UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS
FACULTAD DE CIENCIAS
ECOLOGÍA

RELACIONES ENTRE LAS CARACTERÍSTICAS DEL PAISAJE Y LA DIVERSIDAD VEGETAL EN UN PAISAJE COMPLEJO DEL SUR DE MÉXICO: UN ENFOQUE MESOESCALAR

TESIS

QUE PARA OPTAR POR EL GRADO DE

DOCTOR EN CIENCIAS

PRESENTA

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MÉXICO, D.F. FEBRERO 2013

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VNIVERSIDAD NACIONAL
AVTONOMA DE
MEXICO

POSGRADO EN CIENCIAS BIOLÓGICAS
FACULTAD DE CIENCIAS
DIVISIÓN DE ESTUDIOS DE POSGRADO

OFICIO FCIE/DEP/048/13

ASUNTO: Oficio de Jurado

Dr. Isidro Ávila Martínez
Director General de Administración Escolar, UNAM
Presente

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **26 de noviembre de 2012**, se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del (la) alumno (a) **GALLARDO CRUZ JOSÉ ALBERTO** con número de cuenta **95254438** con la tesis titulada: **"Relaciones entre las características del paisaje y la diversidad vegetal en un paisaje complejo del sur de México: un enfoque mesoescalar"**, realizada bajo la dirección del (la) **DR. JORGE ARTURO MEAVE DEL CASTILLO:**

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De acuerdo con lo anterior, el(a) alumno(a) se acogió a la nueva normatividad, con base en el artículo QUINTO TRANSITORIO en apegó a lo establecido en el Artículo 31 del Reglamento General de Estudios de Posgrado (9 octubre de 2006).

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

Atentamente
"POR MI RAZA HABLARA EL ESPIRITU"
Cd. Universitaria, D.F. a 1de febrero de 2013.
M. del Coro Arizmendi
Dra. María del Coro Arizmendi Arriaga
Coordinadora del Programa

MCAA/MJFM/ASR/mnm

Agradecimientos

La tesis recibió el apoyo y financiamiento del Posgrado en Ciencias Biológicas, del CONACyT (becario 199528; proyecto CB-2009-01-128136) y del PAPIIT (proyecto IN-216007). Agradezco en particular a mi director de tesis, Dr. Jorge Arturo Meave del Castillo y a los miembros de mi comité tutoral, Dra. Angelina Martínez Yrízar y Dr. José Luis Hernández Stefanoni, quienes se embarcaron conmigo en esta aventura.

Agradecimientos personales

Este proyecto lo termino de la mano de más de 60 personas que en el camino me impulsaron a seguir avanzando. El impulso vino en forma de ideas, escritos, revisiones, dinero, retos, discusiones, cumplidos, regaños, ánimos, canciones, caminatas, paciencia, tiempo... En fin, la lista es interminable.

Con todas estas personas estoy en deuda y a todas ellas les doy las gracias. Estos son sus nombres:

Abril Heredia
Alberto Búrquez
Alberto Echeverría
Alejandra Mena
Angelina Martínez
Antonio Rivero
Armando Peralta
Arturo Sánchez
Azalea Guerra
Baudel Aranjo
Baudel Aranjo hijo
Bartolino Reyes
Carlos Martorell
Claudia Flores
Claudia Manuel
Coral Cruz
Daniela González
David Ortiz
Delfín Montañana
Dietmar Moser
Edgar González
Eduardo Pérez
Edwin Lebrija
Elizabeth Campos
Emily Lott
Enrique Martínez
Erika Tetetla
Eunice Romero
Gerardo Cervantes
Gerardo Reyes
Guillermo Ibarra
Héctor Arita
Jesús Pérez
Jorge Meave
José Luis Gallardo
José Luis Hernández
José Luis Villaseñor
Lizzette Luna
Lucio Lozada
Lydie Menadier
Marco Romero
Martha Martínez
Melbi Ramos
Martín Zurita
Patricia Balvanera
Rodrigo Gallardo
Rodrigo Martínez
Román Hernández
Sandra Piña
Sara Amozurrutia
Sergio Nicasio
Silvia Cruz
Silvia Salas
Stefan Schindler
Sergi Llobet
Susana Valencia
Thomas Wiedenmann
Vanessa Maldonado
Yanus Dechnik
Yoke van der Meer

Una vez más, a quienes creyeron en mí…

Índice

Resumen

Los procesos que afectan la diversidad biológica en la mesoescala pueden ser evaluados a través del análisis de la relación de los atributos paisajísticos con los patrones espaciales en la distribución de especies. La idea se basa en que tanto la composición como la configuración de un paisaje reflejan la heterogeneidad ecológica de un sistema. Además de estudiar los patrones espaciales de la diversidad vegetal y su relación con los atributos del paisaje, este estudio analizó cómo el cambio de escala modifica dicha relación. Se buscaron respuestas a las siguientes preguntas: ¿cómo se distribuyen en el espacio las especies de plantas vasculares de una región tropical?, ¿qué efecto tienen las variaciones topográficas sobre la diversidad de especies de la región?, ¿en qué medida la estructura espacial se asocia con los cambios en la diversidad β?, ¿qué relación existe entre la diversidad de especies y la estructura del paisaje analizada siguiendo el paradigma clásico de parche-matriz?, ¿qué relación existe entre la diversidad de especies y la estructura continua del paisaje analizada a partir de métricas de textura? y, ¿es posible modelar la diversidad y los atributos de la vegetación secundaria empleando métricas de textura derivadas de una imagen satelital?

La tesis consta de ocho capítulos. El primero y el último presentan el marco conceptual y sintetizan el alcance de la investigación. El contenido del resto de los capítulos de describe a continuación. Capítulo 2: sintetiza los fundamentos teóricos planteados por las principales teorías sobre los determinantes bióticos y abióticos de la diversidad biológica en diversas escalas, y evalúa su uso en la mesoescala. Capítulo 3: usando la información recabada durante más de 11 años de prospección biológica se actualizó el listado florístico de la región de Nizanda y se analizó el grado de diferenciación biótica entre las principales comunidades en función de las distintas características de las especies. El listado cuenta con 920 especies de plantas vasculares desglosado para los principales tipos de vegetación presentes en el paisaje. La información biológica de este estudio sirvió de base para desarrollar los objetivos de los siguientes estudios. Capítulo 4: este capítulo examinó el cambio en la diversidad de especies asociado con la variación topográfica empleando una modelación de la energía solar potencial. Las variaciones de altitud y orientación del relieve

estructuran el paisaje al modificar los patrones de insolación y el balance hídrico en el terreno. En términos generales se observó que dichos cambios afectan la diversidad β pero no así los atributos estructurales de las comunidades vegetal. Capítulo 5: se analizaron los patrones en la diversidad β asociados con la estructura espacial de las cuatro principales comunidades vegetales de la región. El análisis del comportamiento de la autocorrelación espacial reveló que en la región operan fuertes limitaciones en la dispersión que generan cambios en el arreglo espacial de la diversidad vegetal en el paisaje. Capítulo 6: se estudió la importancia de considerar al paisaje como una entidad sin límites definidos, y se comparó la relación entre la riqueza de especies y la estructura del paisaje analizada bajo dos perspectivas. Los resultados apoyan la idea de cambiar el paradigma clásico para predecir la diversidad de especies vegetales en sistemas con un alto nivel de conservación. Capítulo 7: se analizó si la textura de una imagen satelital se asocia con la diversidad de especies y con la complejidad estructural de la vegetación secundaria. Las correlaciones más fuertes fueron obtenidas para los modelos de la riqueza de especies, el área basal, la edad del acahual, la altura y la cobertura de la vegetación.

El análisis de las comunidades vegetales basado en la textura abre una amplia gama de posibilidades que difieren de los esfuerzos clásicos basados en el análisis de las propiedades espectrales de una imagen satelital. Los resultados de este proyecto permitieron identificar procesos y factores críticos que determinan la distribución espacial de la diversidad en un paisaje muy complejo. Asimismo, abren la puerta a nuevas rutas de investigación que incorporen variables paisajísticas y de percepción remota en la modelación de la diversidad de especies en extensiones territoriales circunscritas a la mesoescala.

Abstract

Examination of the relation between landscape attributes and the spatial distribution of species may assist in understanding the main biodiversity drivers at the mesoscale. This statement derives from the interpretation of landscape configuration as a reflection of the system's ecological heterogeneity. Besides assessing the spatial patterns of plant diversity and its association with the landscape attributes, this study analyzed how changes of scale modify such relation. We sought answers to the following questions: what is the spatial distribution of vascular plant species in a tropical dry region? How is plant species diversity affected by topographic variation? What is the association between spatial structure and β-diversity? What is the relation between species diversity and patch-matrix landscape descriptors? What is the relation between species diversity and texture-based landscape descriptors? What is the potential of texture metrics derived from a satellite image to model secondary vegetation attributes measured in the field? The thesis comprises eight chapters. The first and the last present the conceptual framework and summarize the reach of the investigation, respectively. The contents of the remaining chapters are as follows.

