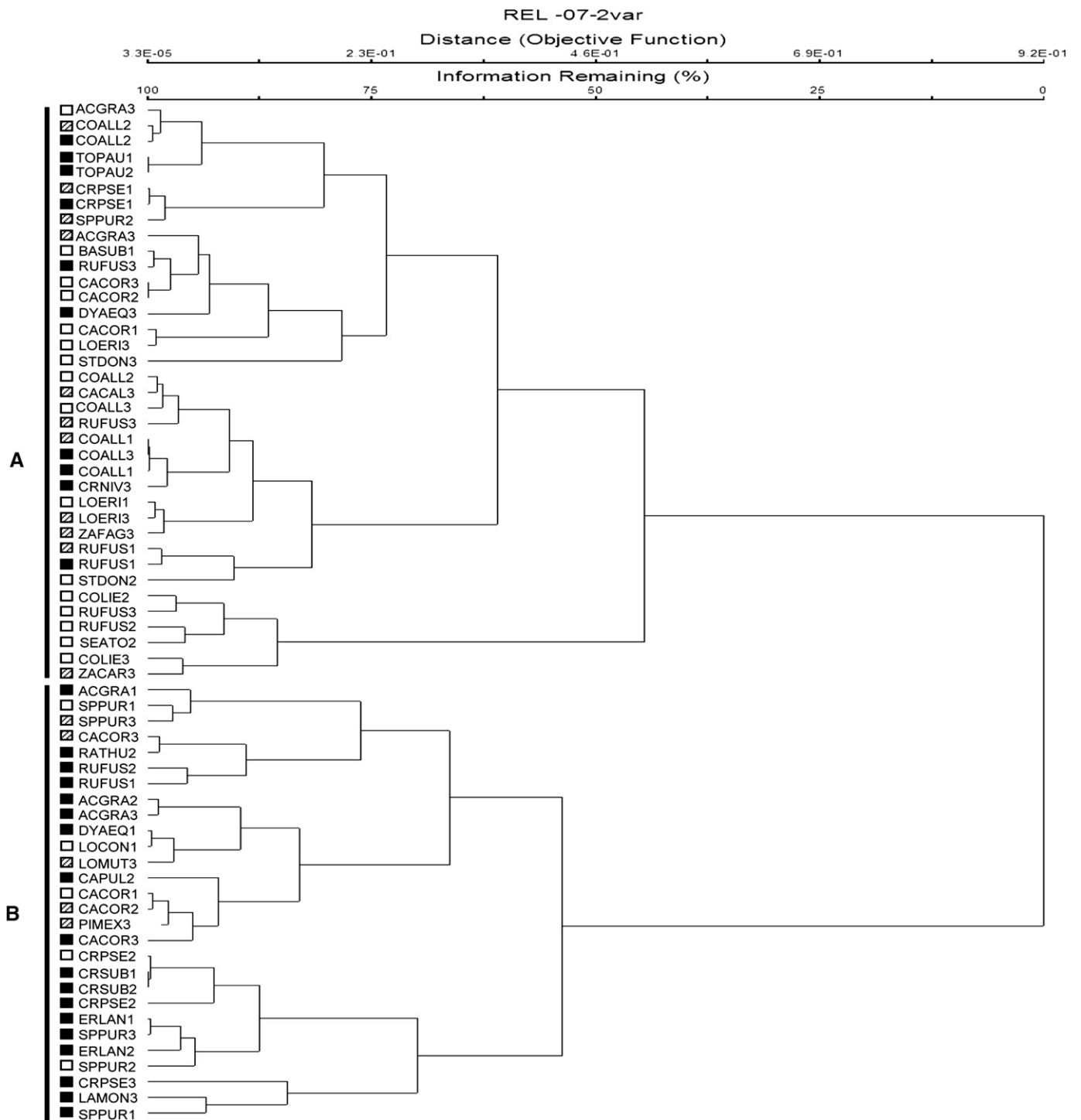


Fig. 2. Hierarchical clustering analysis results. Two functional groups, A and B, were identified on the basis of plant functional traits evaluated in 25 species growing in three seasonally dry tropical forest successional stages. Data points in the graph correspond to the mean per species per plot, and an abbreviation of the correspondent species identifies them. Names of species (Table 1) are shortened by using the first two letters of the genus and the first three letters of the species (i.e., *Achatocarpus gracilis* = ACGRA) and are followed by the number of the plot in which they were measured. Every abbreviation is preceded by a symbol that represents the successional stage in which the individuals were growing: early (open squares), intermediate (dashed squares), or late (solid squares).

light availability, high air temperature, and low relative humidity in the early stages of another Mexican SDTF successional gradient described by Lebrija-Trejos et al. (2010, 2011). The authors found that from young to old-growth forest sites, a

predictable environmental gradient exists in which temperature and light decrease, whereas relative humidity increases. This is also consistent with the significant differences we found among the stages in our daily measures of air relative humidity and leaf

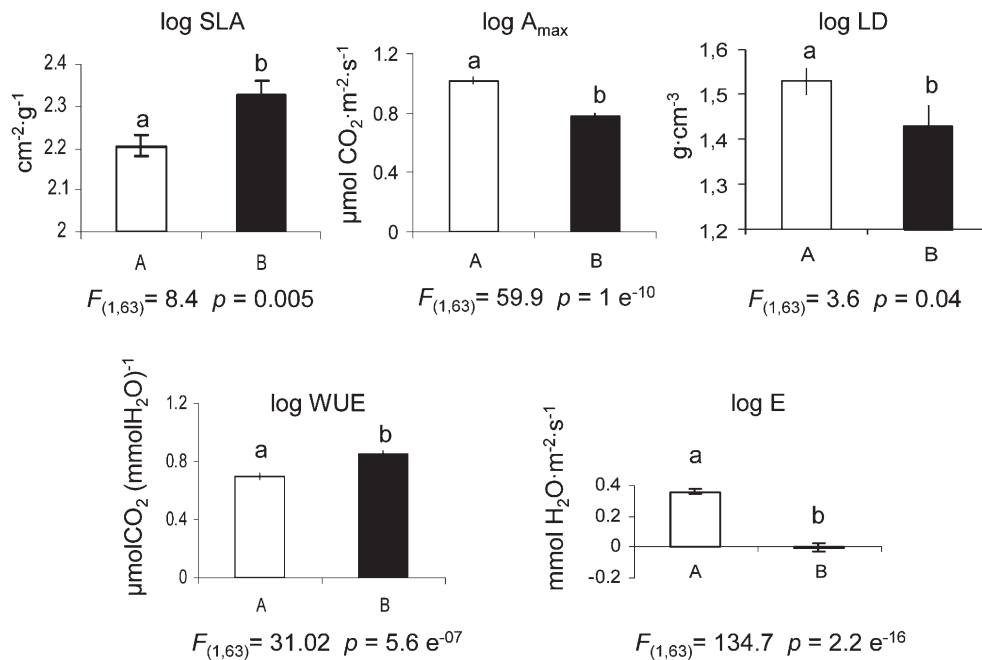


Fig. 3. Average values and standard error of five functional traits significantly differing between two functional groups, A and B.  $F$ , degrees of freedom, and  $P$  values as obtained from ANOVA are indicated for every trait. Different letters in bars indicate significant differences ( $P < 0.05$ ). SLA = specific leaf area;  $A_{\max}$  = maximum net photosynthesis; LD = leaf density; WUE = water use efficiency; E = transpiration rate.

temperature (as measured by the gas analyzer LI-COR 6400 at a constant height ranging from 4 to 6 m). From early to late successional plots, relative humidity increased ( $F_{2,797} = 94.63$ ,  $P = 8.74 \times 10^{-5}$ ), whereas leaf temperature decreased ( $F_{2,797} = 70.18$ ,  $P = 9.5 \times 10^{-4}$ ). Thus, as hypothesized, plant functional change along succession follows gradients in temperature, water availability, and light imposed by successional stages. This implies changes in photosynthetic efficiency, water use, and heat dissipation capabilities of species, which is evident in PRI and WUE trends.

**Functional groups**—Changes in temperature, water, and light availability would favor different plant strategies along successional stages. Group A, exhibiting a pioneer species

strategy, showed a lower WUE and a higher transpiration rate than group B (Fig. 3). Hence, group A strategy could be centered more on evaporative cooling and high growth (high  $A_{\max}$ ) than on water saving. Plants with a higher capacity to use solar energy by photosynthetic processes and, simultaneously, with higher dissipative efficiency through transpiration have an ecological advantage in areas with both high radiation and high temperature (Souza et al., 2004). High efficiency in heat dissipation then could be critical in the success of early successional plants, and those not able to efficiently dissipate heat would be excluded from early successional stages. The favoring of heat dissipation over an efficient water use suggests that elevated temperature could be a more severe environmental constraint than

TABLE 3.  $K$ ,  $P$ , and  $Z$  values for every functional trait as obtained from phylogenetic signal analysis. Any  $K$  value  $< 1$  represents less phylogenetic signal than the one predicted from a given phylogeny. Because  $P$  is nonsignificant ( $> 0.05$ ), functional traits are assumed to be randomly distributed across the phylogeny provided by Phylomath software (Webb and Donoghue, 2005).

Functional traits	$K$	$P$	$Z$
SLA	0.461	0.173	0.913
LT	0.490	0.110	-1.338
LWC	0.453	0.209	-0.827
LD	0.399	0.444	-0.043
LFM	0.454	0.175	-0.923
WUE	0.405	0.473	0.077
$A_{\max}$	0.379	0.639	0.386
E	0.366	0.697	0.569

Notes: Abbreviations: SLA = specific leaf area; LT = leaf thickness; LWC = leaf water content; LD = leaf density; LFM = leaf fresh mass; WUE = water use efficiency;  $A_{\max}$  = maximum net photosynthesis; E = transpiration rate.

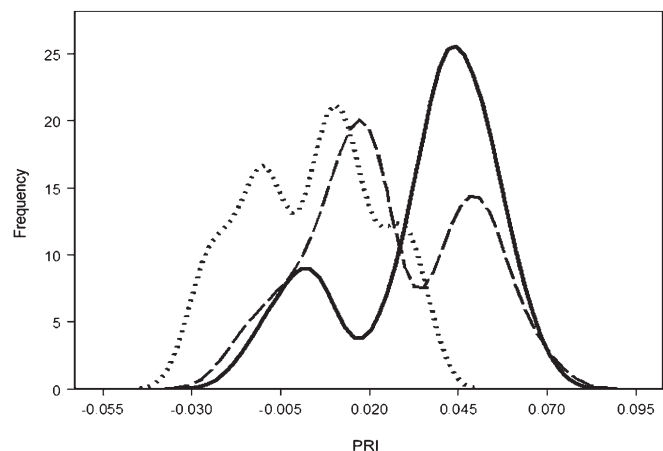


Fig. 4. Distribution of photochemical reflectance index (PRI) values for leaves of 25 tree species growing in three successional stages of the Chamela-Cuixmala seasonally dry tropical forest: early (dotted line), intermediate (dashed line), and late (continuous line).



limited water availability. Indeed, temperature has been suggested as one of the most important factors of community differentiation in a dry tropical system (Lebrija-Trejos et al., 2010). Souza et al. (2004) compared heat dissipation capacities of two SDTF species typical of late and early succession and found that higher  $A_{\max}$  levels of the pioneer species were supported by the efficiency of the whole dissipative structure. Group A species also are characterized by low SLA and high LD. A low SLA is strongly associated with an allocation strategy that increases  $N_{\text{area}}$  and photosynthetic capacity per unit leaf area. According to Cornwell and Ackerly (2009), this constitutes an advantage at dry sites. In the same sense, SLA is negatively correlated with irradiance and decreases with decreasing water availability through increases in leaf density (Witkowski and Lamont, 1991; Groom and Lamont, 1997; Niinemets, 2001). The lower PRI values of early successional plants suggest greater heat dissipation also occurs at the level of light energy distribution associated with PSII. In general, a lower PRI is associated with a higher investment in photoprotective xanthophyll cycle and carotenoid pigments relative to chlorophyll, which shunt excess light away from the photosynthetic reaction centers and toward heat production, thereby protecting the photosynthetic apparatus from damage under high light (Demmig-Adams and Adams, 1996). Therefore, group A individuals deal with high temperatures and high radiation loads by maximizing heat dissipation (high E, high PRI) and minimizing water loss (low SLA, high LD) while maintaining photosynthetic performance (high  $A_{\max}$ ). Group B, in contrast, shows opposite trends, implying a strategy consisting of larger leaves, lower E and  $A_{\max}$ , and, accordingly, higher WUE. In this sense, group B reveals a strategy more centered on water conservation and light acquisition than on heat dissipation/evaporative cooling and photoprotection. High temperature then appears to be the strongest environmental constraint in early stages of SDTF succession, while constraints in light may be more determinative in late successional communities.

Our functional groups now can be considered as forming two major successional groups: the early successional group (A) and the late successional group (B). These groups are clearly separated by species because most of the species (75%) are not shared between them, as they are exclusive to some successional stage. This reinforces the idea of two different dominant strategies in SDTF succession. The grouping would be mainly determined by the functional response of plants to the contrasting environmental conditions present at different successional stages as implied by (1) the organization of most MSP according to successional stage and (2) the lack of phylogenetic signal.

**Successional stage discrimination by spectral reflectance data**—Vegetation functional differences can be reflected in leaf spectra as demonstrated by PRI, a reflectance index related to photoprotection and photosynthetic light-use efficiency. This index differentiated between early-intermediate and late stages (Fig. 4). These results provide further evidence that differences in traits among successional stages are largely defined by microclimate and that characterizing successional communities as functional units would allow us the use of remote sensing technology in the study of SDTF succession. Structural differences can be traced back in the same way through indices related to vegetation structure, such as the canopy structure index, vegetation reflectance indices (Kalacska et al., 2007), or even through data from radar and

LiDAR (light detection and ranging) sensors, which provide information about forest structure. We propose the combination of functional and structural traits to achieve higher accuracy in discriminating successional stages, as proposed by Ustin and Gamon (2010). In the future, the combination of different “markers” of each successional stage and appropriate (hyperspectral) remote sensing technology could provide powerful tools for the identification and characterization of the tropical dry secondary forests.