Chapter 2: it summarizes the theories about the main biotic and abiotic determinants of biodiversity at different scales, and evaluates their applicability at the mesoscale. Chapter 3: the floristic list of the study site was updated using the information collected during 11 years of biological prospection, and the degree of biological differentiation between communities was analyzed in terms of different attributes of their plant species. The list includes 920 species of vascular plants classified by occurrence in the major vegetation types of the region. This information was the basis for the following studies. Chapter 4: it examines plant community variation associated with solar radiation patterns across the landscape. Vegetation structure did not show significant changes linked to the environmental gradients analyzed, but altitude and slope aspect did affect β-diversity. Chapter 5: we analyzed patterns of β-diversity associated with the spatial structure of the four main plant communities in the region. The analysis of autocorrelation patterns revealed strong dispersal limitations in the region, which in turn cause shifts in the spatial distribution of

plant diversity. Chapter 6: we studied the importance of conceiving the landscape as a limitless entity, and compared the relationship between species richness and landscape structure while analyzing the latter under two different perspectives. The results support the idea of forsaking the classic landscape paradigm for predicting plant diversity distribution in highly conserved systems. Chapter 7: we assessed the power of texture to describe and predict vegetation attributes, while identifying those texture variables with the highest predictive potential. Basal area, vegetation height and cover, species richness, and stand age were the attributes best described by textural variables. New and exciting research opportunities emerge by simplifying the analysis of the extent and complexity of successional vegetation through the spatial variation of its spectral information.

This project contributed in the identification of some of the processes and factors that determine the spatial distribution of species in a highly complex landscape. It also opens new avenues of research that seek to incorporate landscape variables and remote sensing in the modeling of species diversity within the framework of the mesoscale.

CAPÍTULO 1

Introducción

Entender los factores causales de la diversidad biológica y los procesos que permiten su mantenimiento es un tema central en la ecología (e.g. MacArthur 1965, Owen 1989, Rohde 1992, Wright et al 1993, He y Legendre 2002, Brown 2003). Durante décadas se ha documentado un gran número de relaciones entre la riqueza específica y algunos factores ecológicos, geográficos y ambientales como el clima (Walter 1973), la productividad biológica (Tilman 1982), la latitud (Pianka 1966, Currie 1991, Willig et al 2003) y la heterogeneidad ambiental (Nichols et al 1998, Stewart et al 2000). La precisión y validez de dichas relaciones han servido para distinguir y modelar regiones geográficas de alta diversidad (Gaston y David 1994, Gaston 1996, Elith et al 2006). No obstante, muchos de los estudios en la materia han señalado que la interpretación y la capacidad predictiva de estos modelos dependen de la escala de análisis (Wiens 1989).

Para explicar y predecir los patrones en la distribución de especies es preciso que exista una correspondencia escalar entre la información biológica y las variables utilizadas en su modelación (e.g. información ambiental). Sin embargo, esta condición es difícil de satisfacer. En la actualidad es posible obtener información climática y topográfica global o hacer mediciones ambientales a escalas finas con un alto nivel de precisión. En contraste, la información disponible sobre los determinantes potenciales de la riqueza de especies y de su comportamiento en la mesoescala es todavía insuficiente (Atauri y de Lucio 2001, Gillespie et al 2005, Gillespie 2005, Harte et al 2005). Por ello, la mayoría de los estudios sobre los patrones de la riqueza específica se han enfocado en arreglos observados en áreas pequeñas (e.g. Schluter y Ricklefs 1993, Tilman y Pacala 1993, Pausas 1994) o en los patrones biogeográficos observados en regiones grandes (e.g.Wright et al 1993, Mourelle y Ezcurra 1996, Wohlgemuth 1998).

Recientemente se ha propuesto que los procesos que afectan la diversidad biológica en la mesoescala pueden ser evaluados relacionando los atributos paisajísticos en grandes extensiones de terreno con los patrones espaciales de la diversidad biológica (Luoto 2000, Luoto et al 2002, Luoto et al 2004). Esta idea se basa en que tanto la composición como la configuración de un paisaje reflejan la heterogeneidad ecológica del sistema que resulta de las interacciones espaciales entre numerosos factores bióticos y abióticos, de las respuestas diferenciales de los organismos a dichos factores y de los atributos propios de cada especie.

A pesar de su importancia innegable, la relación entre las propiedades del paisaje y las medidas de diversidad vegetal apenas comienza a ser analizada. A la fecha se han publicado pocos estudios basados en este enfoque; la mayoría de ellos fueron realizados en paisajes con poca variación geomorfológica de regiones templadas y boreales de Europa y Norteamérica (Heikkinen 1996, Moser et al 2002, Honnay et al 2003). En contraste, a pesar de que las regiones tropicales del mundo concentran la gran mayoría de la diversidad biológica del planeta (Huston 1994, Gaston 2000), para ellas hay muy pocos estudios con este enfoque particular (e.g. Hernández-Stefanoni 2005, 2006).

Además del papel clave para la ecología descriptiva y de las implicaciones teóricas de este enfoque, la capacidad para detectar zonas de alta diversidad biológica y la identificación de los factores que la determinan usando atributos del paisaje es de suma importancia para la biología de la conservación (Prendergast et al 1993). En particular, el uso de estas herramientas en países muy diversos pero limitados en infraestructura científica, permitiría evaluar de forma rápida amplias extensiones de territorio y así localizar áreas prioritarias para la conservación.

A continuación se detallan los conceptos y definiciones comunes a todos los capítulos de este estudio.

El paisaje

Al igual que para otros términos utilizados de manera cotidiana en ecología, para el concepto de paisaje existen varias definiciones (Forman 1995, Farina 2000, Turner et al 2001). Desde las primeras propuestas hasta las más actuales, el término ha sufrido una notable transformación que ha generado debates importantes sobre la concepción del espacio y la escala en el paisaje (e.g. Turner 1989, Levin 1992, Wiens 1992, Hobbs 1997, Lang et al 2004, Mac Nally 2005, Wiens 2005). El debate más fuerte se ha dado en torno a si la definición debiera establecer los límites de la escala del paisaje, además de referirse exclusivamente a grandes extensiones de terreno, o si ésta debiera ser menos restrictiva en cuanto a sus criterios de inclusión (Baatz y Schäpe 2000). Gran parte del problema deriva de que la palabra paisaje en sí posee una fuerte carga semántica que sugiere un significado antropocéntrico. Este hecho es particularmente notorio en las dos primeras definiciones científicas propuestas para el término. Humboldt (1808) habló del paisaje como “el carácter total de una región” incluyendo el hogar del hombre con dimensiones culturales, económicas y físicas, mientras que Troll (1968) lo definió como “... la entidad espacial total del espacio humano habitado”.

A medida de que la ecología del paisaje progresaba, a la definición del concepto se fueron incorporaron tanto procesos ecológicos como atributos geomorfológicos que denotaban la existencia de una configuración espacial en el paisaje (Risser et al 1984). Por ejemplo, Forman y Godron (1986) afirmaron que “el paisaje es visto como un área de tierra compuesta por grupos de ecosistemas que interactúan y se repiten a lo ancho y largo de su extensión”, mientras que Green et al (1996) definieron el paisaje como “una configuración particular de topografía, cobertura vegetal, uso de suelo y patrones de asentamientos que delimitan cierta coherencia en los procesos naturales y en las actividades culturales". Todas estas definiciones están sesgadas hacia un paisaje visto desde la perspectiva humana, ya sea en la escala (grandes extensiones de terreno) o en los elementos que lo conforman (Turner 1989, Farina 2000, Bastian 2001).

En la década de 1990, justo cuando la ecología del paisaje se constituyó como una de las disciplinas científicas de mayor crecimiento (Turner 2005a), se hizo patente la necesidad de generar una definición que abarcara la gran variedad de estudios publicados en este campo, de manera que la definición de paisaje permitiera estudiar los procesos ecológicos en la escala y desde la perspectiva del objeto de estudio (Wiens 1992, Forman 1995, Bastian 2001). El paisaje tenía que ser algo más que un lugar, algo más que un sitio geográfico o que un mosaico de tipos de coberturas. En realidad, el paisaje debía ser el contexto físico y funcional en el que los procesos ecológicos y sus organismos involucrados tuvieran lugar a diferentes escalas espacio-temporales (Swanson y Sparks 1990). En ese entonces incluso surgió la propuesta de considerar al paisaje como un nivel de organización que, al igual que el organismo, carece de escala (Allen 1998). En este sentido, es importante reconocer que los procesos ecológicos son multiescalares, por lo que la dimensión del paisaje está en función del proceso particular que se desee estudiar (Wiens 1989, Wiens y Milne 1989, Levin 1992, Forman 1995, Cushman y McGarigal 2002, Scott et al 2002). Por ello, la escala o el nivel de paisaje no debiera existir.

A la par de la eliminación de la escala como componente integral del concepto de paisaje, se hizo evidente que tanto la configuración espacial como la heterogeneidad en el sistema son dos elementos comunes y esenciales en todas las definiciones (Turner 2005b), ya que la heterogeneidad espacial existe en todas las escalas de análisis (Levin 1992). Esto motivó el planteamiento de dos nuevas definiciones que son el resultado de la transformación de cómo se concibe el paisaje. Así, Farina (2000) lo definió como "una configuración espacial de parches de las dimensiones relevantes para el fenómeno bajo consideración", mientras que Turner et al (2001) establecieron que "un paisaje es un área espacialmente heterogénea en por lo menos un factor de interés. En este trabajo el paisaje se concibe como un mosaico espacialmente definido de elementos que difieren en sus propiedades cuantitativas o cualitativas (Wiens 2005). Esta definición abarca tanto paisajes acuáticos como terrestres de cualquier dimensión (i.e. aescalar) y conserva a la heterogeneidad espacial del sistema como un elemento crucial para definir y estudiar el paisaje.

Estructura del paisaje

Los patrones que resultan del arreglo espacial y de la composición de los elementos presentes en el sistema definen la estructura del paisaje. Dichos patrones pueden tomar la forma de agregados, de arreglos aleatorios o gradientes, y son el resultado de procesos exógenos o endógenos (Forman 1995, Fortin y Dale 2005). Levin (1976) identificó las principales fuerzas generadoras de patrones en el paisaje y las agrupó en tres grandes conjuntos. El primero agrupa las condiciones abióticas de un sitio y las transformaciones impuestas por el uso del terreno. A este conjunto pertenecen las variaciones ambientales asociadas con la topografía, la cual genera cambios en las concentraciones de humedad, temperatura, insolación, contenido de nutrientes y flujo de materiales de un sitio. El segundo conjunto agrupa a los procesos que ocasionan un cambio de fase (e.g. estadios sucesionales) en los elementos del sistema. Bajo este esquema un paisaje puede ser un mosaico de sitios de distintas etapas de sucesión que surgen como resultado de muchos eventos de disturbio a lo largo del tiempo. Finalmente, los procesos ecológicos espaciales como la dispersión y la inhibición poblacional se agrupan en el tercer conjunto. Dichos procesos crean estructura en un paisaje aun en ausencia de variaciones ambientales en el sistema.

El estudio del paisaje

La cuantificación de la estructura del paisaje es fundamental para entender las relaciones recíprocas entre los procesos ecológicos (e.g. biodiversidad) y los patrones espaciales (Lang et al 2004). La estructura del paisaje puede ser medida de muchas maneras. La práctica más difundida inicia con la generación de un mapa temático usando imágenes satelitales del área de interés. A partir de dicho mapa se describe la composición y la configuración espacial usando métricas del tamaño, número, área, perímetro, frecuencia, relaciones área-perímetro, linealidad, elongación, deformación, densidad, contraste, distancia y agregación de las unidades que conforman el paisaje (Gustafson 1998, McGarigal et al 2002, Li y Wu 2004). En la práctica, lo que se delimita como una unidad de paisaje (i.e. parche) depende del objetivo a seguir, de la escala de análisis y del sistema de medición usado (Lang et al 2004, Ivits et al 2005). No obstante, en general se acepta que un parche es un área relativamente homogénea que difiere de su entorno en naturaleza o apariencia (Forman 1995, Turner et al 2001).

Otra manera de cuantificar la estructura del paisaje es analizando la organización y la variación de los pixeles (e.g. textura) directamente de una imagen de satelital. Este procedimiento permite medir la heterogeneidad en una imagen sin necesidad de delimitar arbitrariamente parches en el sistema. Recientemente se propuso que la estructura medida por este procedimiento se relaciona con la heterogeneidad vegetacional del sistema (Rocchini et al 2010, Rocchini y Vannini 2010). Sin embargo, esta idea no ha sido comprobada en su totalidad.

Por último, la estructura del paisaje también puede ser analizada estudiando los patrones de autocorrelación espacial presentes en la variable de interés (Farina 2000, Fortin y Dale 2005). Esta aproximación permite dilucidar la existencia de factores estructuradores propios del sistema como son los procesos de dispersión.

Bajo cualquiera de los tres esquemas, la elección de la escala de análisis es crucial para estudiar la relación paisaje-proceso, ya que distintos procesos abarcan distintas escalas (Wiens 2005). La escala está determinada tanto por la extensión total del paisaje como por la resolución espacial de los datos (grano; Legendre y Legendre 1998). Un cambio en la magnitud de cualquiera de los dos componentes se considera un cambio de escala (Turner et al 2001). Debido a que no existe un protocolo para seleccionar *a priori* la escala de estudio es muy recomendable realizar estudios multiescalares para medir el poder explicativo de un conjunto de variables en distintas escalas (e.g. Pearson 1993).

Objetivo y preguntas de investigación

Este proyecto centra su atención en el estudio de los patrones espaciales de la diversidad vegetal, en su relación con los atributos del paisaje, y en el efecto del cambio de escala sobre dicha relación. En él se analiza también la estructura del paisaje derivada de las tres principales fuerzas generadoras de patrones descritas con anterioridad. El proyecto busca responder las siguientes preguntas:

1. ¿Cómo se distribuyen en el espacio las especies de plantas vasculares de la región de Nizanda?

2. ¿Qué efecto tienen las variaciones topográficas sobre la diversidad de especies de la región?

3. ¿En qué medida la estructura espacial se asocia con los cambios en la diversidad β?

4. ¿Qué relación existe entre la diversidad de especies y la estructura del paisaje analizada siguiendo el paradigma clásico de parche-corredor-matriz?

5. ¿Qué relación existe entre la diversidad de especies y la estructura continua del paisaje analizada a partir de métricas de textura?

6. ¿Es posible modelar la diversidad y los atributos de la vegetación secundaria empleando métricas de textura derivadas de una imagen satelital?

Estructura de la tesis

La tesis está formada por ocho capítulos. Los Capítulos I (Introducción) y VIII (Discusión general) constituyen el marco conceptual del trabajo y sintetizan el alcance de la investigación. El resto de los Capítulos abordan las preguntas y los objetivos planteados arriba. Su contenido es el siguiente:

Capítulo 2 - La diversidad biológica en la mesoescala. Sintetiza los fundamentos teóricos planteados por las principales teorías sobre los determinantes bióticos y abióticos de la diversidad biológica en diversas escalas, y evalúa su uso en la mesoescala.

Capítulo 3 - Vegetation heterogeneity and life-strategy diversity in the flora of the heterogeneous landscape of Nizanda, (Oaxaca) Mexico. Usando la información recabada durante más de 11 años de prospección biológica se actualizó el listado florístico de la región de Nizanda. El listado cuenta con 920 especies de plantas vasculares desglosado para los principales tipos de vegetación presentes en el paisaje. En este capítulo también se analizan los espectros biológicos de los conjuntos florísticos para cada comunidad. La información biológica de este estudio sirvió de base para desarrollar los objetivos de los siguientes estudios.

Capítulo 4 - β-Diversity and vegetation structure as influenced by slope aspect and altitude in a seasonally dry tropical landscape. Este capítulo examina el cambio en la diversidad de especies asociado con la variación topográfica de la región empleando una modelación de la energía solar potencial. Las variaciones de altitud y orientación del relieve estructuran el paisaje al modificar los patrones de insolación y el balance hídrico en el terreno. En términos generales se observó que dichos cambios afectan la diversidad β sin modificar los atributos de las comunidades vegetales.

Capítulo 5 - Spatial structure of plant communities in a complex tropical landscape: implications for β-diversity. Aquí se analizan los patrones en la diversidad asociados con la estructura espacial de cuatro comunidades vegetales de la región (bosque tropical caducifolio, vegetación xerofítica, sabana y bosque subdeciduo). Las pruebas de Mantel multivariadas revelaron que en la región existen fuertes limitaciones en la dispersión que generan cambios en el arreglo espacial de la diversidad vegetal en el paisaje. A lo largo del estudio se discute la importancia de incorporar al componente espacial dentro del marco teórico de la ecología.

Capítulo 6 - Relating species richness to the structure of continuous landscapes: alternative methodological approaches. La ecología del paisaje ha seguido durante décadas el paradigma de la existencia de unidades discretas en paisaje (parche-corredor-matriz. En este capítulo se estudia la importancia de considerar al paisaje como una entidad sin límites definidos, y compara la relación entre la riqueza de especies y la estructura del paisaje analizada bajo estas dos perspectivas. Los resultados obtenidos apoyan la idea de cambiar el paradigma clásico para predecir la diversidad de especies vegetales en sistemas con un alto nivel de conservación.

Capítulo 7 - Predicting Tropical Dry Forest Successional Attributes from Space: Is the Key Hidden in Image Texture? En este capítulo se analiza si la textura de una imagen satelital (i.e. variabilidad espacial de los pixeles) se relaciona con la diversidad de especies y con la complejidad estructural de la vegetación secundaria de la región. Las relaciones más altas fueron obtenidas para modelar la riqueza de especies, el área basal, la edad, la altura y la cobertura de la vegetación. El análisis de las comunidades vegetales basado en la textura abre una amplia gama de posibilidades que difieren de los esfuerzos clásicos basados en el análisis de las propiedades espectrales de una imagen satelital. Este estudio también demostró que las variables de textura tienen un gran potencial para predecir distintos atributos de la vegetación secundaria.