**Conclusions**—The functional approach is contrasting to the structural or compositional assessment of SDTF succession. A complete recovery of SDTF could take longer than the time inferred when the process is evaluated from just a floristic and/or structural perspective. Consequently, the functional performance of the system must be evaluated when describing succession and recovery. In general, plant functional traits along SDTF succession change from those that maximize heat dissipation in early successional stages to those that enhance light acquisition and water use in late successional stages. Spectral reflectance data related to pigment composition, photoprotection, and photosynthetic performance were useful for the discrimination of successional stages, indicating that functional traits are traceable through optical measurements. These results suggest that characterization of successional communities as functional units would facilitate the application of hyperspectral remote sensing technologies to the study of tropical succession. To do so, all relevant dimensions of forest dynamics must be recognized and assessed; this implies that the functional approach must be incorporated as a regular descriptor of processes for an integrative evaluation of these systems.

#### LITERATURE CITED

- ACKERLY, D. D., AND F. A. BAZZAZ. 1995. Leaf dynamics, self-shedding and carbon gain in seedlings of a tropical pioneer tree. *Oecologia* 101: 289–298.
- ALVAREZ-AÑORVE, M., L. AVILA-CABADILLA, R. BERBARA, J. CALVO-ALVARADO, P. CUEVAS-REYES, M. ESPIRITO SANTO, A. FERNÁNDEZ, ET AL. 2008b. Ecology procedures. In J. Nassar, J. Rodríguez, G. A. Sánchez-Azofeifa, T. Garvin, and M. Quesada [eds.], Manual of methods. Human, ecological and biophysical dimensions of tropical dry forests, 15–46. Ediciones IVIC, Caracas, Venezuela.
- ALVAREZ-AÑORVE, M., M. QUESADA, AND E. DE LA BARRERA. 2008a. Remote sensing and plant functional groups detection: Physiology, ecology and spectroscopy in tropical systems. In M. Kalacska and G. A. Sanchez-Azofeifa [eds.], Hyperspectral remote sensing of tropical and sub-tropical forests, 27–45. CRC Press, Boca Raton, Florida, USA.
- ALVAREZ-BUYLLA, E. R., AND M. MARTINEZ-RAMOS. 1992. Demography and allometry of *Cecropia obtusifolia*, a neotropical pioneer tree: An evaluation of the climax–pioneer paradigm for tropical rain forests. *Journal of Ecology* 80: 275–290.
- ASNER, G. P., AND R. E. MARTIN. 2008. Spectral and chemical analysis of tropical forests: Scaling from leaf to canopy levels. *Remote Sensing of Environment* 11: 3958–3970.
- ASNER, G. P., AND R. E. MARTIN. 2009. Airborne spectranomics: Mapping canopy chemical and taxonomic diversity in tropical forests. *Frontiers in Ecology and the Environment* 7: 269–276.
- AVILA-CABADILLA, L., K. STONER, M. HENRY, AND M. ALVAREZ-AÑORVE. 2009. Composition, structure and diversity of phyllostomid bat assemblages in different successional stages of a tropical dry forest. *Forest Ecology and Management* 258: 986–996.
- BORCHERT, R. 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology* 75: 1437–1449.

- BULLOCK, S. H., H. A. MOONEY, AND E. MEDINA. 1995. Seasonally dry tropical forests. Cambridge University Press, Cambridge, UK.
- CASTRO-ESAU, K. L., G. A. SANCHEZ-AZOFEIFA, B. RIVARD, J. WRIGHT, AND M. QUESADA. 2006. Variability in leaf optical properties of Mesoamerican trees and the potential for species classification. *American Journal of Botany* 93: 517–530.
- CAVENDER-BARES, J., K. KITAJIMA, AND F. A. BAZZAZ. 2004. Multiple trait associations in relation to habitat differentiation among 17 Floridian oak species. *Ecological Monographs* 74: 635–662.
- CECCON, E., I. OMSTEAD, C. VÁZQUEZ-YANES, AND J. CAMPO-ALVES. 2002. Vegetation and soil properties in two tropical dry forests of differing regeneration status in Yucatán. *Agrociencia* 36: 621–631.
- CHAZDON, R. 2003. Tropical forest recovery: Legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics* 6: 51–71.
- CHAZDON, R. 2008. Chance and determinism in tropical forest succession. In W. Carson and F. Schnitzer [eds.], *Tropical forest community ecology*, 384–408. Wiley-Blackwell, Sussex, UK.
- CHAZDON, R., S. LETCHER, M. VAN BREUGEL, M. MARTINEZ-RAMOS, F. BONGERS, AND B. FINEGAN. 2007. Rates of change in tree communities of secondary neotropical forests following major disturbances. *Philosophical Transactions of the Royal Society of London* 362: 273–289.
- CHAZDON, R. L., C. A. HARVEY, M. MARTINEZ-RAMOS, P. BALVANERA, K. E. STONER, J. E. SCHONDUPE, L. D. AVILA-CABADILLA, AND M. FLORES-HIDALGO. 2011. Seasonally dry tropical forest biodiversity and conservation value in agricultural landscapes of Mesoamerica. In R. Dirzo, H. S. Young, H. A. Mooney, and G. Ceballos [eds.], *Seasonally dry tropical forests*, 195–220. Island Press, Washington, D.C., USA.
- CORNELISSEN, J. H. C., S. LAVOREL, E. GARNIER, S. DIAZ, N. BUCHMANN, D. E. GURVICH, P. B. REICH, ET AL. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335–380.
- CORNWELL, W. K., AND D. D. ACKERLY. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs* 79: 109–126.
- DEMIGG-ADAMS, B., AND W. W. ADAMS III. 1996. The role of xanthophyll cycle carotenoids in the protection of photosynthesis. *Trends in Plant Science* 1: 21–26.
- DIAZ, S., M. CABIDO, M. ZAK, E. MARTÍNEZ-CARRETERO, AND J. ARANÍBAR. 1999. Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina. *Journal of Vegetation Science* 10: 651–660.
- EAMUS, D., AND L. PRIOR. 2001. Ecophysiology of trees of seasonally dry tropics: Comparisons among phenologies. *Advances in Ecological Research* 32: 113–197.
- EVANS, J. R. 1989. Photosynthesis and nitrogen relationships in leaves of C<sub>3</sub> plants. *Oecologia* 78: 9–19.
- EWEL, J. 1977. Differences between wet and dry successional tropical ecosystems. *Geo-Eco-Trop* 1: 103–117.
- FOLEY, S. L., B. RIVARD, G. A. SANCHEZ-AZOFEIFA, AND J. CALVO-ALVARADO. 2006. Foliar spectral properties following leaf clipping and implications for handling techniques. *Remote Sensing of Environment* 103: 265–275.
- GAMON, J. A., J. PEÑUELAS, AND C. B. FIELD. 1992. A narrow-waveband spectral index that tracks diurnal changes in photosynthetic efficiency. *Remote Sensing of Environment* 41: 35–44.
- GAMON, J. A., L. SERRANO, AND J. S. SURFUS. 1997. The photochemical reflectance index: An optical indicator of photosynthesis radiation use efficiency across species, functional types and nutrient levels. *Oecologia* 112: 492–501.
- GARCÍA-OLIVA, F., J. M. MAASS, AND L. GALÍCIA. 1995. Rainstorm analysis and rainfall erosivity of a seasonal tropical region with a strong cyclonic influence in the Pacific Coast of Mexico. *Journal of Applied Meteorology* 34: 2491–2498.
- GARNIER, E., B. SHIPLEY, C. ROUMET, AND G. LAURENT. 2001. A standardized protocol for the determination of specific leaf area and leaf dry matter content. *Functional Ecology* 15: 688–695.
- GITAY, H., AND I. R. NOBLE. 1997. What are plant functional types and how should we seek them? In T. M. Smith., H. H. Shugart, and F. I. Woodward [eds.], *Plant functional types*, 3–19. Cambridge University Press, Cambridge, UK.
- GROOM, P. K., AND B. B. LAMONT. 1997. Xerophytic implications of increased sclerophylly: Interactions with water and light in *Hakea psilorrhyncha* seedlings. *New Phytologist* 136: 231–237.
- GRUBB, P. J. 1977. Maintenance of species-richness in plant communities: Importance of regeneration niche. *Biological Reviews of the Cambridge Philosophical Society* 52: 107–145.
- GUARIGUATA, M., AND R. OSTERTAG. 2001. Neotropical secondary forest succession: Changes in structural and functional characteristics. *Forest Ecology and Management* 148: 185–206.
- HUANTE, P., AND E. RINCON. 1998. Responses to light changes in tropical deciduous woody seedlings with contrasting growth rates. *Oecologia* 113: 53–66.
- JARAMILLO, V. J., AND R. L. SANFORD. 1995. Nutrient cycling in tropical deciduous forests. In S. H. Bullock., H. A. Mooney, and E. Medina [eds.], *Seasonally dry tropical forests*, 346–361. Cambridge University Press, Cambridge, UK.
- KALACSKA, M., G. A. SANCHEZ-AZOFEIFA, B. RIVARD, T. CAELLI, H. P. WHITE, AND J. C. CALVO-ALVARADO. 2007. Ecological fingerprinting of ecosystem succession: Estimating secondary tropical dry forest structure and diversity using imaging spectroscopy. *Remote Sensing of Environment* 108: 82–96.
- KEMBEL, S. W., P. D. HELMUS, M. R. CORNWELL, W. K. MORLON, D. ACKERLY, S. BLOMBERG, AND C. WEBB. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics (Oxford, England)* 26: 1463–1464.
- LEBRÍJA-TREJOS, E., E. PÉREZ-GARCÍA, J. A. MEAVE, F. BONGERS, AND L. POORTER. 2010. Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology* 91: 386–398.
- LEBRÍJA-TREJOS, E., E. PÉREZ-GARCÍA, J. A. MEAVE, L. POORTER, AND F. BONGERS. 2011. Environmental changes during secondary succession in a tropical dry forest in Mexico. *Journal of Tropical Ecology* 27: 477–489.
- LOTT, E. J. 1993. Annotated checklist of the vascular flora of the Chamela Bay Region, Jalisco, Mexico. *Occasional Papers of the California Academy of Sciences* 148: 1–60.
- MARKESTEIJN, L., AND L. POORTER. 2009. Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. *Journal of Ecology* 97: 311–325.
- MARTÍNEZ-YRIZAR, A., M. MAASS, A. PÉREZ-JIMÉNEZ, AND J. SARUKHÁN. 1996. Net primary productivity of a tropical deciduous forest on the coast of Jalisco, Mexico. *Journal of Tropical Ecology* 6: 433–444.
- MAZA-VILLALOBOS, A., P. BALVANERA, AND M. MARTÍNEZ-RAMOS. 2011. Early regeneration of tropical dry forest from abandoned pastures: Contrasting chronosequence and dynamic approaches. *Biotropica*.
- MC CUNE, B., AND M. J. MEFFORD. 1999. Multivariate analysis of ecological data, version 4.01. MjM Software, Glenden Beach, Oregon, USA.
- MURPHY, P. G., AND A. E. LUGO. 1986. Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* 17: 67–88.
- NIINEMETS, U. 2001. Global-scale climatic controls of leaf dry mass per area, density and thickness in trees and shrubs. *Ecology* 82: 453–469.
- ODUM, E. P., AND G. W. BARRETT. 2005. *Fundamentals of ecology*, 5th ed. Thomson Brooks/Cole, Belmont, California, USA.
- OKSANEN, J. 1983. Ordination of boreal health-like vegetation with principal component analysis, correspondence analysis and multidimensional scaling. *Vegetatio* 52: 181–189.
- PARKER, G., C. TINOCO-OJANGUREN, A. MARTÍNEZ-YRIZAR, AND M. MAASS. 2005. Seasonal balance and vertical pattern of photosynthetically active radiation within canopies of a tropical dry deciduous forest ecosystem in Mexico. *Journal of Tropical Ecology* 21: 283–295.
- PASCARELLA, J., T. AIDE, AND J. ZIMMERMAN. 2004. Short-term response of secondary forests to hurricane disturbance in Puerto Rico, USA. *Forest Ecology and Management* 199: 379–393.
- PILLAR, V. D. 1999. On the identification of optimal plant functional types. *Journal of Vegetation Science* 10: 631–640.
- POORTER, L. 2009. Leaf traits show different relationships with shade tolerance in moist versus dry tropical forests. *New Phytologist* 181: 890–900.
- POORTER, L., AND L. MARKESTEIJN. 2008. Seedling traits determine drought tolerance of tropical tree species. *Biotropica* 40: 321–331.