El paisaje de Nizanda

La región de Nizanda constituye una de las regiones más interesantes desde el punto de vista biológico en el Istmo de Tehuantepec (Pérez-García et al 2001). Nizanda se sitúa en una región conocida como "Paso de Chivela" y marca la transición entre la Serranías Centrales del Istmo y la Planicie Costera de Tehuantepec (Williams 1939). La región se ubica en la Vertiente Pacífica del Istmo de Tehuantepec, en el Distrito de Juchitán. Su clima es cálido, subhúmedo y marcadamente estacional. En esta región el paisaje está dominado por lomeríos de filitas de baja altitud (< 200 m snm) donde se presentan algunos altozanos calcáreos dentro de una matriz de rocas metamórficas (Pérez-García et al 2001, Pérez-García y Meave 2004). La heterogeneidad ambiental generada por las variaciones en la litología, el relieve, la profundidad del suelo, el drenaje y la disponibilidad de agua, así como por los diferentes regímenes de disturbio explican en gran medida la variabilidad en la vegetación regional. En la región se distinguen parches correspondientes a ocho tipos de vegetación primaria y secundaria, así como áreas de uso antropogénico, lo que resulta en una cubierta vegetal notablemente heterogénea y diversa que reúne una flora estimada en más de 1,000 especies de plantas vasculares. La selva baja caducifolia domina claramente el paisaje. Esta comunidad presenta el mayor número de especies y la mayor variación entre áreas de un mismo tipo vegetacional (Pérez-García et al 2001). Los estudios florísticos de la región indican la existencia de una enorme diferenciación florística espacial (Gallardo-Cruz et al 2005, Pérez-García et al 2005). Por ejemplo, ninguna de las 740 especies registradas por Meave y Pérez-García (2000) se distribuyeron en todos los tipos de vegetación reconocidos en ese momento. En otro estudio restringido a la vegetación presente en los afloramientos calcáreos, Pérez-García y Meave (2004) mostraron que las diferencias florísticas van acompañadas de diferencias notables en los atributos de la vegetación; en ese estudio se encontró que en los sitios desprovistos de suelo predominan las plantas crasicaules espinosas y las suculentas rosetófilas; además, se encontró que la riqueza de monocotiledóneas es mayor en estos sitios, mientras que grandes grupos florísticos están ausentes de ellos, como las hierbas graminoides (Poaceae y Cyperaceae) y las leguminosas herbáceas y rastreras (Pérez-García 2002, Pérez-García y Meave 2004). En las sabanas de la región, las hierbas graminoides son las plantas dominantes (López-Olmedo et al 2006), mientras que muchas de las especies propias de la vegetación ribereña son exclusivas de ambientes expuestos a inundaciones frecuentes (Lebrija-Trejos 2001).

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CAPÍTULO 2

La diversidad biológica en la mesoescala

La diversidad biológica es un fenómeno fascinante. Sorprendidos por la espléndida variedad de vida, los naturalistas y los biólogos han invertido cientos de años en la recolección, descripción y clasificación de los organismos vivientes para entender los factores causales de la diversidad biológica y los procesos que permiten su mantenimiento (Brown 2003, He y Legendre 2002, MacArthur 1965, Owen 1989, Rohde 1992, Wright et al 1993). Esta labor inconclusa se ha concentrado principalmente en el estudio de algunos grupos como las aves, los mamíferos, los moluscos y las plantas vasculares lo cual ha generado un vacío en el conocimiento de grandes grupos como los ácaros, nemátodos, hongos y procariontes (Brown 2003).

Actualmente sabemos que apenas hemos comenzado a entender a profundidad los procesos que generan y mantienen la diversidad. En parte, el desconocimiento se deriva de que los patrones observados en la biodiversidad y los procesos que los producen son extremadamente complejos (Storch y Gaston 2004, Storch et al 2005b). Éstos abarcan desde los eventos evolutivos ocurridos millones de años atrás hasta las interacciones contemporáneas entre los individuos y su ambiente; desde los procesos biogeográficos a nivel continental y oceánico hasta las interacciones locales que suceden en escalas espaciales minúsculas (Storch y Gaston 2004). Por otro lado, dicho desconocimiento puede explicarse simplemente por el hecho de que la biodiversidad está determinada por un sinfín de procesos exclusivos para cada taxón y ambiente (Gaston 2000, Storch et al 2005a, Storch y Gaston 2004): Cada tipo de organismo es único debido a las restricciones evolutivas que afectan sus estrategias de supervivencia y reproducción, cada hábitat tiene propiedades particulares de composición biótica, de condiciones abióticas y de dinámica, y cada masa de tierra y cuerpo de agua tiene una historia geológica, climática y orgánica propia. Por ello, la búsqueda de leyes universales puede parecer una tarea desalentadora.

Se ha reconocido, sin embargo, patrones generales en la diversidad biológica, lo cual sugiere que existen también procesos subyacentes generales que los originan (Gaston 2000). Por ejemplo, se han documentado relaciones entre la riqueza específica y numerosos factores ecológicos, biogeográficos y espaciales como el clima (Walter 1973), la productividad biológica (Tilman 1982), la latitud (Currie 1991, Pianka 1966, Willig et al 2003), el tamaño, la forma y la distancia entre islas de hábitat (Meave y Kellman 1994, Schluter y Ricklefs 1993) y la heterogeneidad ambiental (Nichols et al 1998, Stewart et al 2000). Se han planteado cuantiosas explicaciones, algunas mutuamente excluyentes, para estas relaciones (Gaston 2003). Seleccionar una de entre todas las existentes requiere formular y poner a prueba cuantitativamente modelos formales que relacionen los patrones y procesos (Storch y Gaston 2004).

La diversidad biológica depende de la escala de observación (Arrhenius 1921). Aun cuando esta idea es antigua, entender con precisión cómo varía y cómo se debería trasladar la información existente entre escalas es un tema de investigación actual (Storch et al 2007). No obstante, la mayoría de los estudios de los patrones de la riqueza específica se han enfocado en arreglos observados en escalas pequeñas (e.g. Pausas 1994, Schluter y Ricklefs 1993, Tilman y Pacala 1993) o en patrones biogeográficos de gran escala (e.g. Currie y Paquin 1987, Mourelle y Ezcurra 1996, Wohlgemuth 1998, Wright et al 1993). Este sesgo ha provocado que la información disponible sobre los determinantes potenciales de la riqueza de especies y sobre su comportamiento en escalas espaciales intermedias (mesoescala) sea todavía insuficiente (Atauri y de Lucio 2001, Gillespie 2005, Harte et al 2005). La generación de la información necesaria para entender la biodiversidad en esta escala requeriría de un enorme esfuerzo dirigido específicamente a la obtención y el análisis de datos. Sin embargo, con el fin de avanzar en esta dirección y basado en la idea de que es posible trasladar entre escalas la información disponible (Wu et al 2006), este capítulo pretende extraer los fundamentos e ideas planteados en las principales teorías y evaluar la factibilidad de emplearlos en la mesoescala.

Determinantes bióticos y abióticos de la diversidad biológica en diversas escalas

Desde hace más de dos siglos, la variación espacial de la diversidad ha motivado el planteamiento de numerosas hipótesis que buscan explicarla (Palmer 1994, Willig et al 2003). Debido a que la riqueza de especies varía dentro de una amplia gama de escalas espaciales y temporales (Willis y Whittaker 2002), esta tarea ha estado limitada históricamente por la falta de consenso respecto a las expresiones para referirse a la biodiversidad de un sitio (e.g. riqueza de especies, de familias o de géneros, índices de diversidad, densidad de especies, recambio de especies, número de endemismos) y a la gran cantidad de definiciones de escala que se han propuesto (Schneider 2001).

A partir de aquí se considerará a la biodiversidad como el número de especies observadas o estimadas por unidad de área (riqueza de especies), mientras que el concepto de escala integrará dos componentes reconocidos por la mayoría de los estudios espacio-temporales de la diversidad: el grano y la extensión (Schneider 1994, Wiens 1989). El grano es el tamaño de la unidad de muestreo elemental, mientras que la extensión es la magnitud espacio-temporal sobre la cual se examina el fenómeno de interés (Legendre y Legendre 2000). Un cambio de escala involucra el cambio en la magnitud de por lo menos uno de los dos componentes. Establecer la escala de estudio es de suma importancia ya que permite comparar entre sistemas y derivar patrones generales. Típicamente los ecólogos centran sus estudios en tres categorías espacio-temporales de extensión. La macroescala ($> 10^9$ m^2; $> 10^2$ años), la escala local ($<10^4$ m^2; < 1 año) y la mesoescala, comprendida entre las dos anteriores (Ricklefs y Schluter 1993, Schneider 2001, Turner 1989, Turner et al 1989, Willis y Whittaker 2002). Es importante destacar que la escala no es un agente causal *per se*, ya que no produce ni patrones ni procesos, sólo permite percibirlos y, dado el caso, cuantificarlos. No obstante, se ha encontrado que existe una fuerte correlación entre cierto tipo de patrones y procesos con determinadas escalas (Schneider 2001, Turner 1989). Aun cuando algunos estudios macroecológicos señalan que no existen variables que tengan el mismo poder explicativo en todas las escalas, es probable que algunas relaciones sean tan esenciales que operen en todas las escalas, a pesar de no ser detectables en todas ellas (Whittaker et al 2001). Esta idea sintetiza la necesidad de realizar estudios multiescalares en el análisis de la diversidad.