- QUESADA, M., G. A. SANCHEZ-AZOFEIFA, M. ALVAREZ-AÑORVE, K. STONER, L. AVILA-CABADILLA, J. CALVO-ALVARADO, A. CASTILLO, ET AL. 2009. Succession and management of tropical dry forests in the Americas: Review and new perspectives. *Forest Ecology and Management* 258: 1014–1024.
- QUESADA, M., AND K. E. STONER. 2004. Threats to the conservation of tropical dry forest in Costa Rica. In G. W. Frankie., A. Mata, and S. B. Vinson [eds.], *Biodiversity conservation in Costa Rica: Learning the lessons in a seasonal dry forest*, 266–280. University of California Press, Berkeley, California, USA.
- R DEVELOPMENT CORE TEAM. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, website <http://www.R-project.org>. [accessed 10 January 2010].
- REICH, P., I. WRIGHT, J. CAVENDER-BARES, J. CRAINE, J. OLESKYN, M. WESTOBY, AND M. WALTERS. 2003. The evolution of plant functional variations: Traits, spectra and strategies. *International Journal of Plant Sciences* 164: S143–S164.
- RODERICK, M. L., S. L. BERRY, I. R. NOBLE, AND G. D. FARQUHAR. 1999. A theoretical approach to linking the composition and morphology with the function of leaves. *Functional Ecology* 13: 683–695.
- RUIZ, J., M. C. FANDINO, AND R. L. CHAZDON. 2005. Vegetation structure, composition, and species richness across a 56-year chronosequence of dry tropical forest on Providencia island, Colombia. *Biotropica* 37: 520–530.
- RZEDOWSKI, J. 1978. *Vegetación de México*. Editorial Limusa, Mexico, D.F.
- SANCHEZ-AZOFEIFA, G. A., M. QUESADA, J. P. RODRÍGUEZ, J. M. NASSAR, K. E. STONER, A. CASTILLO, T. GARVIN, ET AL. 2005. Research priorities for neotropical dry forest. *Biotropica* 37: 477–485.
- SEGURA, G., P. BALVANERA, E. DURÁN, AND A. PÉREZ. 2003. Tree community structure and stem mortality along a water availability gradient in a Mexican tropical dry forest. *Plant Ecology* 169: 259–271.
- SHEIL, D. 2001. Long-term observations of rain forest succession, tree diversity and responses to disturbance. *Plant Ecology* 155: 183–199.
- SIMS, D., AND J. A. GAMON. 2002. Relationships between leaf pigment content and spectral reflectance across a wide range of species, leaf structures and developmental stages. *Remote Sensing of Environment* 81: 337–354.
- SOUZA, G. M., R. V. RIBEIRO, M. G. SANTOS, H. L. RIBEIRO, AND R. F. OLIVEIRA. 2004. Functional groups of forest succession as dissipative structures: An applied study. *Brazilian Journal of Biology* 64 (3B): 707–718.
- SPSS. 1999. SigmaScan Pro Image Analysis, version 5. SPSS Inc., Chicago, Illinois, USA.
- STEFFEN, W., A. SANDERSON, P. D. TYSON, J. JÄGER, P. A. MATSON, B. MOORE III, F. OLDFIELD, ET AL. 2005. Global change and the earth system: A planet under pressure. Springer-Verlag, Berlin Heidelberg, Germany.
- STYLINSKI, C. D., J. A. GAMON, AND W. C. OECHEL. 2002. Seasonal patterns of reflectance indices, carotenoid pigments and photosynthesis of evergreen chaparral species. *Oecologia* 131: 366–374.
- SWAINE, M. D., AND T. C. WHITMORE. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75: 81–86.
- TINOCO-OJANGUREN, C., AND R. W. PEARCY. 1992. Dynamic stomatal behavior and its role in carbon gain during lightflecks of a gap phase and an understory *Piper* species acclimated to high and low light. *Oecologia* 92: 222–228.
- TOLEDO, M., AND J. SALICK. 2006. Secondary succession and indigenous management in semideciduous forest fallows of the Amazon Basin. *Biotropica* 38: 161–170.
- TURNER II, B. L., W. C. CLARK, R. W. KATES, J. F. RICHARDS, J. T. MATHEWS, AND W. B. MEYER. 1990. The earth as transformed by human action: Global and regional changes in the biosphere over the past 300 years. Cambridge University Press, New York, New York, USA.
- USTIN, S., AND J. GAMON. 2010. Remote sensing of plant functional types. *New Phytologist* 186: 795–816.
- VIEIRA, D. L. M., AND A. SCARIOT. 2006. Principles of natural regeneration of tropical dry forests for restoration. *Restoration Ecology* 14: 11–20.
- WARD, J. H. 1963. Hierarchical grouping to optimize an objective function. *Journal of the American Statistical Association* 58: 236–244.
- WEBB, C. O., AND M. J. DONOGHUE. 2005. Phylomatic: Tree assembly for applied phylogenetics. *Molecular Ecology Notes* 5: 181–183.
- WESTOBY, M., D. S. FALSTER, A. T. MOLES, P. A. VESK, AND I. J. WRIGHT. 2002. Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33: 125–159.
- WITKOWSKI, E. T. F., AND B. B. LAMONT. 1991. Leaf specific mass confounds leaf density and thickness. *Oecologia* 88: 486–493.
- WRIGHT, I. J., P. B. REICH, M. WESTOBY, D. D. ACKERLY, Z. BARUCH, F. BONGERS, J. CAVENDER-BARES, ET AL. 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.
- WRIGHT, S. J., AND H. C. MULLER-LANDAU. 2006. The future of tropical forest species. *Biotropica* 38: 287–301.

APPENDIX 1. Summary statistics (mean  $\pm$  standard error per species) of plant functional traits measured in 25 seasonally dry tropical forest tree species.  $A_{\max}$  = maximum net photosynthesis ( $\mu\text{mol CO}_2\text{-m}^{-2}\text{-s}^{-1}$ ); E = transpiration rate ( $\text{mmol H}_2\text{O}\text{-m}^{-2}\text{-s}^{-1}$ ); LD = leaf density ( $\text{g}\text{-cm}^{-3}$ ); LFM = leaf fresh mass ( $\text{g}\text{-cm}^{-2}$ ); LT = leaf thickness (mm); LWC = leaf water content ( $\text{g}\text{-cm}^{-2}$ ); SLA = specific leaf area ( $\text{cm}^2\text{-g}^{-1}$ ); WUE = water use efficiency ( $\mu\text{mol CO}_2$  ( $\text{mmol H}_2\text{O}$ ) $^{-1}$ ).

Species	$A_{\max}$	E	LD	LFM	LT	LWC	SLA	WUE
<i>Achatocarpus gracilis</i>	8.7583 $\pm$ 1.0768	1.8194 $\pm$ 0.2743	0.5705 $\pm$ 0.0474	0.0205 $\pm$ 0.0014	0.1397 $\pm$ 0.0118	0.0148 $\pm$ 0.0012	199.6266 $\pm$ 11.3845	5.4727 $\pm$ 0.6491
<i>Bahinia subrotundifolia</i>	11.4881 $\pm$ 2.3930	2.6427 $\pm$ 0.2030	0.2958 $\pm$ 0.0079	0.0157 $\pm$ 0.0008	0.2148 $\pm$ 0.0165	0.0099 $\pm$ 0.0006	229.087 $\pm$ 23.6229	4.2344 $\pm$ 0.5981
<i>Caesalpinia pulcherrima</i>	6.9954 $\pm$ 0.1643	1.0991 $\pm$ 0.3390	0.4230 $\pm$ 0.0302	0.0090 $\pm$ 0.0006	0.1070 $\pm$ 0.0046	0.0048 $\pm$ 0.0005	252.6972 $\pm$ 10.5459	7.6322 $\pm$ 1.7828
<i>Casearia corymbosa</i>	7.6555 $\pm$ 0.7337	1.7648 $\pm$ 0.2326	0.5206 $\pm$ 0.0601	0.0181 $\pm$ 0.0013	0.1442 $\pm$ 0.0062	0.0110 $\pm$ 0.0007	149.3966 $\pm$ 9.4912	6.0640 $\pm$ 0.4338
<i>Cordia alliodora</i>	11.2714 $\pm$ 0.6762	1.7725 $\pm$ 0.1062	0.4016 $\pm$ 0.0309	0.0166 $\pm$ 0.0009	0.1870 $\pm$ 0.0106	0.0100 $\pm$ 0.0004	162.3639 $\pm$ 10.9519	5.9922 $\pm$ 0.4323
<i>Coccoloba liebmannii</i>	11.8126 $\pm$ 0.6990	2.8987 $\pm$ 0.1982	0.4829 $\pm$ 0.0340	0.0293 $\pm$ 0.0026	0.2918 $\pm$ 0.0311	0.0178 $\pm$ 0.0022	107.7965 $\pm$ 5.2702	4.5213 $\pm$ 0.3363
<i>Croton pseudoniveus</i>	6.4190 $\pm$ 0.4351	1.4956 $\pm$ 0.1543	0.1859 $\pm$ 0.0748	0.0151 $\pm$ 0.0014	0.1708 $\pm$ 0.0078	0.0120 $\pm$ 0.0010	365.4436 $\pm$ 17.1258	6.3178 $\pm$ 0.5087
<i>Croton niveus</i>	10.2631 $\pm$ 0.9928	1.6976 $\pm$ 0.0452	0.2191 $\pm$ 0.0036	0.0206 $\pm$ 0.0004	0.2625 $\pm$ 0.0134	0.0152 $\pm$ 0.0005	206.1495 $\pm$ 7.8164	6.0888 $\pm$ 0.4780
<i>Croton suberosus</i>	8.3778 $\pm$ 0.5693	1.0259 $\pm$ 0.2107	0.1526 $\pm$ 0.0044	0.0166 $\pm$ 0.0003	0.2484 $\pm$ 0.0054	0.0129 $\pm$ 0.0004	279.2539 $\pm$ 9.5126	9.8032 $\pm$ 3.7631
<i>Diospyros aequorioris</i>	4.0606 $\pm$ 0.2980	1.709 $\pm$ 0.5683	0.3367 $\pm$ 0.0210	0.0138 $\pm$ 0.0018	0.1931 $\pm$ 0.0196	0.0096 $\pm$ 0.0008	169.5183 $\pm$ 4.7864	3.7027 $\pm$ 1.1062
<i>Erythrina lanata</i>	4.4217 $\pm$ 0.2738	0.8078 $\pm$ 0.1448	0.1581 $\pm$ 0.0106	0.0167 $\pm$ 0.0009	0.2127 $\pm$ 0.0213	0.0135 $\pm$ 0.0007	327.0403 $\pm$ 15.9349	6.8153 $\pm$ 1.0362
<i>Lagrezia monosperma</i>	3.9625 $\pm$ 0.2649	0.355 $\pm$ 0.0352	0.2895 $\pm$ 0.0196	0.0193 $\pm$ 0.0003	0.1637 $\pm$ 0.0065	0.0147 $\pm$ 0.0001	230.3719 $\pm$ 3.9286	12.1173 $\pm$ 0.9536
<i>Lonchocarpus   ertocarinidis</i>	14.0145 $\pm$ 1.2696	2.6149 $\pm$ 0.1862	0.3707 $\pm$ 0.0093	0.0191 $\pm$ 0.0003	0.2368 $\pm$ 0.0051	0.0115 $\pm$ 0.0002	142.4255 $\pm$ 2.7132	5.8646 $\pm$ 0.5256
<i>Lonchocarpus mutans</i>	6.3525 $\pm$ 0.6555	1.2007 $\pm$ 0.1453	0.4069 $\pm$ 0.0237	0.0170 $\pm$ 0.0007	0.1908 $\pm$ 0.0042	0.0092 $\pm$ 0.0006	134.724 $\pm$ 8.1086	5.5009 $\pm$ 0.3546
<i>Lonchocarpus constrictus</i>	7.7000 $\pm$ 0.2867	1.4263 $\pm$ 0.1855	0.4467 $\pm$ 0.0269	0.0144 $\pm$ 0.0014	0.1405 $\pm$ 0.0053	0.0085 $\pm$ 0.0012	167.8244 $\pm$ 6.9729	6.0359 $\pm$ 0.6890
<i>Caesalpinia caladana</i>	9.2588 $\pm$ 0.6492	1.7777 $\pm$ 0.1505	0.4978 $\pm$ 0.0105	0.0176 $\pm$ 0.0019	0.1727 $\pm$ 0.0110	0.0090 $\pm$ 0.0012	129.3059 $\pm$ 14.2795	5.2480 $\pm$ 0.1348
<i>Pithecellobium mexicanum</i>	5.5688 $\pm$ 0.6442	0.9988 $\pm$ 0.1633	0.9448 $\pm$ 0.0377	0.0167 $\pm$ 0.0026	0.1425 $\pm$ 0.0033	0.0072 $\pm$ 0.0010	124.9034 $\pm$ 12.7111	8.1949 $\pm$ 2.4918
<i>Randia thurberi</i>	6.9808 $\pm$ 1.9654	1.2431 $\pm$ 0.3827	0.4136 $\pm$ 0.1144	0.0251 $\pm$ 0.0040	0.2402 $\pm$ 0.0292	0.0156 $\pm$ 0.0023	119.3848 $\pm$ 15.1622	6.5621 $\pm$ 0.8444
<i>Ruprechtia fusca</i>	9.5049 $\pm$ 0.4393	2.0793 $\pm$ 0.1107	0.2525 $\pm$ 0.0134	0.0238 $\pm$ 0.0023	0.4015 $\pm$ 0.0438	0.0147 $\pm$ 0.0012	125.2009 $\pm$ 9.7305	4.9658 $\pm$ 0.0745
<i>Senna atomaria</i>	12.7367 $\pm$ 1.9394	3.4291 $\pm$ 0.4703	0.2893 $\pm$ 0.0405	0.0291 $\pm$ 0.0026	0.3508 $\pm$ 0.0458	0.0194 $\pm$ 0.0016	107.5452 $\pm$ 15.4347	3.7985 $\pm$ 0.0463
<i>Spondias purpurea</i>	6.5837 $\pm$ 0.6132	1.0813 $\pm$ 0.2390	0.2489 $\pm$ 0.0311	0.0222 $\pm$ 0.0008	0.1680 $\pm$ 0.0059	0.0182 $\pm$ 0.0005	292.5452 $\pm$ 15.0165	7.4977 $\pm$ 0.9287
<i>Stemmadenia donnell-smithii</i>	12.5312 $\pm$ 0.5232	3.1685 $\pm$ 0.6170	0.2572 $\pm$ 0.0263	0.0271 $\pm$ 0.0006	0.2402 $\pm$ 0.0129	0.0209 $\pm$ 0.0009	182.6632 $\pm$ 10.0655	5.4273 $\pm$ 2.4241
<i>Thouinia paucidentata</i>	9.5733 $\pm$ 0.1604	2.1196 $\pm$ 0.0495	0.6527 $\pm$ 0.0726	0.0099 $\pm$ 0.0005	0.0816 $\pm$ 0.0051	0.0058 $\pm$ 0.0004	255.8939 $\pm$ 9.3345	4.8955 $\pm$ 0.4124
<i>Zanthoxylum fagara</i>	13.3587 $\pm$ 3.1504	2.5753 $\pm$ 0.7803	0.3426 $\pm$ 0.0177	0.0227 $\pm$ 0.0014	0.2120 $\pm$ 0.0186	0.0156 $\pm$ 0.0010	149.2808 $\pm$ 11.9364	6.4030 $\pm$ 1.2364
<i>Zanthoxylum caribaeum</i>	13.3812 $\pm$ 3.5423	2.5326 $\pm$ 0.8605	0.7075 $\pm$ 0.1075	0.0309 $\pm$ 0.0023	0.1985 $\pm$ 0.0737	0.0175 $\pm$ 0.0002	81.1396 $\pm$ 12.0916	5.6756 $\pm$ 0.8696

## **CAPÍTULO 4**

**Datos espectrales en el estudio de los caracteres funcionales de la vegetación y los procesos ecológicos: la próxima herramienta en el estudio de la dinámica de los bosques tropicales.**

**Spectral data in the study of tropical vegetation functional traits and ecological processes: a forthcoming tool for the study of tropical forest dynamics.**

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## ABSTRACT

At present, most tropical areas are conformed by a mosaic of secondary (disturbed) forests under different stages of succession. The high rate of degradation/disappearance of our tropical systems requires of the development of faster, simpler and scalable techniques of study and monitoring. As the spectral reflectance of vegetation is highly correlated to its structural and functional properties, it could be possible to detect the plant functional change associated to succession/disturbance with spectral data (e.g. vegetation indices). In this study we assessed the functional and spectral properties of the most abundant tree species along a successional gradient in a seasonally dry tropical forest (SDTF). The SDTF is one of the most widespread and endangered tropical ecosystem in the world. Specifically, we evaluated 1) the species functional performance along succession, 2) the relationship between the leaf functional traits varying along succession and leaf spectral reflectance 2) the variation of spectral data in the different successional stages and 3) which spectral data are most useful to discriminate between the stages. We found that five spectral vegetation indices showed significant correlations to most of the functional traits varying along succession. The intermediate successional stage (IS) showed a greater variation in their spectral data than the early and late successional stages (ES and LS). This coincides with the intermediate disturbance hypothesis which implies a greater functional diversity at intermediate successional stages. These results and previous reports on the behavior of leaf functional traits, suggest that some niche processes could explain the behavior of spectral data. The ES and IS, which are functionally similar, were found to be spectrally similar as well. Thus, the most accurate discrimination (86% of accuracy) was achieved between ES and LS by using two spectral indices highly correlated to our plant functional traits varying along succession. These results suggest that spectral are potentially useful to infer not only the functional and successional status of tropical vegetation, but also the ecological processes influencing such status. This would make possible the upcoming of simpler, faster and, in the long term, spatially scalable techniques, in the study/monitoring of tropical forests dynamics.

## INTRODUCTION

In an age of major anthropogenic disturbance and climatic change, the study of ecological succession is fundamental to understand how natural systems respond to disturbance. The development of techniques to “diagnose” the successional and functional status of natural systems in simpler (faster) ways and/or at larger scales, will allow us to study the ecosystems dynamics at the rapid pace imposed by their high rates of degradation.

Tropical systems, in particular, are highly endangered by human activities and most of their area is constituted by a mosaic of secondary forests under different stages of succession (Sanchez-Azofeifa et al. 2005, Quesada et al. 2009). Along tropical succession, there are predictable environmental changes determining detectable shifts in plant functional traits (Swaine and Whitmore, 1988; Alvarez-Buylla and Martínez-Ramos, 1992, Lebrija-Trejos et al. 2010, Alvarez-Añorve et al. 2012). Plant functional traits are correlated with leaf optical (spectral) properties and consequently they can be traceable through spectral data/techniques (i.e. Peñuelas et al. 1994, Gamon et al. 1995, Asner 1998). This means that spectral data correlated with functional processes most sensitive to environmental change along succession will probably be useful to discriminate between the different successional stages of tropical systems (Alvarez-Añorve et al. 2008, 2012). Additionally, niche processes such as environmental filtering, must affect the range of variation of leaf spectral data. By inferring plant functional traits and certain niche processes influencing community assembly through spectral data, we could be taking an important step into the study of forest dynamics. The use of spectral data for inferring the functional and successional status of vegetation is especially important for tropical forests which, being highly diverse and heavily disturbed, need urgently the development of simpler and faster study techniques.

Previous studies (Alvarez-Añorve et al. 2012) have demonstrated that spectral data such as the Photochemical Reflectance Index (PRI), an index related to plant photosynthetic performance, pigment composition and photoprotection (Gamon et al. 1992), is significantly different between early succession (ES) and late succession (LS) in a seasonally dry tropical forest (SDTF). The SDTFs are the most widespread tropical systems and they also are among the most threatened ecosystems of the world (Murphy and Lugo,



1986; Bullock et al., 1995; Quesada and Stoner, 2004; Sanchez-Azofeifa et al., 2005; Quesada et al., 2009). Studies on SDTF succession are relatively recent and plant functional change along succession has received attention only until the last years (i.e. Lebrija-Trejos et al. 2010, Alvarez-Añorve et al. 2012).

At present, plant functional data from a SDTF successional gradient in Jalisco, México, have shown evidence of environmental filtering and niche partitioning (limits to similarity) in ES and intermediate succession (IS) for traits related to evaporative cooling (water use efficiency, transpiration rate), water use (leaf water content and fresh mass) and photosynthetic capacity (net photosynthesis) (Alvarez-Añorve et al. submitted). Environmental filtering, however, showed a stronger effect than niche partitioning in these plant communities, favoring a combination of traits that allow for evaporative cooling at the time that enhance photosynthetic potential. Species lacking this combination would be excluded from these communities. This produces a reduction in the range of functional traits values in ES and IS. Late successional stages, in contrast, appear to be dominated by environmental filtering and niche partitioning processes with similar force (but with opposite influence in the range of functional traits values); consequently, the range of functional traits values is less restricted in these communities. In general, LS plants enhance light acquisition (larger leaves) and water conservation (higher water use efficiency). Then, high temperature appears to be the strongest environmental constraint in early stages of SDTF succession while constraints in light may be more determinant in late successional communities (Alvarez-Añorve et al. 2012).

In this study we explore the utility of leaf level spectral data to infer the functional status of tropical plant communities, to evidence niche processes influencing community assembly and to discriminate between different successional stages. Specifically we aimed to: 1) evaluate the variation in plant functional traits among different SDTF successional stages, 2) evaluate the correlation between spectral indices and most variable plant functional traits, 3) evaluate the variation of the spectral data in the different successional stages, and 4) evaluate the power of spectral data related to the functional traits most variable along succession, to discriminate between successional stages.

For this purpose, in a SDTF successional gradient, we evaluated leaf level tree functional traits and spectral data. We selected widely recognized functional traits that are

mainly related to radiation and water acquisition or use (Cornelissen et al. 2003), given that these two factors vary greatly with succession and are often negatively correlated across environmental gradients (Niinemets, 2001; Markesteijn and Poorter, 2009). Leaf spectral reflectance was evaluated through the visible and near infrared regions of the spectra (400-1100 nm) with a high resolution hyperspectral sensor.

In the long term, the combination of sensors detecting functional traits with sensors detecting structural aspects of vegetation, may provide innovative approaches to increase our understanding of physiological functioning at regional scales (Asner and Martin, 2008; Ustin and Gamon, 2010). These regional level studies could constitute a powerful tool for the study of SDTF dynamics (Alvarez-Añorve et al. 2012).

## **MATERIAL AND METHODS**

### **Study region and sampling sites**

The study was conducted in and surrounding the Chamela-Cuixmala Biosphere Reserve (CCBR), located in the central western coast of Mexico in the state of Jalisco (19°22' - 19°35'N, 104°56' - 105°03'W). The CCBR has an extension of 13,200 ha and is covered by a well preserved SDTF (Lott 2002) and some small areas of riparian forest, among other vegetation types (Lott 2002). In this region, the precipitation regime follows a markedly seasonal pattern as most of the rainfall occurs during June-October. Average annual precipitation is  $763 \pm 258$  (SD) mm and average annual temperature is 24.6°C (<http://www.ibiologia.unam.mx/ebchamela/index.html>).

We selected nine sampling sites representing a SDTF successional gradient (chronosequence) of three successional stages. Each set of sites have different ages of abandonment: 3 early stage plots (5 – 7 years old), 3 intermediate stage plots (13 – 15 years old) and 3 late stage plots (at least 50 years old, located in the CCBR). Early and intermediate plots consisted of a quadrat of 120 \* 90 m embedded within a matrix of similar vegetation and were distributed around the reserve in order to generate a research design reasonably balanced. More details on characteristics and land use history of plots can be found in Avila-Cabadilla et al. (2009) and Alvarez-Añorve et al. (2012).

### **Vegetation sampling and species selection**

A vegetation census of all woody individuals above 2.5 cm DBH (diameter at breast height) were conducted in a 50 m \* 20 m (0.1 ha) subplot at every plot. In order to include >70% of biomass of each plot in our study, we analyzed 31 species corresponding to 22 genera and 14 families (table 1). Of these 31 species, seven occur in all three stages (“shared”) and 24 in just one given stage (“exclusives”).

### **Functional traits**

Provided that different leaf traits/processes can be optimal in different regeneration opportunities (Grubb, 1977), we selected for evaluation the following fundamental leaf traits and processes: 1) processes related to CO<sub>2</sub> acquisition and use: net photosynthesis ( $A_{\max}$ ) (Evans, 1989), 2) traits/processes related to water use and conservation: leaf water content (LWC, the difference between leaf fresh and dry mass per unit area), transpiration (E) and water use efficiency (WUE, the ratio of  $A_{\max}$  to E) (Reich et al., 2003), 3) traits related to light acquisition and/or heat load regulation: specific leaf area (SLA, leaf area per dry mass) and leaf density (LD, leaf dry mass/ (leaf area \* leaf thickness, Wright *et al.*, 2004), 4) traits related to nutrient conservation or use: leaf thickness (LT) and leaf fresh mass per unit area (LFM) (Roderick et al. 1999; Garnier et al., 2001; Sims and Gamon, 2002) and 5) traits related to leaf spectral reflectance: the percentage of air space in the spongy mesophyll (ASM) and spongy mesophyll thickness (MT) (Slaton et al. 2001). Several of these traits reflect plant responses in more than one function and can be used as indicators of different survival mechanisms, including physical protection, resistance to drought stress, competitive ability, etc (Wright et al., 2004).

### **Spectral reflectance data**

Candidate optical indices were identified from literature and grouped into 3 categories, based on the spectral region of the wavelengths considered in their calculation: visible (VIS, 400 to 700 nm), red edge (680 to 730 nm) and near infrared (NIR, 800 to 1100 nm). In total, from leaf spectral reflectance metrics, we calculated five spectral indices that are correlated to different aspects of vegetation functional performance as specified in table 2.

## **Data collection**

Leaf collection and measurement were conducted during the rainy season of three years, 2006 to 2008, following standard methods (Cornelissen et al. 2003). At least five adult individuals were selected per species in each plot. To reach the crown, we used a 4 m long portable ladder and climbed trees when necessary to collect only sunlit leaves. Per individual, we collected 15 - 25 fully expanded, sun exposed, mature leaves without herbivore damage. We collected 9000 leaves of 450 individuals in total. Additionally, three leaves per individual were fixed under vacuum in a formalin aceto-alcohol (5% formalin) solution for posterior histological analysis. Collected (non-fixed) leaves were immediately placed in sealed plastic bags containing moistened paper towels and transported to the laboratory in a cooler. Maintaining leaf moisture prevents significant changes in leaf reflectance during transport (Foley et al., 2006). Once in the laboratory, from the non fixed leaves, we obtained: 1) spectral reflectance, 2) weight, 3) thickness and 4) area. Leaf spectral reflectance was analyzed using an spectral analysis system VIS/NIR UNISPEC (PPSystems, Amesbury MA, USA). Its spectral range is 350–1100 nm, with a sampling interval of 3.3 nm and a spectral resolution of < 10 nm. A bifurcated fiber optic delivers light from an internal 7.0 W halogen lamp via one branch and receives reflected light via the other (Castro-Esau et al., 2006). To measure spectral reflectance of leaves, we employed a leaf clip that holds the foreoptic at 60° and maintains a 2.3 mm diameter field of view. Sample reflectance was measured by comparing leaf reflectance to reflectance of a white standard of spectralon. Ten scans were averaged per recorded spectrum. We measured three different parts of the leaf in order to capture the potential variation of each leaf, and these three samples were expressed as a single average value for that leaf. Dark scans and white reference scans were performed frequently to detect instrument drift on the spectra. For more details on leaf traits measurement see Alvarez-Añorve et al. (2012).

In respect to the fixed leaves, following Castro-Esau et al. (2006), small pieces of blade (approximately 1 cm<sup>2</sup>) were cut from each leaf. Blades were run through an ethanolic dehydration and embedded in paraffin molds following López-Curto et al. (2005). Thin sections (5 µm) were cut from the mounted samples using a microtome (Spencer 280). Slides were mounted, stained (Harris' haematoxylin stain) and viewed with a ZEISS light microscope at 25x (figure 1). Digital photos were taken of the stained samples. The

percentage of air space in the spongy mesophyll was determined by classifying the photos for cells vs. air space (Sigma Scan Pro 5.0). Spongy mesophyll thickness was calculated using a 100- $\mu\text{m}$  scale in each photo. These two measurements were obtained only for the subset of 7 shared species (table 1).

Gas exchange measurements ( $A_{\text{max}}$  and E) were evaluated in an average of four adult trees per species in each plot. Per tree, we selected 3 - 5 sun exposed, mature and healthy leaves. To reach the crown, we used a portable 4 m long ladder which allowed us to measure the top leaves of trees six meters height or less, and the outer lateral (but totally sun exposed) leaves of taller trees. We measured a total of 800 leaves from 240 individuals. All measurements were recorded between 0900 and 1200 hours local time in days with no clouds and similar climatic conditions. We used a portable gas exchange system (LI-COR 6400, LI-COR, Nebraska, USA) to measure the photosynthetic rates of selected plants. For more details about photosynthesis measurements see Alvarez-Añorve et al. (2012).

### **Data analysis**

The spectral and functional variables that were not normally distributed were log-transformed to allow for parametric statistical analyses. To incorporate the variation per plot and because the unit of analysis is the species level, individuals were averaged per species and per plot to constitute databases. We will then use the abbreviation MSP (mean per species per plot) to name these averages in the rest of the text. Every MSP represents an average of four individuals at least. Except when another program is specified, all statistical analysis were performed in R (R Development Core Team, 2011).