Uno de los primeros patrones descritos por la ecología es la relación entre el número de especies y el área (Arrhenius 1921). Generalmente dicha relación se representa con una gráfica de dispersión de puntos para la que se ajusta una curva que representa la relación especies-área. Del análisis de las curvas a nivel global y local para distintos grupos taxonómicos se han generalizado los patrones descritos a continuación (Rosenzweig 1995). Al fijar los demás factores, la diversidad incrementa conforme lo hace el esfuerzo en el muestreo. El número de especies registradas incrementa rápidamente al principio debido a que se examinan más individuos, pero invariablemente éste se estabiliza a medida de que un número constante de especies raras permanece sin ser descubierto. La forma exacta de la curva depende de la distribución de la abundancia entre las especies; ésta será exponencial negativa si la abundancia pertenece a la serie log y potencial si la abundancia es log-normal. Si el área de muestreo es amplia el número de especies también incrementa. Esto se debe a que una extensión grande puede albergar una mayor gama de condiciones y a que en ésta se pueden colectar más individuos. A medida de que el área de muestreo aumenta el número de especies registradas sigue una ley potencial con exponente de aproximadamente 0.25 (Connor y McCoy 1979, Crawley y Harral 2001). En realidad, el exponente cambia de acuerdo con la escala y el tipo de datos incluidos (Connor y McCoy 1979, Rosenzweig 1995). Por ejemplo, la pendiente (z) de las curvas acumulativas especies-área, en escala logarítmica, para la Flora Británica tiene un valor bajo para la escala local ($z = 0.1 - 0.2$), alto para la mesoescala ($z = 0.4 - 0.5$) y bajo para la macroescala ($z = 0.1 - 0.2$). Estos resultados sugieren que no existe un único proceso que determine el cambio en la riqueza de especies en un intervalo amplio de escalas sino que son distintos los procesos que actúan para determinar la biodiversidad a diferentes escalas espaciales (Bell 2001, Condit et al 2002, Lennon et al 2001). Al considerar las implicaciones de la relación especies-área, es evidente que para evaluar el papel relativo de las variables bióticas y abióticas en la determinación de los patrones espaciales en la diversidad y evitar confusiones, las áreas comparadas deben de ser equivalentes (Whittaker et al 2001, Willis y Whittaker 2002).

Una elevada proporción de especies se concentra en las zonas tropicales del mundo. Al alejarse de estas zonas, el número promedio de especies por unidad de muestreo disminuye de manera gradual (Willig et al 2003). Este gradiente no sólo existe a nivel global (Gotelli y Ellison 2002). Un meta-análisis comparativo del comportamiento de 571 gradientes de distintos grupos taxonómicos (349 macroescalares *vs.* 222 mesoescalares) reveló que el patrón se mantiene entre escalas, aunque el decremento latitudinal en la diversidad es significativamente mayor para la escala macro (Hillebrand 2004). Aun cuando la explicación definitiva para este gradiente latitudinal aún no está disponible, recientemente se ha acotado el número de hipótesis plausibles. Particularmente, los modelos climáticos basados en la hipótesis especies-energía (Wright 1983) han recibido una notable atención debido a la correlación dada entre el clima y la latitud. En términos generales, la hipótesis especies-energía propone que el clima regula la cantidad de energía en el sistema, lo que a su vez establece los límites en la riqueza del sistema, ya sea mediante cascadas tróficas (Mittelbach et al 2001, Wright et al 1993) o a partir de restricciones fisiológicas (Currie 1991, Humboldt 1808). Indudablemente, el clima está relacionado con la riqueza de especies (Hawkins et al 2003). Sin embargo, la intensidad de la relación depende de la variable climática empleada, del grupo taxonómico y de la región geográfica explorada. Ésta fue la conclusión a la que Hawkins et al (2003) llegaron al estudiar 85 gradientes (> 800 km) de diversidad asociados con variables climáticas. Específicamente, reportaron que a nivel global la riqueza vegetal está determinada por la dinámica agua-energía medida a partir de la evapotranspiración anual (EA; relacionada con la productividad) y que en las regiones situadas al sur del paralelo 45° N dicha riqueza se asocia mejor con la precipitación (P). Por otro lado, encontraron que la riqueza de los vertebrados e invertebrados se relaciona fuertemente con la EA y con la P tanto a nivel global como para las regiones al sur de dicho paralelo, pero que en las regiones frías (al norte de 45° N) el potencial anual de evapotranspiración (PAE), una medida de la energía ambiental, explica mucho mejor la variación encontrada. Basados en esta evidencia, Hawkins et al (2003) concluyeron que la disponibilidad de energía ambiental explica la diversidad animal sólo en una pequeña fracción de la Tierra (al norte de 45° N), mientras que la disponibilidad de agua determina los gradientes del resto de la biodiversidad en la mayor parte del planeta. La medición de estos patrones sirve para generar modelos predictivos de la riqueza de especies a nivel macroescalar. El mejor ejemplo lo ofrece el trabajo de O'Brien (1998), quien desarrolló un modelo del potencial climático sobre la riqueza de especies, géneros y familias de plantas vasculares de Sudáfrica. El modelo establece que la riqueza se relaciona linealmente con la precipitación y parabólicamente con la energía del sistema (PAE). Según O'Brien, la riqueza y el clima están íntimamente relacionados debido a que los parámetros fundamentales, tanto de la actividad biológica (i.e. fotosíntesis) como del clima (i.e. ciclo hidrológico), dependen de la dinámica agua-energía. Otros esfuerzos por explicar las causas que subyacen al gradiente latitudinal se encuentran en los postulados de las teorías de la velocidad evolutiva y del área geográfica. La primera propone que la diversidad se incrementa en los trópicos debido a que las altas temperaturas aceleran las tasas de especiación como resultado del efecto combinado de las elevadas tasas de mutación, los reducidos tiempos generacionales y la fuerte presión de selección (Rohde 1992). Aun cuando esta teoría ofrece una explicación mecanicista basada en la teoría evolutiva, encontrar evidencia que la sustente es en sí una tarea desafiante y poco alentadora. En particular, los reportes para el grupo de las aves refutan los postulados centrales (Bromham y Cardillo 2003). La segunda teoría se sustenta en la relación especies-área descrita con anterioridad. Específicamente, ésta propone que los trópicos albergan más diversidad simplemente porque abarcan una mayor extensión geográfica. La evidencia en la que descansa esta teoría es confusa (Rohde 1997) y en algunos casos contradictoria (Kaufman y Willig 1998), por lo cual no se han podido generalizar sus predicciones. Es importante resaltar que el gradiente latitudinal en la diversidad es una abstracción burda de la realidad que en ocasiones se interrumpe tajantemente por el efecto de otros factores que sólo se hacen evidentes al analizar la mesoescala y la escala local (Stevens y Willig 2002). Un claro ejemplo de ello son las alteraciones en los patrones macroescalares provocados por los gradientes altitudinales presentes en el relieve. En varias ocasiones se ha propuesto que dichos gradientes generan un patrón en el comportamiento de la diversidad representado gráficamente (altitud vs. riqueza) con una curva en forma de joroba (hump-shaped). Sin embargo, el análisis cuantitativo de 204 gradientes altitudinales asociados con la riqueza de especies reveló que el efecto de la altitud depende completamente de la escala (Rahbek 2005). La curva de joroba domina claramente el patrón observado tanto a nivel local como en la mesoescala, pero en los grandes gradientes altitudinales (macroescala) la diversidad decrece linealmente conforme aumenta la altitud (Rahbek 2005). Al igual que con el gradiente latitudinal, los patrones observados no son generados por la altitud en sí, sino por los cambios en las variables asociadas al gradiente altitudinal (e.g. dinámica agua-energía).

Las variaciones en el relieve regional también promueven un incremento en la heterogeneidad ambiental (Huggett 1995). Dicho incremento se relaciona de forma positiva con la biodiversidad analizada en la mesoescala (Wilson 2000). Para sustentar esta aseveración emplearemos el estudio de la flora de la Península Ibérica. En dicho estudio se usaron más de un millón de registros de riqueza y datos ambientales para 315 unidades de 10 km × 10 km repartidas a lo largo y ancho de la península. A partir de un análisis ponderado de devianza, Pausas et al (2003) encontraron que tanto el número de sustratos geológicos como la superficie efectiva por unidad de análisis explican *ca.* 2/3 partes de la devianza registrada, lo que sugiere que la heterogeneidad ambiental juega un papel central en la determinación de los patrones de riqueza a nivel mesoescalar al proveer una mayor variedad de condiciones donde las especies puedan coexistir. La importancia de la heterogeneidad ambiental también ha sido reportada para la escala local (Vivian-Smith 1997). No obstante, los patrones descritos no han sido tan recurrentes como en la mesoescala. Mientras que algunos estudios reportan una relación positiva (e.g. Harner y Harper 1976), otros describen una relación neutral (e.g.Wilson 2000) o incluso negativa (e.g. Kleb y Wilson 1997) entre la heterogeneidad y la riqueza de especies. Por ello, Pausas y Austin (2001) sugieren que sin dejar de ser importante, la heterogeneidad ambiental podría jugar un papel secundario en la determinación de los patrones de distribución a nivel local al depender de otros factores ambientales como la disponibilidad de nutrientes (Wilson y Tilman 1995). A este respecto es importante mencionar que para esta escala se ha reportado que la riqueza de especies es baja en niveles bajos de nutrientes, alcanza el máximo en niveles intermedios y decrece gradualmente en niveles altos de nutrientes (Braakhekke y

Hooftman 1999). Al parecer ésta es una respuesta generalizada ante la disponibilidad de nutrientes a nivel local.