To evaluate the change in plant functional traits along succession (objective 1), we compared the performance of the functional traits across different successional stages through ANOVA tests for the MSP. In this model, successional stages were the independent variables and the MSP of every functional trait the response variable. When F-values revealed significant variation among successional stages, we used Tukey's means separation tests to determine how the stages differed from one another. For consistency, this analysis was only performed for the functional traits measured in the whole set of 31 species.

We used Pearson correlations to evaluate the relation between spectral indices and functional traits differing significantly among the stages (objective 2). We also performed Pearson correlations between spectral indices and the two functional traits measured exclusively in the subset of seven shared species (ASM and MT).

To evaluate the variation of the spectral data in the different successional stages (objective 3), we mapped the observed dissimilarities on MSPs for the five spectral indices through a non-metric multidimensional scaling ordination (NMDS) on a matrix of standardized Euclidean distances. We employed the stress value, expressed on a scale from 0-100, to evaluate how successfully the between-species distances in the ordination space reflected the distances in the original space (distance matrix). In this sense, lower values of stress indicate a more reliable ordination. Finally, we used the “envfit” function from the R package “vegan” to statistically test for differences among successional stages (Oksanen 2011, Oksanen et al. 2012). This function calculates the centroids for each successional stage in the ordination space and evaluates if the observed differences among centroids are greater than expected by chance. The significance ( $\alpha = 0.05$ ) of the differences was evaluated through a randomization test (10000 permutation).

Finally, to assess whether it was possible to discriminate between successional stages based on different combinations of the spectral indices (objective 4), we used classification analysis. Classification analysis was performed through a set of algorithms that assigns a label (i.e. successional stage) to an object (i.e. MSP) based on its properties (i.e. spectral reflectance). We used a set of supervised parametric and nonparametric classifiers *sensu* Castro-Esau et al. (2004). The classifiers are part of a classification toolbox developed by Stork and Yom –Tov (2004) for use within MATLAB (v.7.4, Mathworks, 2007). Twenty percent of our MSP were labeled according to their successional stage or functional group to train the classifiers. Then, the trained classifiers classified the rest of the data to validate the robustness of the model. The percentage of incorrectly classified MSP (classification error) was determined for both the training and the testing data.

## RESULTS

### Functional change along succession

When every functional trait was evaluated separately through ANOVAs, five of them showed significant differences among stages (figure 2); in four of them (SLA, LD,  $A_{\max}$  and E) differences occurred between LS vs IS and LS vs ES. Traits showing differences among stages were related to the acquisition or use of water (E), light (SLA, LD), nutrients (LFM) and  $\text{CO}_2$  ( $A_{\max}$ ). In general, LFM, LD, E and  $A_{\max}$  decreased along succession while SLA increased.

### Correlations of spectral and functional data.

We found that spectral indices were significantly related to one or more of the functional traits differing among successional stages ( $A_{\max}$ , LFM, SLA and LD, table 3). Additionally, for the smaller set of shared species we found that four spectral indices were significantly correlated to the percentage of air spaces in the mesophyll (ASM, table 3). Spectral indices related to plant functional traits involve wavelengths from the visible and near infrared regions of the spectra (table 2).

### Spectral data variation

We only considered two axes for the NMDS ordination of MSPs for spectral indices (Fig. 3) due to additional dimensions did not substantially diminish the stress value (4.40, scaled between 0 and 100). In addition, this stress value corresponds to an excellent representation of the dissimilarities among the MSPs, with no prospect of misinterpretation (McCune and Grace 2002). The resulting ordination did not show a clear separation between successional stages ( $r^2$ : 0.08, p-value: 0.15). Nevertheless, we found a tendency toward a higher variability among the MSPs of spectral indexes in the IS (see ellipses representing the standard deviations on fig. 3), while ES and LS showed lower variability. Thus, IS trees encompass a greater spectral variation than trees from ES and LS. Along both axis, ES and IS centroids appear closer to each other than LS (fig.3), suggesting an slightly higher similitude between these two stages in spectral and functional terms.

### **Successional stages discrimination.**

Among the different successional stages, ES vs LS were more easily discriminated than ES vs IS or LS vs IS, whereas, among the different combination of indices tested, the discrimination between ES and LS was best achieved using the spectral indices PRI and mNDVI (figure 4). These successional stages were discriminated with an accuracy of 86% by the least squares algorithm. Then, at least two successional stages (early and late) can be discriminated by using spectral indices related to fundamental functional traits.

## **DISCUSSION**

The use of spectral, easy-to-measure data for inferring functional and successional status of tropical vegetation has been poorly explored until now. Tropical forests, however, need urgently the development of “shortcuts” allowing for a faster study of their status and dynamics, especially if such shortcuts allow for landscape-level studies, as is the case of spectral data.

Leaf spectral reflectance is determined by its biochemical (water content, pigments content, structural carbohydrates) and morphological (cell wall thickness, mesophyll air spaces, cuticle) properties (Grant 1987, Asner 1998). Leaf biochemical properties affect the absorption of specific wavelengths whereas morphological properties affect photons dispersion (Grant 1987, Asner 1998). The energy absorbed by a leaf in the visible region of the electromagnetic spectrum (400-700 nm) is primarily related to the content of pigments. Thus, the vegetation spectral reflectance in the visible wavelengths is highly determined by the content and composition of chlorophyll (a and b) and carotenoids (Tucker and Garrett 1977). On the other hand, the energy reflected in the near infrared wavelengths (700-1300 nm) is a function of the number and configuration of air spaces in the spongy mesophyll of the leaf (Danson 1995). In this way, the successional change in the biochemical and morphological properties of leaves (i.e. functional traits) should modify the spectral properties of vegetation along the successional process.



### **Functional change along succession**

Change in functional traits values along succession clearly respond to environmental changes along the successional gradient. As from young to old forest sites, there are environmental gradients that go from sunny to shady, hot to cool and dry to moist (Lebrija-Trejos et al. 2010, Alvarez-Añorve et al. 2012), the observed decrement of  $E$  along succession (fig. 2) can be attributed to a decrement in temperatures and radiation loads as well as to an increment in humidity from early to late successional stages. Early successional trees would experiment higher vapour pressure deficits and higher transpiration rates than late successional ones. This is an obvious adaptive advantage for early-successional species, as transpiration is the main process through which latent heat dissipates in plants, preventing plant damage induced by heat stress (Nilsen & Orcutt, 1996). On the other hand, lower light levels and higher humidity could contribute to lower transpiration rates in the LS plants.

Several studies at local and regional scales (Pillar 1999; Fonseca *et al.* 2000; Cornwell & Ackerly 2009) have found a decrease in leaf area with an increasing in dryness as well as an association of low SLA values with high stress tolerance. Trees from ES tend to have smaller leaves, reducing transpiration and water loss due to lower transpiring leaf area per unit plant mass. Leaf area can also influence the thermal conductance of the leaf boundary layer (Cornwell & Ackerly 2009), consequently smaller leaves may keep lower temperatures under high temperatures of exposed ES sites. In contrast, trees from the LS experiencing lower light availabilities, could be enhancing their light interception by producing thin leaves with a high specific leaf area (SLA, fig. 2). Differences across successional stages in light availability could also explain the decrement of LD toward LS (fig.2). The patterns of LD and LFM, can be related to a higher stress tolerance and to water conservation strategies in ES and IS plants. Indeed, when water becomes a major limiting resource, leaves tend to be thicker (Pillar 1999), which would improve plant photosynthetic performance under low water availability that might occur at ES. Regarding  $A_{max}$ , a higher rate in the ES and IS (fig.2) can be an indicative of higher leaf nitrogen concentration per unit area ( $N_{area}$ ) in these stages, which is associated with the low values of SLA, as SLA and  $N_{area}$  are related (Cornwell & Ackerly 2009).

### **Correlations of spectral and functional data.**

The spectral indices significantly correlated to two or more of the functional traits varying along succession. This suggests that this kind of spectral data are potentially useful to differentiate among SDTF successional stages. The PRI relation to LFM, LD, and SLA, in example, indicates that thicker, denser and smaller leaves show higher values of PRI and consequently higher light use efficiency (table 3). This is the case of leaves from ES trees (figure 2). Light use efficiency is highly related to carbon uptake efficiency and vegetative growth rates, and is somewhat related to fractional absorption of photosynthetically active radiation (Gamon et al. 1997). In general, PRI is sensitive to changes in carotenoid pigments (particularly xanthophyll pigments) in live foliage. Carotenoid pigments are indicative of photosynthetic light use efficiency, or the rate of carbon dioxide uptake by foliage per unit of energy absorbed (Gamon et al. 1992).

The red edge refers to the region of rapid change in reflectance of vegetation in the near infrared range of electromagnetic spectrum. Consequently, red edge indices, such as mNDVI and VOG, are sensitive to small changes in vegetation health and are intended for use with high spectral resolution data, such as that acquired by hyperspectral sensors (Zarco-Tejada et al. 2001). Chlorophyll contained in vegetation absorbs most of the light in the visible part of the spectrum but becomes almost transparent at wavelengths greater than 700 nm. In this way, vegetation cellular structure takes its major part in the reflectance because each cell acts like an elementary corner reflector (Fillela and Peñuelas 1994). This explains why our red edge indices showed a high degree of correlation to most morphological functional traits (LFM, LD and ASM, table 3). Indeed, ASM, a trait greatly influencing photon dispersion patterns, is highly correlated to mNDVI even when it was analyzed for a small subset of species. LFM is also well correlated to both spectral indices. Additionally, increases in leaf chlorophyll concentration or leaf area, can contribute to increases in the reflectance of red and blue wavelengths, thereby causing an increase in the values of indices involving these wavelengths (Datt 1999), which is the case of our red edge indices. Note that blue (450 nm) and near red wavelengths (720 nm) are considered in the calculation of mNDVI and VOG respectively (table 2). This explains the high correlation coefficients between the red edge indices and  $A_{\max}$ , a process that tends to be enhanced by higher chlorophyll concentration.

Indices combining visible and near infrared wavelengths, such as the NDVI and SR (table 2), compare reflectance measurements from the reflectance peak of vegetation in the near-infrared range to another measurement taken in the red range, where chlorophyll absorbs photons to store into energy through photosynthesis (Foley et al. 1998). As vegetation reflectance in the near infrared is highly determined by its structural characteristics (Foley et al, 1998, Peñuelas and Fillela 1998), both spectral indices were significantly correlated to the functional traits related to morphology. On the other hand, because indices include visible wavelengths in the denominator (table 2), higher chlorophyll content determines lower indices values. Hence, low values of NDVI and SR are related to high values of leaf traits that scale with photosynthetic capacity (i.e. negative correlations with LD and LFM). In the same sense, low values of these indices are related to low values of traits that decline with increasing photosynthetic capacity (i.e. positive correlation with SLA). Indeed, SLA, which is indicative of leaf morphology and is also highly related to  $A_{\max}$  (Alvarez-Añorve et al. submitted), showed high correlation coefficients to both indices. In general, VIS-NIR indices are less sensitive to small changes in vegetation health than narrowband indices (mNDVI and VOG).

Spectral indices most related to functional traits varying along succession, were mainly related to light use efficiency, leaf structure and pigments content, emphasizing the importance of considering wavelengths from different regions of the spectra when using spectral data to characterize vegetation functional status. Except for NDVI, evaluated indices were significantly related to several functional traits. Higher correlation coefficients occurred in the red edge indices which are related to both, structural and biochemical vegetation properties. Hence, our spectral data can be sensitive to plant functional change along SDTF succession.

### **Spectral data variation**

Although we found a high correlation between the spectral indices and the functional traits most varying along succession, when we analyzed the entire set of spectral indices, we didn't found separation among the successional stages in the ordination space. This can be a consequence of the high variation observed in the spectral indices among the species occurring in the same successional stage. In fact, this variation is higher in the intermediate

stage, which could be reflecting the pattern expected according to the intermediate disturbance hypothesis (Connell 1978). This hypothesis predicts that at an intermediate moment after disturbance (here the intermediate successional stage) a mix of species characteristic of the early and late stages can coexist in the same area. As a result of this, and considering the different functional strategies observed between the early and late species (see also Alvarez-Añorve et al. 2012), the functional traits and spectral data could encompass a higher variability in the IS communities.

On the other hand, spectral data from ES and LS showed less variation. The variation of values of certain functional traits, such as LFM, LWC and Amax, were found to be restricted in ES because of environmental filtering processes occurring in this successional stage (see Alvarez-Añorve et al. submitted). Environmental filtering prevents the occurrence of functional traits values that do not enhance heat dissipation and photosynthetic capacity, occasioning a reduction in the range of values detected in this stage. The more restricted range of functional traits values in ES could then help to explain the lower variation in spectral data of ES. This would imply that niche processes such as environmental filtering could be preliminarily inferred from spectral data characteristics. The even lower variation in the LS suggest that this stage could also be under niche processes such as environmental filtering even when these processes were not detected in a previous study with functional data probably as a consequence of niche processes acting in opposite direction in the functional traits (see Alvarez-Añorve et al. submitted). In addition, we also observed a tendency toward a higher similitude between the early and intermediate stage (fig. 3), which reinforces the idea that these stages are functionally (and spectrally) similar, as has been suggested in this and other studies (Alvarez-Añorve et al. 2012).

Although the results described in this section are just tendencies and successional stages variation in spectral reflectance must be examined with other techniques and spectral data in posterior studies, to our knowledge, this is a first step in the exploration of spectral data for inferring, not only the functional status of vegetation, but also the ecological forces determining such status. These forces, ultimately, underlie the assembly of biological communities (Webb et al. 2002).

### **Successional stages discrimination.**

When the indices potential to discriminate among successional stages was evaluated in combinations of two indices through classifications, we found some useful combinations. First, because of the functional similarity between ES and IS, the discrimination of these stages with spectral data did not achieve high accuracies. The highest accuracies were achieved between the most functionally dissimilar stages: ES vs LS. It is not surprising that most accurate discriminations involved indices with high correlation coefficients to functional traits varying along succession. The PRI and mNDVI, together, are highly correlated to almost all functional traits varying along succession and involve wavelengths of different regions (blue, green, red and red edge) that are indicative of pigment content, light use efficiency and structural traits of vegetation. This suggests a kind of complementarity in this combination. Thus, functional differences between ES and LS are effectively reflected in these leaf spectral data. Indeed, as  $A_{\max}$  is clearly a discriminant trait of both successional stages, PRI distribution has previously shown significant differences among the stages (Alvarez-Añorve et al. 2012).

These results indicate that spectral indices can be useful to discriminate between different successional stages in tropical systems such as the SDTF. This constitutes an enormous advantage for the study of forest dynamics, not only for the potential of spectral indices to be used at landscape scales, but also because the in situ measurement of spectral data is becoming increasingly easier. In fact, modern portable devices that calculate automatically spectral indices in the field, are being produced currently (i.e. RP-400, Photon Systems Instruments, Czech Republic). The potential of this kind of spectral data to infer functional status of vegetation, ecological forces shaping the communities and, ultimately, forest dynamics, make possible the upcoming of easier, faster and, in the long term, landscape-level study techniques for plant communities. This is especially important for our highly diverse, highly endangered and still insufficiently studied tropical systems.

### **CONCLUSIONS**

Our results indicate that spectral indices, which are widely used for the study of vegetation, are useful for inferring functional and successional status of tropical forests. The analysis of

the variation of spectral data, like the analysis of the variation of functional traits, could also have potential to detect the occurrence of certain niche processes in tropical plant communities. Nevertheless, more studies are needed considering an increasing number of species, spectral data and analytical techniques. The potential of spectral data to infer functional status of vegetation, ecological forces shaping the communities and, ultimately, forest dynamics, make possible the upcoming of easier and faster study techniques for plant communities. Needless to say, only through future studies we will find increasingly more accurate spectral approximations as well as the capacity to extrapolate them to larger spatial scales.

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## REFERENCES

- Alvarez-Añorve M, Quesada M and E. de la Barrera. 2008. Remote sensing and plant functional groups detection: physiology, ecology and spectroscopy in tropical systems. In M. Kalacska and G. A. Sanchez-Azofeifa [eds.], *Hyperspectral Remote Sensing of Tropical and Sub-Tropical Forests*, 27–45. CRC Press. Boca Raton, USA.
- Alvarez-Añorve M, Quesada M, Sánchez-Azofeifa G.A, Avila-Cabadilla, L and J. Gamon. 2012. Functional regeneration and spectral reflectance of trees during succession in a highly diverse tropical dry forest ecosystem. *American journal of Botany* In press.
- Alvarez-Buylla E. R and M. Martinez-Ramos. 1992. Demography and allometry of *Cecropia obtusifolia*, a neotropical pioneer tree: an evaluation of the climax–pioneer paradigm for tropical rain forests. *Journal of Ecology* 80: 275–290.
- Asner G. P and R. E. Martin. 2008. Spectral and chemical analysis of tropical forests: scaling from leaf to canopy levels. *Remote Sensing of Environment* 112: 3958–3970.
- Asner G.P. 1998. Biophysical and biochemical sources of variability in canopy reflectance. *Remote Sensing of Environment* 64(3): 234–253.
- Bullock S.H, Mooney H. A and E. Medina. 1995. *Seasonally dry tropical forests*. Cambridge University Press, Cambridge, UK.
- Castro-Esau K. L, Sanchez-Azofeifa G. A, Rivard B, Wright J, and M. Quesada. 2006. Variability in leaf optical properties of mesoamerican trees and the potential for species classification. *American Journal of Botany* 93(4): 517–530.
- Castro-Esau KL, Sanchez-Azofeifa GA and T. Caelli. 2004. Discrimination of lianas and trees with leaf-level hyperspectral data. *Remote Sensing of Environment* 90: 353–372.
- Connell J.H. 1978. Diversity in tropical rain forest and coral reefs: high diversity of trees and coral is maintained only in a nonequilibrium state. *Science* 199: 1302-1310.
- Cornelissen, J.H.C, S. Lavorel, E. Garnier, S. Diaz, N. Buchmann, D.E. Gurvich, P.B. Reich, et al. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335-380.
- Cornwell W. K and D. D. Ackerly. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs* 79(1): 109–126.
- Danson F and S. E. Plummer. 1995. Red-edge response to forest leaf area index. *International Journal of Remote Sensing* 16(1): 183-188.
- Datt B. 1999. A New Reflectance Index for Remote Sensing of Chlorophyll Content in Higher Plants: Tests Using Eucalyptus Leaves. *Journal of Plant Physiology* 154:30-36.
- Filella I and J. Peñuelas. 1994. The red edge position and shape as indicators of plant chlorophyll content, biomass and hydric status. *Int. J. Remote Sens.* 15:1459–1470.
- Foley S. L, Rivard B, Sanchez –Azofeifa G.A and J. Calvo-Alvarado. 2006. Foliar spectral properties following leaf clipping and implications for handling techniques. *Remote Sensing of Environment* (103): 265-275.

- Foley W, McIlwee A, Lawler I, Aragonés L, Woolnough A and N. Berding. 1998. Ecological applications of near infrared reflectance spectroscopy – a tool for rapid, cost-effective prediction of the composition of plant and animal tissues and aspects of animal performance. *Oecologia* 116(3). 293-305.
- Fonseca C. R., J. M. Overton, B. Collins and M. Westoby. 2000. Shifts in trait-combinations along rainfall and phosphorus gradients. *Journal of Ecology* 88:964–977.
- Gamon J, Field C.B, Goulden M, Griffin K, Hartley A, Joel G, Peñuelas J and R. Valentini. 1995. Relationships between NDVI, canopy structure, and photosynthesis in three Californian vegetation types. *Ecological applications* 5(1): 28-41
- Gamon J, Serrano L and J. Surfus. 1997. The photochemical reflectance index: an optical indicator of photosynthetic radiation use efficiency across species, functional types, and nutrient levels. *Oecologia* 112(4): 492-501
- Gamon J. A, Peñuelas J and C. B. Field. 1992. A narrow-waveband spectral index that tracks diurnal changes in photosynthetic efficiency. *Remote Sensing of Environment* 41: 35-44
- Garnier E, Shipley B, Roumet C and G. Laurent. 2001. A standardized protocol for the determination of specific leaf area and leaf dry matter content. *Functional Ecology* 15:688–695.
- Grant L. 1987. Diffuse and specular characteristics of leaf reflectance. *Remote Sensing of Environment* 22: 309–322.
- Lebrija-Trejos E, Pérez-García E, Meave J.A, Bongers F and L. Poorter. 2010. Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology* 91(2): 386-398.
- Markestijn L and L. Poorter. 2009. Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. *Journal of Ecology*, 97: 311–325.
- Murphy P. G, and A. E. Lugo. 1986. Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* 17: 67–88.
- López-Curto M, Márquez-Guzmán J and G. Murguía. 2005. Técnicas para el estudio del desarrollo en angiospermas. Facultad de Ciencias, UNAM. 178pp.
- Niinemets U. 1999. Components of leaf dry mass per area—thickness and density—alter photosynthetic capacity in reverse directions in woody plants. *New Phytologist* 144: 35–47.
- Nilsen E. T and D. M. Orcutt. 1996. The physiology of plants under stress: abiotic factors. John Wiley, New York, USA.
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Henry M, Stevens H, and Wagner H. 2012. vegan: Community Ecology Package. R package version 2.0-3. <http://CRAN.R-project.org/package=vegan>
- Oksanen J. 2011. Multivariate analysis of ecological communities in R: vegan tutorial, URL: <http://cc.oulu.fi/~jarioksa/opetus/metodi/vegantutor.pdf>
- Peñuelas J and I. Filella. 1998. Visible and near-infrared reflectance techniques for diagnosing plant physiological status. *Trends in Plant Science* 3: 151 – 156.



- Peñuelas J, Gamon J, Fredeen A. L, Merino J and C. B. Field. 1994. Reflectance indices associated with physiological changes in nitrogen- and water-limited sun flower leaves. *Remote Sensing of Environment* 48:135–146.
- Pillar V. D. 1999. On the Identification of Optimal Plant Functional Types. *Journal of Vegetation Science* 10 (5): 631-640.
- Quesada M and K. E. Stoner. 2004. Threats to the conservation of tropical dry forest in Costa Rica. Pages 266-280 in: Frankie, G. W., A. Mata, and S. B. Vinson, editors. Biodiversity Conservation in Costa Rica: Learning the Lessons in a Seasonal Dry Forest. University of California Press. Berkeley, California.
- Quesada M, G. A. Sanchez-Azofeifa, M. Alvarez-Añorve, K. Stoner, L. Avila-Cabadilla, J. Calvo-Alvarado, A. Castillo, M. Espiritu-Santo, M. Fagundes, G. W. Fernandes, J. A. Gamon, M. Lopezaraiza-Mikel, D. Lawrence, P. Morellato, J. Powers, F. Neves, V. Rosas-Guerrero, R. Sayago, G. Sanchez-Montoya. 2009. Succession and management of tropical dry forests in the Americas: Review and new perspectives. *Forest Ecology and Management*, 258: 1014–1024.
- R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Reich P, Wright I, Cavender-Bares J, Craine J, Oleskyn J, Westoby M and M. Walters. 2003. The evolution of plant functional variations: traits, spectra and strategies. *International Journal of Plant Sciences* 164(3): S143-S164
- Roderick M. L, Berry S. L, Noble I.R and G. D. Farquhar. 1999. A theoretical approach to linking the composition and morphology with the function of leaves. *Functional Ecology* 13: 683–695.
- Sanchez-Azofeifa G. A, M. Quesada, J. P. Rodríguez, J. M. Nassar, K. E. Stoner, A. Castillo, T. Garvin, E. L. Zent, J. C. Calvo-Alvarado, M. E. Kalacska, L. Fajardo, J. A. Gamon, and P. Cuevas. 2005. Research Priorities for Neotropical Dry Forest. *Biotropica* 37 (4): 477-485.
- Sims D and J. A. Gamon. 2002. Relationships between leaf pigment content and spectral reflectance across a wide range of species, leaf structures and developmental stages. *Remote Sensing of Environment* 81: 337– 354
- Stork D and E. Yom-Tov. 2004. Computer Manual in MATLAB to accompany pattern classification. Second edition. Wiley-Interscience. New Jersey, USA.
- Swaine M. D and T. C. Whitmore. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75: 81–86.
- Tucker C. J and M.W. Garratt. 1977. Leaf optical system modeled as a stochastic process. *Appl. Optics*, 16, 635.
- Ustin S and J. Gamon. 2010. Remote sensing of plant functional types. *New Phytologist* 186: 795–816
- Webb C.O, Ackerly D.D, McPeck M.A. and M.J. Donoghue. 2002. Phylogenies and community ecology. *Annu. Rev. Ecol.Syst.*, 33, 475–505.
- Zarco-Tejada P. J, Miller J. R, Noland T. L, Mohammed G. H and P.H. Sampson. 2001. Scaling-up and model inversion methods with narrow-band optical indices for chlorophyll content estimation in closed forest canopies with hyperspectral data. *IEEE Transactions on Geosciences and Remote Sensing* 39: 1491 – 1507.

## TABLES

**Table 1.** Family, species and successional stage (S.S) in which species occur. “All” indicates when a species was evaluated in the three successional stages (early, intermediate and late)

Family	Species	Acronyms	Successional stage
Achatocarpaceae	<i>Achatocarpus gracilis</i> (H. Walt.)	ACGRA	All
Amaranthaceae	<i>Lagrezia monosperma</i> (Rose) Standl.	LAMON	Late
Anacardiaceae	<i>Spondias purpurea</i> (L.)	SPPUR	All
Apocynaceae	<i>Stemmadenia donnell-smithii</i> (Rose) Woods.	STDON	Early
Boraginaceae	<i>Cordia alliodora</i> (Ruiz & Pav.) Oken	COALL	All
Ebenaceae	<i>Diospyros aequoris</i> (Standl.)	DIAEQ	Late
Euphorbiaceae	<i>Croton niveus</i> (Jacq.)	CRNIV	Late
	<i>Croton pseudoniveus</i> (Lundell)	CRPSE	All
	<i>Croton suberosus</i> (H.B.K)	CRSUB	Late
	<i>Pyranhea mexicana</i> (Standl.)	PYMEX	Intermediate
Fabaceae	<i>Bauhinia subrotundifolia</i> (Cav.)	BASUB	Early
	<i>Caesalpinia pulcherrima</i> (L.)	CAPUL	Late
	<i>Erythrina lanata</i> (Standl.)	ERLAN	Late
	<i>Lonchocarpus constrictus</i> (Pittier)	LOCON	Intermediate
	<i>Lonchocarpus eriocarinalis</i> (Micheli)	LOERI	All
	<i>Lonchocarpus mutans</i> (Sousa)	LOMUN	Late
	<i>Platymiscium lasiocarpum</i> (Sandwith)	PLLAS	Intermediate
	<i>Senna atomaria</i> (L.)	SEATO	Early
Flacourtiaceae	<i>Casearia corymbosa</i> (H.B.K)	CACOR	All
Polygonaceae	<i>Coccoloba liebmannii</i> (Lindau)	COLIE	Early
	<i>Ruprechtia fusca</i> (Fernald)	RUFUS	All
Rubiaceae	<i>Randia thurberi</i> (S. Watson)	RATHU	Late
Rutaceae	<i>Zanthoxylum fagara</i> (L.)	ZAFAG	Intermediate
	<i>Zanthoxylum caribaeum</i> (Lam.)	ZACAR	Intermediate
Sapindaceae	<i>Thouinia paucidentata</i> (Radlk.)	THPAU	Late

**Table 2.** Spectral indices used to analyze leaf spectral reflectance in 31 tropical tree species. It is specified the index code (“Index”), name, formula, reference, correspondent section of the electromagnetic spectrum (“Section”) as well as the index relation to plant functional traits/performance (“Functional traits”).