Muchos de los patrones que se observan en la distribución de la diversidad resultan de las interacciones biológicas. Las interacciones que más efecto tienen en la distribución son la competencia, la depredación, el parasitismo, el mutualismo y el comensalismo (Crawley 1997). Existe una idea generalizada de que las interacciones biológicas tienen un papel determinante sobre los patrones de distribución de las especies a nivel local y mesoescalar. Particularmente, la competencia es un factor clave entre las teorías que relacionan la riqueza local de especies con el régimen de disturbio (Huston 1994). Muchos estudios descriptivos y experimentales han reportado que la máxima diversidad se mantiene en niveles intermedios (frecuencia o intensidad) de disturbio, idea que sustenta a la llamada teoría del disturbio intermedio (TDI; Connell 1978, Grime 1973, Huston 1979, Tilman 1982). La TDI postula que cuando las tasas de disturbio son altas sólo pocas especies son capaces de recuperarse de los daños asociados al disturbio, mientras que cuando las tasas son bajas la riqueza se reduce debido a la exclusión competitiva causada por las pocas especies dominantes. En niveles intermedios de disturbio, las ventajas del disturbio (reducción competitiva inter- e intra- específica) son mayores que las desventajas debidas a los daños. Usualmente el pastoreo es considerado como una fuente importante de disturbio (Bakker y Ruyter 1981, Fensham et al 1999), y en relación con esta actividad se ha observado que a niveles intermedios de pastoreo la riqueza de especies se maximiza en diferentes tipos de comunidades vegetales, desde pastizales hasta comunidades arbustivas (Helle y Aspi 1983, McIntyre et al 1995, Pandey y Singh 1991). Aunque la TDI es aplicable en todas las escalas, encontrar evidencia para la macroescala es difícil debido a las limitaciones de muestreo después de que un evento de disturbio haya producido una peturbación en grandes extensiones de terreno (e.g. huracanes, erupciones volcánicas).

Desde una perspectiva biológica, es importante identificar otros mecanismos que permitan la existencia de varias especies al minimizar la exclusión competitiva a nivel local. A partir de una extensa revisión bibliográfica, Wilson (1990) identificó doce procesos que, de operar verdaderamente, cada uno permitirían la coexistencia entre especies: (1) diversificación de nicho, (2) presión por plagas, (3) igualdad de oportunidades, (4) cambio climático gradual, (5) disturbio intermedio, (6) diferencias en las historias de vida, (7) composición inicial de parches, (8) efecto espacial de masa, (9) redes competitivas circulares, (10) sucesión cíclica, (11) Agregación, y (12) coevolución estabilizadora. Luego de ponerlos a prueba, Wilson (1990) encontró que en la comunidad vegetal de Nueva Zelanda la coexistencia entre especies se debe al efecto de seis de ellos (1, 2, 4, 8, 10, 11). Aunque cada uno de estos procesos es por sí mismo un tema amplio de discusión, se ha reportado la importancia de los mecanismos 1, 2 y 4 en la determinación de los patrones locales y mesoescalares de diversidad para otras regiones del mundo (Harms et al 2000). Particularmente, la evidencia sugiere que la distribución dispersa de los árboles de la misma especie en las selvas húmedas puede ser explicada por el efecto de la presión por plagas (Barone 2000).

Es importante destacar que el cambio en la escala de análisis modifica nuestra percepción de los patrones observados y de las causas que los generan. En particular, la modificación del tamaño del grano tiene una consecuencia importante: al emplear granos gruesos en los estudios se tiende a homogeneizar los patrones observados, debido al efecto de promediar áreas más grandes. Por lo tanto, el uso de granos gruesos privilegia la observación de patrones generados por causas de efecto global, como lo son el clima o la orografía. El uso de granos finos realza los efectos de causas locales, como las interacciones biológicas o la concentración de nutrientes (Rahbek 2005).

La relación entre la riqueza local y la regional también puede afectar los patrones observados. Básicamente la riqueza local puede ser igual a la regional, directamente proporcional pero menor que la regional o no sobrepasar un límite superior, aun cuando la riqueza regional continúe aumentando (Gaston 2000).

Los factores ambientales y los mecanismos biológicos podrían no ser los únicos elementos involucrados en la determinación de los patrones de diversidad. Recientemente se propuso una teoría que no requiere de gradientes ambientales asociados con la latitud ni que la biota responda a los gradientes ambientales, si éstos realmente existen. La hipótesis del dominio medio (HDM) postula que el acomodo aleatorio de intervalos geográficos de distintos tamaños dentro de un dominio de límites infranqueables genera un pico en la riqueza de especies a la mitad del dominio (Colwell y Hurtt 1994, Colwell y Lees 2000).

Desde que apareció, la HDM ha sido fuertemente cuestionada debido principalmente a que no explica cómo se pueden originar intervalos geográficos de distintos tamaños en ausencia de restricciones ambientales, pero también por faltar a los supuestos generales de los modelos nulos (ver Zapata et al 2005). No obstante dichas objeciones (rebatidas por los postulantes (ver Colwell et al 2005), la idea básica no debe tirarse por la borda ya que como se ha reportado, estos modelos permiten generar patrones conocidos en la diversidad a partir del acomodo aleatorio de intervalos geográficos (e.g. Willig y Lyons 1998). Esto simplifica notablemente el panorama ya que reduce el problema de la distribución de la diversidad a una cuestión matemática. De generalizarse los modelos de dominio medio, la investigación podría enfocarse en la ponderación del efecto de las restricciones geométricas, eliminarlas de la ecuación y así entender mejor el efecto del resto de las variables estudiadas.

Es claro que ninguno de los patrones o procesos mencionados es independiente del resto y que forman parte de un sistema muy complejo y que varía en numerosas dimensiones. Sin embargo, para llegar a poder identificar los que son más importantes se debe considerar sus mecanismos de acción y analizar la posibilidad de escalar la información desde la micro o macroescala hacia la mesoescala (Wu et al 2006). De manera general, la acción de escalar se refiere a la tarea de descubrir y explicar cómo una variable de estado o parámetro dinámico cambia con alguna otra variable (Storch et al 2007). El escalamiento en ecología quizá esté mejor desarrollado en el contexto del escalamiento espacial, por ejemplo, en el análisis de los cambios en los patrones observados con respecto a la escala espacial de observación. Como se mencionó antes, los ecólogos han notado que los patrones y procesos varían con la escala, sin embargo sólo hasta la actualidad ha sido posible formular reglas cuantitativas que describan dichos cambios (Wu et al 2006). Escalar la diversidad es una tarea complicada que requiere de grandes conjuntos de datos, pero éstos no siempre están disponibles (Gaston 2000). No obstante, para plantear qué procesos afectan la diversidad en la mesoescala se pueden analizar los fundamentos expuestos. Por ejemplo, las interacciones biológicas de las plantas vasculares tienen lugar en la micro y mesoescala por depender de otros factores como la contigüidad y el vecindario biológico (Crawley 1997). Por ello, factores como la depredación, el parasitismo, el mutualismo y el comensalismo no son evidentes en la macroescala. Asimismo, la dispersión vegetal es otro factor que generalmente ocurre sólo hasta la mesoescala. La heterogeneidad ambiental y el disturbio se encuentran entre los fenómenos más importantes en la mesoescala (Houle 2007). En diversos estudios se ha demostrado que los paisajes con niveles altos de heterogeneidad albergan más especies que los que son poco heterogéneos (Fahrig 2003). Por otro lado, los factores que actúan en grandes regiones geográficas como el clima dominan las teorías en la macroescala (Gaston 2000).

La tarea de identificar los agentes causales de la diversidad biológica en la mesoescala a partir de las teorías existentes es de suma importancia. Sin embargo, se debe continuar con la obtención de información específica para dicha escala, para así poder generar modelos cuantitativos multiescalares que permitan estudiar el comportamiento de la biodiversidad.

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CAPÍTULO 3

Vegetation heterogeneity and life-strategy diversity in the flora of the heterogeneous landscape of Nizanda, Oaxaca, Mexico

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Folia Geobotanica (2010), 45: 143-161

In the vast territory of North and Central America, only three lowland areas have distances between the Atlantic and the Pacific coasts sufficiently short to enable an intense biotic exchange between these two oceanic watersheds: the Isthmus of Tehuantepec in Mexico, the Isthmus of Panama, and the Isthmus of Papagayo in Nicaragua (Steenburgh et al 1998). Therefore, these areas represent potential biological corridors for the thermophilous biota of Mesoamerica. Among these corridors, the Isthmus of Tehuantepec is the most northerly located, which makes it very relevant for North American biogeographic patterns (Gonzalez-Silvera et al 2004). Mesoamerica is one of the most biologically interesting areas in all of tropical America due to its floristic richness (Kier et al 2005), its endemic component (Lorence and García-Mendoza 1989, Pérez-García et al 2001, García-Mendoza 2004), and its role as a contact zone between the tropical flora of seasonally dry regions of

North America with that of southern Amazonian floras (Rzedowski 1991, Wendt 1993). Undoubtedly, the series of successive biogeographic exchanges that took place in this region through geologic history are very complex; for example, the Isthmus has been proposed as having acted as a selective filter for several taxa (Peterson et al 1999, Cevallos-Ferriz and González-Torres 2005). A complex suite of ecological mechanisms that currently allow the maintenance of a very diverse flora locally (Pérez-García et al 2005) confer additional biological interest to the region.

Considering its large plant diversity, it is surprising that very few detailed floristic studies have been conducted in Oaxaca's Pacific slope, particularly in the Isthmus of Tehuantepec (Zizumbo and Colunga 1980, Torres-Colín 1989, 2004, Torres-Colín et al 1997, Pérez-García et al 2001, Salas-Morales et al 2003, 2007). Moreover, its vegetation has been described mostly based on physiognomy rather than on precise compositional data and species' distributional patterns. Consequently, numerous factors affecting community structure may have been overlooked. An important one refers to the ways in which plants cope with the environment through vegetative features (Bhattarai and Vetaas 2003, Reich et al 2003, Rowe and Speck 2005), which may be correlated with the plant's phenological and reproductive characteristics (Westoby et al 1990, Ramírez 2002), and with their biotic interactions (Çakan and Karataş 2006). Worldwide, few studies have attempted to classify all species of a single flora in ecological groups for any highly diverse seasonally dry tropical region (Gentry 1995, Batalha and Martins 2004). This is relevant, as the characteristic seasonality of these systems may have consequences on species' survival and growth patterns, thus leading to the development of strategies differing from those displayed by the same species under different environmental conditions (see Rowe and Speck 2005).

The first floristic account that provided detailed information on species distributions for a vegetation mosaic in the Isthmian region comes from the surroundings of the village of Nizanda (Pérez-García et al 2001). In that inventory, the occurrence of 746 species distributed in seven primary vegetation types or in secondary vegetation was reported. This preceding work led to the question whether further floristic investigation at this locality was warranted. In this paper we aim to show that additional investigation was needed by presenting new results derived from more than one decade of floristic prospective effort in the region. We report a numerical analysis of the regional flora together with a species classification according to life strategies, as this information allows to approach with fresh eyes the study of the plant distribution patterns within a landscape. Specifically, this study aimed at: *i*) providing an updated floristic checklist for the region, *ii*) characterizing the regional plant communities by pointing out their prevailing plant species, *iii*) providing a description of the local flora based on growth form, life form, growth type, and growth habit spectra, and *iv*) conducting a broad biogeographical analysis of the flora of Nizanda region.

Study Region

Nizanda (16°39′ N, 95°00′ W) is located in the southern portion of the Isthmus of Tehuantepec, Oaxaca State (Figure 1), just in the transition between the Central Isthmian Mountain Ranges and the Tehuantepec Coastal Plain (Williams 1939, Ferrusquía-Villafranca 1993). Elevation ranges from 100 to 750 m a.s.l., but most of the area lies between 150 and 300 m, particularly in the shale hills area. The metamorphic bedrock matrix is occasionally interrupted by faults where limestone rocks outcrop, reaching elevations of up to 450 m (Pérez-García and Meave 2004). Climate is typical of the Pacific watershed lowlands in southern Mexico, i.e., warm sub-humid, with summer (June–September) rains (Aw_0; García 2004). Annual precipitation is ca. 900 mm. After the short rainy season, precipitation is almost non-existent, except for some rain events caused by the arrival of cold polar air masses ("*nortes*") from the Gulf of Mexico during fall and winter. Considering the extent of the study area (ca. 80 km^2), the overall climate is homogeneous, except at the highest reaches of Mount Cerro Naranjo, where humidity is notoriously higher due to the combined effects of elevation and fog persistence. Thus, environmental heterogeneity related to relief and surface lithology appears to be the major determinant of vegetation variability in the region.

Pérez-García et al (2001) described seven primary vegetation types for this region: (1) gallery forest, (2) spiny scrub, (3) xerophytic scrub, (4) savannah, (5) tropical dry forest (TDF), (6) tropical semi-deciduous/semi-evergreen forest, and (7) aquatic vegetation. A considerable surface of secondary vegetation was also reported. Only savannah and TDF cover continuous areas of considerable extent, whereas the remaining types are more limited in area. López-Olmedo et al (2006) examined structure and floristics of savannahs and reported a strong dominance of graminoid herbs (Poaceae and Cyperaceae). Strikingly, these plant groups are lacking in the xerophytic vegetation growing on the limestone outcrops located a few hundred meters away from the savannahs (Pérez-García and Meave 2004, 2006). Pérez-García and Meave (2004) distinguished three plant communities typical of limestone outcrops: TDF on more developed soil, TDF growing directly on the limestone bedrock, and xerophytic scrub. In turn, Lebrija-Trejos (2001) found clear-cut differences in the floristic composition of riparian communities, allowing the distinction between tropical semi-evergreen forest and the structurally more simple gallery forest; the former thrives on relatively shallow soils, whereas gallery forest is typical of floodplain habitats, where soils are deeper and sandier. In Nizanda, previous work indicated that floristic composition is more sensitive to small environmental variations than community structure (Gallardo-Cruz et al 2005, 2009), suggesting that the former is a relevant variable in characterizing regional plant communities.

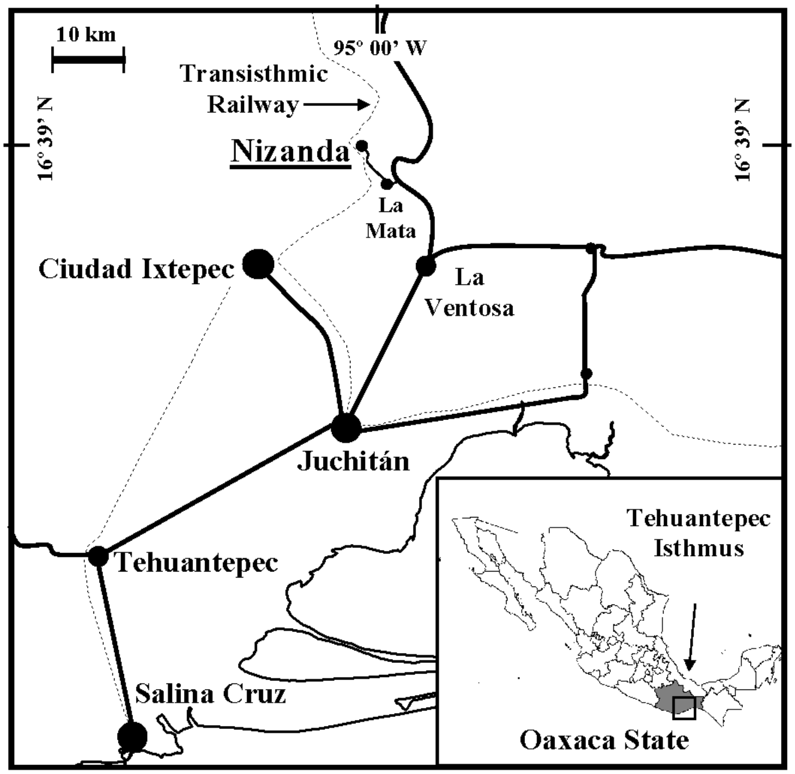

Figure 1. Location of the study site in Oaxaca state, southern Mexico.

Methods

The botanical exploration of this locality resulted in a collection of over 2,500 specimens. Vouchers are deposited in MEXU, MOBOT, SERO and XAL. Concurrently to the preparation of the regional floristic inventory, vegetation was sampled with 188 100-m^2 plots surveyed in different vegetation types; although minor sampling variants existed among them (Lebrija-Trejos 2001, Pérez-García and Meave 2004, Gallardo et al 2005, Sierra-Huelsz 2005), presence-absence data are comparable. For comparative purposes, we constructed a single database for all species recorded in the sampling. Plots were preferentially placed in well-preserved vegetation, i.e., lacking recent disturbance signs such as stumps, fire or overgrazing. The sampling attempted to include as much of the regional topographic and lithologic variability as possible.

We assured taxonomic reliability in plant determinations by involving a set of botanical experts in this task (Electronic Supplementary Material **1**). Nomenclature for genera and families follows Torres-Colín et al (1997) and Pérez-García et al (2001). For each species we recorded the vegetation type where it was found (more than one was possible), using both the information obtained from the sampling and from the regional floristic survey. Clear occasional occurrences in a given vegetation type, mostly corresponding to seedlings and saplings, were excluded from that community's record.

Four categorizations for the flora were performed at the species level based on the following criteria: (1) growth form, (2) life form, (3) growth type, and (4) growth habit. For each of them several categories were established. Each species was assigned to only one category for each criterion. For the first categorization we used the most developed form displayed by the species in the region; that is, if a species was found growing as a tree in the forest and as a shrub in the savannah, it was solely categorized as a tree. Differentiation between trees and shrubs was based on a 3-m height threshold. Non-woody plants capable of attaining large sizes (including arborescent plants such as palms and succulents) were also categorized according to their maximum heights. For the life form categorization we applied Raunkiaer's criteria (Müller-Dombois and Ellenberg 1974). In the suffrutex category of the growth type categorization, we included those plants whose basal portions were perennial, lignified structures, regardless whether the plant's aerial parts die during the unfavourable dry season. The growth habit categorization included the following groups: epiphyte, terrestrial, aquatic and semi-aquatic (this category only applies to flooded open areas, and thus it did not include riparian forest species), and lithophytic (species living on bare rock).