Index	Name	Formula	Reference	Section	Functional traits
PRI	Photochemical reflectance index	$(R_{531}-R_{570}) / (R_{531}+R_{570})$	Gamon et al. (1992)	VIS	Photosynthetic efficiency, pigment composition
mNDVI	Modified normalized difference index	$(R_{750}-R_{450}) / (R_{750}+R_{705}-2R_{450})$	Datt (1999)	RE	Structural traits, amount and quality of photosynthetic material (chlorophyll absorption)
VOG	Vogelmann red edge index	$R_{740} / R_{720}$	Vogelmann et al.(1993)		
NDVI	Normalized difference vegetation Index	$(R_{774}-R_{677}) / (R_{774}+R_{677})$	Rouse et al. (1973)	VIS/NIR	Fractional absorption of photosynthetically active radiation. Chlorophyll absorption. Structure.
SR	Simple ratio index	$R_{774} / R_{677}$	Rouse et al. (1974)		

*Formula: R is the leaf reflectance at the wavelength indicated by the subscript. Section: Visible (VIS, 400 to 700 nm), red edge (RE, 680 to 730 nm) and near infra red (NIR, 800 to 1100 nm).*

**Table 3.** Significant Pearson correlation coefficients between plant functional traits and spectral indices (“index”) in tropical tree species.

<b>Index</b>	<b>Plant functional traits</b>				
	<b>A<sub>max</sub></b>	<b>LFM</b>	<b>SLA</b>	<b>LD</b>	<b>ASM*</b>
PRI	n.s	0,49	-0,74	0,61	0,32
mNDVI	0,63	0,77	n.s	0,48	0,97
VOG	0,53	0,78	n.s	0,48	0,36
NDVI	n.s	-0,53	0,59	n.s	n.s
SR	n.s	-0,53	0,73	-0,48	0,31

*n.s: non significant correlation*

\* Correlations using only data from the seven shared species (table 1).

Plant functional traits: Net photosynthesis ( $A_{max}$ ), Leaf fresh mass (LFM), Specific leaf area (SLA), Leaf density (LD) and Percentage of air spaces in the mesophyll (ASM). Spectral indices names are as specified in Table 2.

**FIGURES**

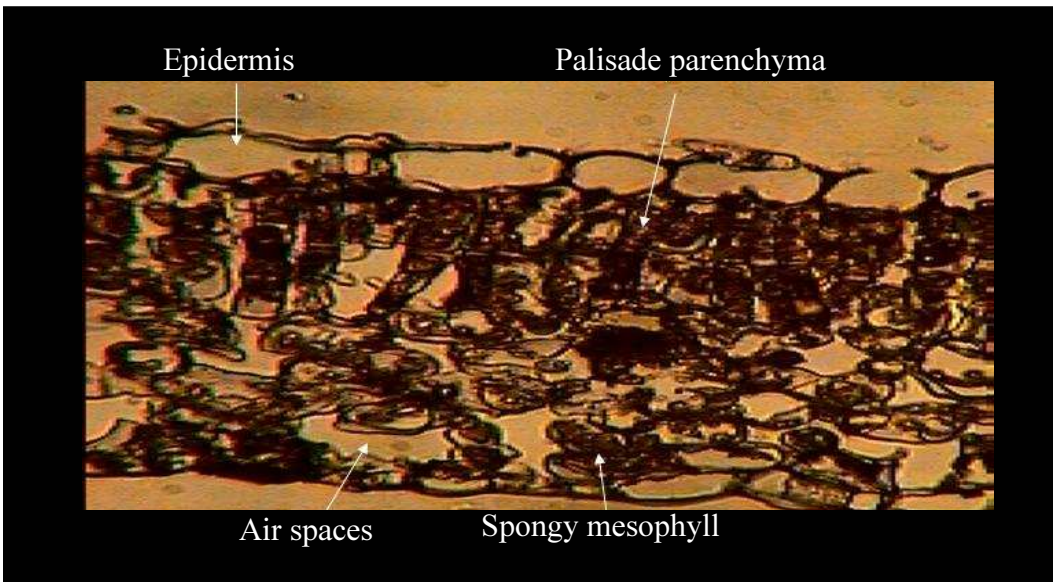


Figure 1.

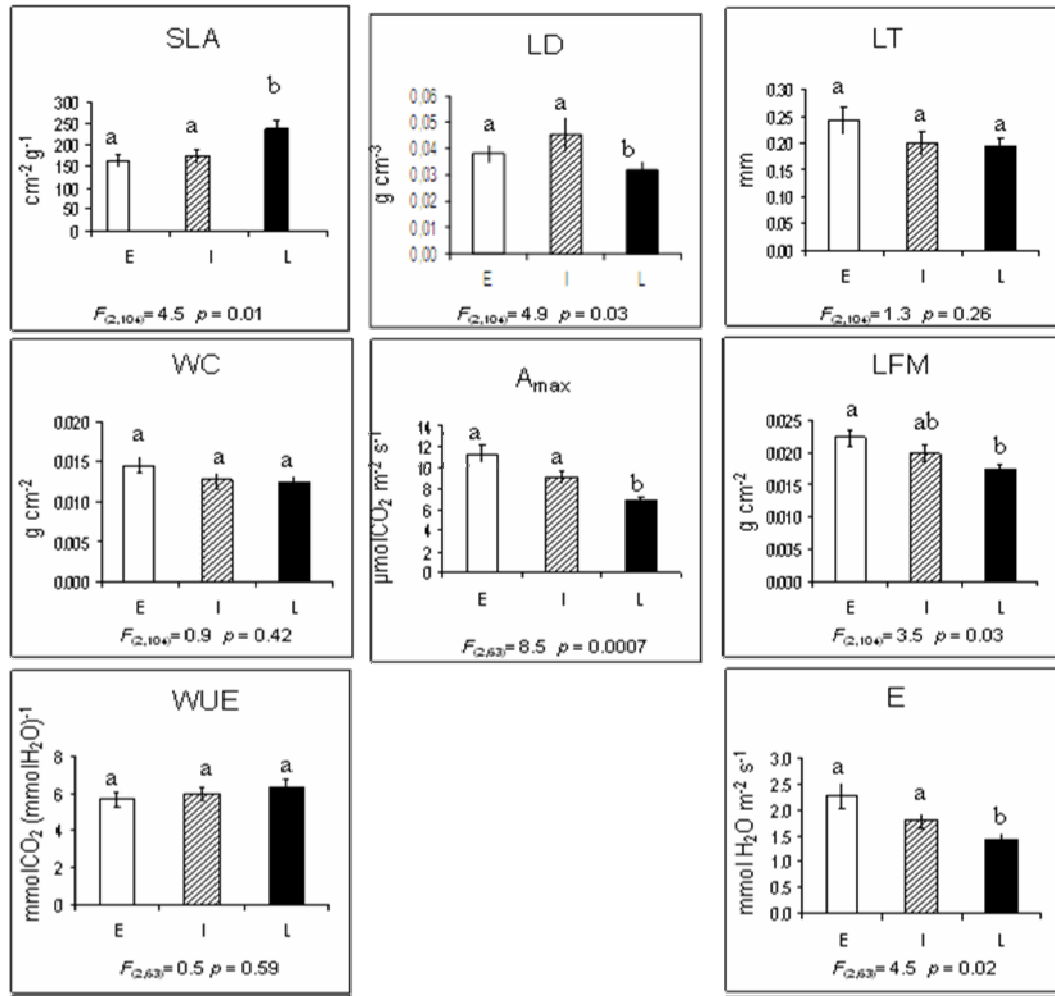


Figure 2.

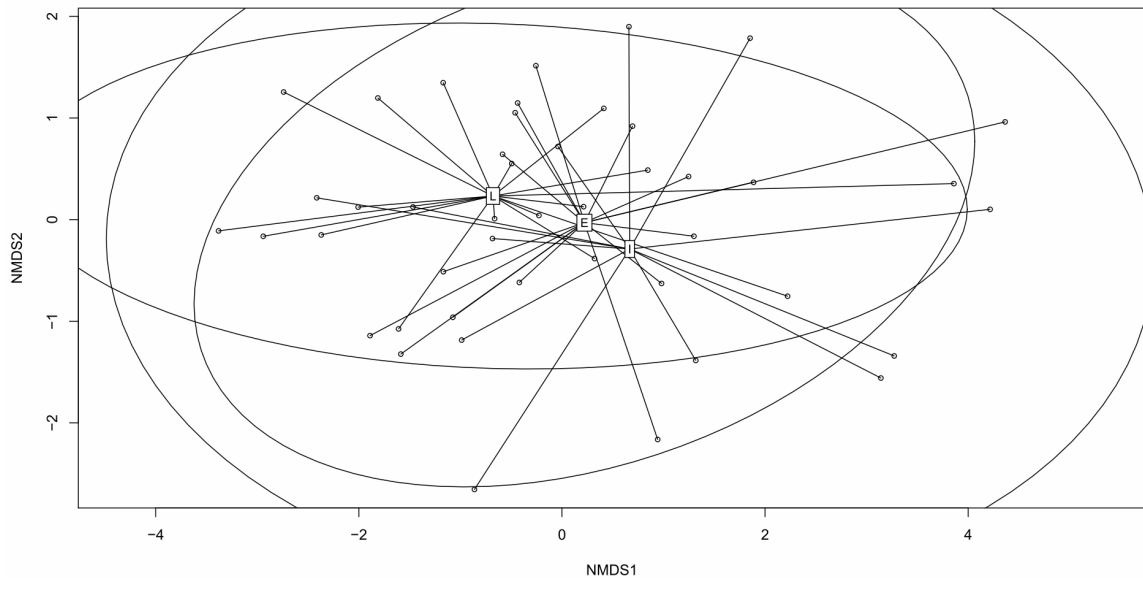


Figure 3.

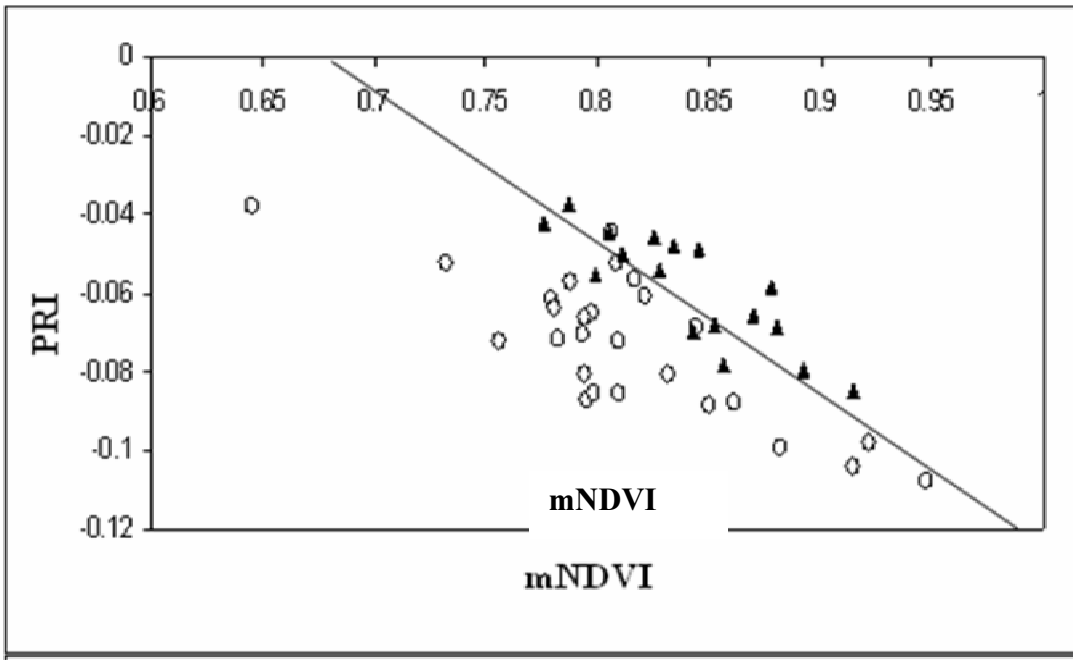


Figure 4.



## FIGURE LEGENDS

**Figure 1.** Leaf cross section of *Cordia alliodora* (25X) stained with Harris Haematoxylin and indicating the position of the spongy mesophyll and mesophyll air spaces.

**Figure 2.** Average values and standard error of eight functional traits evaluated in individuals of 31 species from three successional stages of Chamela SDTF.  $F$  and  $p$  values as obtained from ANOVA are indicated for every trait. Degrees of freedom are shown with the  $F$  value. Bars sharing a letter are not significantly different ( $p < 0.05$ ). E=early succession, I = intermediate succession and L=late succession. Functional traits abbreviations are defined in the text.

**Figure 3.** Non-metric multidimensional scaling ordination of MSPs for spectral indices. Ordination axes: axis 1 (NMDS1), and axis 2 (NMDS 2). Centroids for each successional stage, early (E), intermediate (I) and late (L), are marked by a square. Ellipses represent the standard deviation for each stage.

**Figure 4.** Graph showing results of classification between early and late successional stages based on spectral indices PRI and mNDVI. The diagonal line delimits the classification areas of the classifier (least square algorithm). Data points above the line are labeled as early successional and data points below the line are labeled as late successional by the classifier. Solid triangles and open circles represent the values of PRI and mNDVI for MSPs from early and late successional stages respectively.

## **CONCLUSIONES GENERALES**

Con las graves amenazas que se ciernen sobre nuestros sistemas tropicales en una era de gran perturbación antropogénica y de rápido cambio climático, el entendimiento de las causas y consecuencias de la estructura de las comunidades tropicales es de gran importancia. La protección de estos sistemas requiere forzosamente del entendimiento acerca de como se conforman sus comunidades y como responden a las fuerzas de cambio.

A lo largo de este estudio, hemos logrado comprender qué fuerzas podrían estar implicadas en la conformación de las comunidades de plantas del BTS (e.g. filtros ambientales, límites a la similaridad) y cómo la acción de éstas fuerzas se reflejan en las características funcionales de las diferentes comunidades sucesionales (e.g. grupos funcionales) así como en el cambio funcional de la vegetación a lo largo de la sucesión. Asimismo, esta información se ha utilizado para explorar el uso de datos/técnicas (e.g. reflectancia espectral) que nos permitan estudiar la dinámica de las comunidades tropicales en una forma más simple, rápida y también extrapolable a grandes escalas espaciales.

Primeramente, la combinación de datos filogenéticos y datos funcionales en el estudio del ensamblaje de las comunidades tropicales (muy poco utilizada hasta el momento), nos resultó sumamente útil para detectar tanto los patrones (e.g. estructura filogenética), como los procesos (e.g. procesos de nicho) existentes detrás de ellos. De manera general, se encontró que el ensamblaje de las diferentes comunidades sucesionales del BTS estaba dirigido por procesos de nicho más que por procesos neutrales. Esto es particularmente importante si pensamos que la teoría neutral (Hubbell 2001) nació en el mismo tipo de comunidad que estamos estudiando (árboles tropicales), y por tanto, estos resultados constituyen una prueba de que los procesos de nicho tienen un papel importante en la conformación de las comunidades tropicales, tal y como ha sido estipulado por otros estudios (e.g. Kelly and Bowler 2002, Kraft et al. 2008, Kelly 2008, Swenson and Enquist 2009, Letcher 2010).

En los estadios tempranos e intermedios del BTS, predomina la acción de filtros ambientales que solo permiten la ocurrencia de especies con alta capacidad de dispersión de calor y con altas tasas fotosintéticas. Como consecuencia, la relación filogenética de las

especies del estadio temprano, fue mayor que lo esperado por el azar (agrupamiento filogenético). En los estadios tempranos e intermedios, también se detectaron procesos de partición de nicho (límites a la similaridad) actuando en sentido contrario pero con menor intensidad que los filtros ambientales. Esto ejemplifica cómo fuerzas “opuestas” pueden estar actuando simultáneamente en una comunidad provocando, incluso, una ausencia de estructura filogenética en las comunidades, misma que podría ser interpretada como ausencia de procesos de nicho, es decir, procesos neutrales. Muestra de esto es el estadio tardío, en donde ni en la estructura filogenética, ni en la distribución de los caracteres funcionales, se encontró evidencia de procesos de nicho que estuviesen estructurando las comunidades arbóreas. Sin embargo, con base en lo que ocurre en los estadios tempranos e intermedios, pensamos que esto también podría ser una consecuencia de que los límites a la similaridad aumentan en intensidad a lo largo de la sucesión, anulando, en los estadios avanzados, la evidencia (pero no necesariamente la acción) de los filtros ambientales.

Los cambios en diversidad funcional (riqueza, equitatividad y divergencia) a lo largo del proceso sucesional, reflejan esta visión acerca de los cambios en intensidad de las fuerzas dirigiendo el ensamblaje de comunidades. Desde los estadios tempranos hasta los tardíos, la riqueza funcional aumentó, indicando una disminución en la intensidad de los filtros ambientales. Asimismo, también se registró un aumento en la equitatividad hacia los estadios tardíos, lo que sugiere una mayor regularidad en las distancias funcionales entre las especies (límites a la similaridad). La mayor dominancia de leguminosas en el estadio temprano refleja también la acción de estos procesos en los caracteres funcionales de la vegetación, ya que estas especies presentan características funcionales útiles para evadir los efectos perjudiciales de la alta radiación (disipación de calor) y para optimizar el uso del agua.

Cuando exploramos los patrones del proceso sucesional del BTS desde una perspectiva más amplia (ecosistémica), evaluando su regeneración en términos florísticos, estructurales y funcionales, encontramos que la regeneración integral de este sistema es más lenta de lo que se infiere a partir de estudios que no evalúan el componente funcional. Esto implica que la evaluación de la regeneración en términos meramente estructurales y/o florísticos

podría llevarnos a subestimar el tiempo real de regeneración de los sistemas naturales y, por tanto, esta visión no sería suficiente para caracterizar ni el proceso sucesional ni la dinámica de las comunidades en general.

A lo largo del gradiente sucesional del BTS, se identificaron dos grandes grupos funcionales de plantas asociados a diferentes estadios sucesionales. Los procesos de nicho moldeando el ensamblaje de las diferentes comunidades sucesionales se reflejaron también en las características de los grupos identificados. Así, un primer grupo asociado a los estadios tempranos e intermedios, se caracterizó por su mayor capacidad para disipar calor, minimizar la pérdida agua y mantener un alto potencial fotosintético. Características opuestas se encontraron en un segundo grupo sucesional asociado al estadio tardío. Este segundo grupo mostró caracteres relacionados con una captación más eficiente de la luz. Las características de los grupos funcionales estuvieron estrechamente asociadas a las características ambientales de los diferentes estadios pues, a lo largo de la sucesión, la intensidad de radiación y la temperatura disminuyen, mientras que la humedad aumenta.

Dadas las características de los grupos funcionales identificados, las condiciones ambientales asociadas a cada estadio y el efecto de filtro ambiental detectado en los caracteres funcionales asociados a la disipación de calor (en los estadios temprano e intermedio), se puede decir que la alta temperatura es un factor limitante en los estadios tempranos, mientras que, hacia los estadios tardíos, la luz podría ser mas limitante. Otros estudios han descrito también el gradiente ambiental a lo largo de la sucesión del BTS y el papel de la temperatura como un factor decisivo para el ensamblaje de las comunidades (Lebrija-Trejos et al. 2010).

El hecho de que las comunidades sucesionales del BTS hayan sido caracterizadas como unidades funcionales, facilita el uso de sus caracteres funcionales para identificarlas y discriminarlas. Esto se debe al alto nivel de correlación que existe entre los caracteres funcionales de la vegetación y la reflectancia espectral de la misma, específicamente, en forma de índices espectrales (e.g. Grant 1987, Fillela et al. 1994, Peñuelas et al. 1994, Gamon et al. 1995, Asner 1998). Este alto nivel de correlación se corroboró en la relación

existente entre varios de los caracteres funcionales evaluados en este estudio y cinco índices espectrales relacionados con distintas longitudes de onda y con distintos caracteres funcionales de la vegetación. Muestra de ello es que el índice de reflectancia fotoquímica (Gamon et al. 1992), un índice espectral asociado a la eficiencia fotosintética, al contenido de pigmentos y al nivel de fotoprotección de la hoja, características todas que varían a lo largo de la sucesión, fue significativamente distinto entre los estadios temprano e intermedio. Asimismo, este índice combinado con otro índice “complementario” en términos de longitudes de onda y de los caracteres funcionales con los cuales guarda relación, fueron de utilidad para discriminar el estadio temprano del tardío con un 86% de precisión. Esto demuestra que el uso de los datos espectrales resulta útil para “rastrear” las semejanzas y/o diferencias de las comunidades en términos funcionales. Refinar la discriminación de los estadios sucesionales con datos espectrales, tal vez considerando índices indicadores de características estructurales, puede convertirse en una herramienta poderosa para estudiar la dinámica de los sistemas tropicales a mayores escalas espaciales.

De manera preliminar, nuestros resultados sugieren que los patrones del proceso sucesional del BTS, en relación a los caracteres funcionales, se pueden reflejar también en los datos espectrales. La similitud funcional entre los estadios temprano e intermedio, por ejemplo, se manifestó también en los datos espectrales dado que ambos estadios mostraron similitud desde el punto de vista espectral. De hecho, esto fue lo que dificultó la discriminación espectral entre el estadio temprano e intermedio. Asimismo, las huellas de los procesos determinando los patrones sucesionales, podrían ser observables en los datos espectrales. Por ejemplo, el efecto del filtro ambiental al restringir la variación de los caracteres funcionales en el estadio temprano, determina también en una menor variación de los datos espectrales en este estadio. Esto significa que, redoblando los esfuerzos en la realización de este tipo de estudios, tanto los patrones como los procesos influenciando el ensamblaje de las comunidades podrían ser rastreados a través de datos espectrales de rápida (y fácil) medición. Al margen de que este tipo de datos podrían también, en el largo plazo, escalar a nivel regional o de paisaje, su uso “in situ” supone ya una gran simplificación en el estudio de la funcionalidad y por tanto, de los procesos ecológicos que operan en las comunidades vegetales. Por ello, en este estudio se propone: 1) el uso creciente de este tipo

de datos en el estudio de las comunidades tropicales, 2) el perfeccionamiento de estas técnicas para inferir de forma cada vez más precisa los patrones y procesos relativos al desempeño funcional de la vegetación y 3) el desarrollo de métodos enfocados a extrapolar dichas inferencias a grandes escalas espaciales.

Indudablemente, mientras mejor entendamos cuáles son las causas y consecuencias de la estructura de las comunidades tropicales, mejor entenderemos cómo éstas son afectadas por la perturbación humana. Esto nos permitirá dimensionar las consecuencias de la perturbación así como las condiciones necesarias para su recuperación. Esto facilitará también, el desarrollo de técnicas cada vez más eficientes para monitorear su dinámica. En este sentido, en el presente estudio se ha explorado, en cierta medida, la aplicación del conocimiento generado para la implementación de técnicas de estudio más rápidas, enfatizando siempre en la necesidad de producir conocimiento al ritmo impuesto por las tasas de modificación/desaparición de nuestros altamente diversos, gravemente amenazados y hasta emblemáticos bosques tropicales.

No se puede dejar de señalar, sin embargo, que la tasa a la que estos, y otros ecosistemas, se modifican y desaparecen por la acción humana, sobrepasan por mucho la capacidad de cualquier técnica o escala de estudio. Como científicos debemos percatarnos de que no hay técnica, tamaño o calidad de estudio, que esté impactando la conservación de los sistemas naturales de una forma apenas suficiente. Por supuesto, la profundización en el estudio de este o cualquier otro tema relativo a la ecología de los sistemas naturales reviste gran importancia para su conservación, pero mientras la mayoría de nuestros resultados y esfuerzos no tengan un impacto importante en la conciencia de la sociedad y en sus leyes, muy poco es lo que la ciencia de este país podrá contribuir al conocimiento, aprecio y conservación de la naturaleza y de los procesos que mantienen la vida en nuestro planeta. Muchas veces, estos esfuerzos ni siquiera llegan a tener impacto en el acervo de conocimiento de nuestras sociedades simplemente por la barrera del idioma. Un claro ejemplo de ello es esta tesis, escrita casi en su totalidad en inglés, con el objetivo usual de ser publicada en revistas internacionales. Este también es el caso de una gran proporción de la producción científica que, por este motivo, queda inaccesible para el resto de la sociedad.

Son muchas entonces las barreras que debemos derribar para que el conocimiento generado gracias al esfuerzo de los científicos, impacten, primero, a la sociedad, y a través de ella, al aprecio y conservación de nuestros sistemas naturales. Una barrera que habrá que romper tal vez sea el idioma, garantizando así que el conocimiento generado con recursos públicos esté al alcance de la sociedad y pueda ser usado en su provecho. La constitución de una alta diversidad de revistas científicas mexicanas con altos estándares académicos, por ejemplo, podría ser una alternativa entre muchas otras. Una vez que el conocimiento generado sea accesible para la sociedad, éste puede constituirse en una herramienta para la misma. Esto facilitaría también la vinculación del conocimiento con el rubro legal y el ámbito político. Y es que la aún insuficiente vinculación del quehacer científico con estos ámbitos constituye, indudablemente, otra barrera que como comunidad científica debemos vencer. Mientras la mayoría del conocimiento no sea plasmado en leyes, no podrá haber un progreso sustancial en la protección de los sistemas naturales y consecuentemente nos seguiremos enfrentando a la pérdida creciente de nuestros recursos bióticos.

Más que delinear un panorama pesimista, he querido en éstos párrafos reflexionar no sólo sobre la utilidad y el alcance de este estudio, sino también sobre las limitaciones reales que enfrentan este y la mayoría de los estudios ecológicos, particularmente a causa de un impacto muy limitado en la sociedad y, por tanto, en la preservación de los sistemas naturales, misma que constituye nuestro principal interés. Así, el objetivo de esta reflexión ha sido delinear lo que, a mi juicio, son los próximos pasos en la conservación de nuestros sistemas y recursos naturales. Necesitamos más estudios, sí, es innegable, pero adicionalmente necesitamos que estos estudios lleguen, toquen, sean útiles y hasta transformen a nuestra sociedad.



## REFERENCIAS

- Asner G.P. 1998. Biophysical and biochemical sources of variability in canopy reflectance. *Remote Sensing of Environment* 64(3): 234– 253.
- Filella I and J. Peñuelas. 1994. The red edge position and shape as indicators of plant chlorophyll content, biomass and hydric status. *Int. J. Remote Sens.* 15:1459–1470
- Gamon J, Field C.B, Goulden M, Griffin K, Hartley A, Joel G, Peñuelas J and R. Valentini. 1995. Relationships between NDVI, canopy structure, and photosynthesis in three Californian vegetation types. *Ecological applications* 5(1): 28-41
- Gamon J. A, Penuelas J and C. B. Field. 1992. A narrow-waveband spectral index that tracks diurnal changes in photosynthetic efficiency. *Remote Sensing of Environment* 41: 35-44
- Grant L. 1987. Diffuse and specular characteristics of leaf reflectance. *Remote Sensing of Environment* 22: 309– 322.
- Hubbell S. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.
- Kelly C.K and M.G. Bowler. 2002. Coexistence and relative abundance in forest tree species. *Nature* 417:437–440.
- Kelly C.K, Bowler M.G, Pybus O and P.H. Harvey. 2008. Phylogeny, niches, and relative abundance in natural communities. *Ecology*, 89, 962–970.
- Kraft N.J, Valencia R and D. Ackerly. 2008. Tree Community Assembly in an Amazonian Forest. *Science* 322: 580-582.
- Lebrija-Trejos E, Pérez-García E, Meave J.A, Bongers F and L. Poorter. 2010. Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology* 91(2): 386-398.
- Letcher S. 2010. Phylogenetic structure of angiosperm communities during tropical forest succession. *Proc. Biol. Sci.* 277(1678): 97–104.
- Peñuelas J, Gamon J, Fredeen A. L, Merino J and C. B. Field. 1994. Reflectance indices associated with physiological changes in nitrogen- and water-limited sun flower leaves. *Remote Sensing of Environment* 48:135–146.
- Swenson N.J and B. Enquist. 2009. Opposing assembly mechanisms in a Neotropical dry forest: implications for phylogenetic and functional community ecology. *Ecology*, 90,2161–2170.