The distributional patterns of the flora of Nizanda were examined to assess the biogeographical role of the Isthmus of Tehuantepec. To this end, we performed an extensive search beyond Nizanda's limits of localities where these species have been collected. Moreover, we extracted biogeographical information from the unpublished database of J.L. Villaseñor. This database was constructed by compiling information from 265 floristic checklists, florulas and floras of Mexico, which enabled the gathering of information on 23,951 species growing wild in Mexico (last update, January 2009). This database also includes information on worldwide occurrence of these species obtained from published floras and botanical surveys elsewhere. Our analysis was restricted to the species level and included both native and alien taxa, but excluded undescribed species. The database was also used to calculate Sørensen's similarity index (Magurran 2004) between pairs of Mexican localities that met the following criteria: (1) that they had a floristic inventory available that included some low-elevation areas (<2,000 m a.s.l.); and (2) that the inventories came preferably from relatively small areas. Floristic lists used to calculate the Sørensen index, for binary data (presence/absence) of species occurrence were as follows: La Sepultura, Chiapas (Castillo 1996), La Vainilla, Guerrero (Gallardo 1996), Northern Veracruz (Gutiérrez 1993), Los Tuxtlas, Veracruz (Ibarra-Manríquez and Sinaca 1987), Cape Region, Baja California Sur (Lenz 1992), Tabasco Mountains (López-Hernández 1994), Chamela, Jalisco (Lott 1993), Sierra de Huautla, Morelos (Maldonado 1997), Río Mayo, Sonora (Martin et al 1998), La Lacandona, Chiapas (Martínez et al 1994), Calakmul, Campeche (Martínez et al 2001), Central Depression, Chiapas (Reyes-García and Sousa 1997), Zimatán, Oaxaca (Salas-Morales et al 2003), Río Hondo, Puebla-Oaxaca (Tenorio 1997), Álamos, Sonora (Van Devender et al 2000), Rincón de la Vía, Guerrero (Verduzco and Rodríguez 1995), Tenabo, Campeche (Zamora 2003).

To further examine the geographical connections of the vascular flora of Nizanda, we verified the occurrence of these species in seven regions, many of which represent well-defined biogeographical regions (Morrone 2005). Each species could be present in none, one or several localities of these regions, thus their percent representation does not add up to 100%. The first such region was the Pacific watershed of Mexico; although Nizanda is located in this region, for a species to be tallied as being present here, it had to occur in at least some other locality. The remaining areas for this analysis were the Mexican Atlantic watershed, North America (excluding Mexico), Central America, South America, the West Indies, and Eurasia/Africa. Finally, we identified two sets of species for which the Isthmus of Tehuantepec represents one geographical boundary, i.e., their (east) southern or (west) northern distribution limit. Unlike the previous analysis, assignment of the species to any of these categories was mutually exclusive.

Sample Classification and Ordination

We performed three classifications of the floristic information from the 188 sampling plots (presence/absence data), using Ward's method and Euclidean distances (Kent and Coker 2003, Aho et al 2008). The analyses were performed at the species, genus and family levels. The inclusion of the latter two higher-level taxa allowed us to gain insight on the differentiation of evolutionary histories in the region (Magurran 2004, Pérez-García and Meave 2006), as well as of life strategies (Reich et al 2003), as they are potential indicators of lineage-related morphological and physiological constraints and adaptations (Webb et al 2002). In addition, a DCA ordination was performed on the sampling plots at the species level only. The classification analyses where conducted using STATISTICA 6.0 (StatSoft, Inc. 2001), whereas for the DCA Community Analysis Package 1.2 was used (Pisces Conservation Ltd. 1999).

Results

Regional Floristic Inventory

The updated regional inventory included a total of 920 species, distributed in 553 genera and 124 families (Electronic Supplementary Material 2). In comparison with the previously published checklist, the updated inventory resulted in the exclusion of 12 species, but included an additional 187; this numerical change represents an increase of ca. 25%. Families added in the current inventory are mainly represented by species collected in the montane evergreen forests (Araliaceae, Begoniaceae, Davaliaceae, Valerianaceae, Violaceae, and one of two Melastomataceae), but also in tropical dry forests (Lythraceae, Opiliaceae and Polemoniaceae). Considering all taxonomic levels, there were 51 taxonomic modifications in respect of the previous publication by Pérez-García et al (2001). Excluded from the present list were Lemnaceae (now in Araceae), Moringaceae (occurring in Nizanda only as cultivated plants) and Lomariopsidaceae (now in Aspleniaceae), so that the final figure for family richness apparently reflects an increase of only five families, but it is actually of nine.

Forty-three families (34.6%) were represented by a single species. In contrast, the 10 most diverse families had 397 species (43%), and 28 families had more than nine species each (71.2% of the species). Among the most species-rich families were Fabaceae (66 species), Poaceae (59), Asteraceae (49), Orchidaceae (48) and Euphorbiaceae (43, Table **1**). Species were also unevenly distributed among genera. The nine most diverse genera (≥ 8 species) had together 83 species (9% of total species richness), whereas 381 genera were represented by a single species. The richest genera were *Ipomoea* (12 species), *Croton* (11) and *Tillandsia* (10; Table 1).

Table 1. The most diverse taxa of the flora of Nizanda. S: number of species; G: number of genera.

Richest families				Richest genera	
By species	S	By genera	G	Genus (family name)	S
Fabaceae	66	Asteraceae	37	*Ipomoea* (Convolvulaceae)	12
Poaceae	59	Poaceae	35	*Croton* (Euphorbiaceae)	11
Asteraceae	49	Orchidaceae	32	*Tillandsia* (Bromeliaceae)	10
Orchidaceae	48	Fabaceae	30	*Euphorbia* (Euphorbiaceae)	9
Euphorbiaceae	43	Rubiaceae	19	*Acacia* (Mimosaceae)	8
Mimosaceae	36	Euphorbiaceae	17	*Dioscorea* (Dioscoreaceae)	8
Rubiaceae	28	Cactaceae	16	*Cyperus* (Cyperaceae)	8
Caesalpiniaceae	26	Mimosaceae	16	*Cordia* (Boraginaceae)	8
Convolvulaceae	21	Acanthaceae	14	*Mimosa* (Mimosaceae)	8
Cactaceae	21	Bignoniaceae	14		

Biogeographical Relations

Although the flora of Nizanda consists mostly of native species, there was a small fraction (22 species) of wild alien species. Poaceae was the family with more exotic species (12), followed by Caesalpiniaceae and Cyperaceae with two species each. The remaining six species each belong to different families.

The most noticeable aspect of the geographical relations of Nizanda was that most species (>90%) in its flora also occur in the two major oceanic watersheds of Mexico (Table 2). The next region showing a strong relationship with Nizanda was Central America, as more than three-quarters of its species also occur there. As expected, increasingly distant regions and stronger geographical barriers resulted in weaker affinities, the lowest one being with Eurasia/Africa, where only 11.4% of Nizanda's species occur. When focusing on those species in the flora of Nizanda for which the Isthmus of Tehuantepec represents one of its geographical boundaries, this region turned out to be the northern limit for many more of them (582; 63.2% of the flora) than their southern limit (84, 9.1%).

Table 2. Extended occurrence of the species present in the flora of Nizanda in further biogeographical regions. Note that the occurrence of any species in one area is not mutually exclusive with its occurrence in any other area, and therefore the shown percentages do not total 100.

Geographical region	Number of species (%)
Mexican Pacific watershed	894 (97.1)
Mexican Atlantic watershed	854 (92.7)
Central America	707 (76.8)
South America	473 (51.4)
West Indies	377 (40.9)
North America (excluding Mexico)	246 (26.7)
Eurasia/Africa	105 (11.4)

The largest floristic similarity of the flora of Nizanda according to Sørensen's index (SI) was found with Zimatán region (SI=43.2%), located nearby (<250 km) on the Pacific coast of Oaxaca state. This strong link was followed by an also high similarity with Chiapas

Central Depression (SI=36.5%), a region equally distant from and climatically similar to Nizanda, although technically it is a basin draining towards the Gulf of Mexico (Atlantic watershed). Nizanda also had high SI values (>20%) with localities from the two oceanic watersheds, in this order: Chamela, Jalisco (33.7%), Calakmul, Campeche (27.3%), La Vainilla, Guerrero (26.3%), Northern Veracruz (22.4%), and Sierra de Huautla, Morelos (21.4%). High similarities were found even with very distant localities of the Pacific watershed (e.g., Los Álamos, Sonora, 1,820 km from Nizanda, SI=19.4%), whereas some similarities with nearby Atlantic watershed localities were smaller (e.g., Los Tuxtlas, Veracruz , 210 km, SI=17.4%).

Classification and Ordination Analyses

In the 188 sampling plots 716 species were recorded, of which 502 were determined to species level; this set was used for classification and ordination analyses. In the dendrograms corresponding to the three taxonomic levels all savannah samples formed a single cluster, and it was in all cases the best-differentiated one (linkage distance ≤70 for the three levels; Figure 2).

The distinctly different floristic character of the savannah was confirmed by the DCA ordination, as all savannah samples concentrated on the right end of Axis 1, and it was the only set showing very little variation on axis 2 (Figure 3). The remaining samples tended to be distributed on the left side of axis 1 (<600), but were spread along axis 2. Within this large cluster, differences were observed between the xerophytic scrub and TDF on bare rock (on the upper end of axis 2) and the two more mesophytic communities (riparian forests and mountain evergreen forest (MEF)), located near the lower end of axis 2 and the left side of axis 1). TDF samples were situated in the lower-middle section of the ordination space, in an arch-like sample cluster.

The species level classification split riparian vegetation samples (*sensu* Lebrija-Trejos 2001) in two groups: riparian forest ("selva mediana" according to the classification by Miranda and Hernández-X. 1963) and gallery forest. The riparian forest was the second best differentiated set, as it kept its individuality up to a linkage distance slightly over 40

(Figure 2a). The distinction of these samples from other vegetation types decreased when moving up in the taxonomic hierarchy. At the genus level classification riparian vegetation became a single group (gallery forest and riparian forest) at a linkage distance of ca. 20, but this group also included MEF samples (Figure 2b). At the family level classification this group was less well differentiated from TDF samples, and some piedmont TDF plots became mixed with those from riparian forests (Figure 2c).

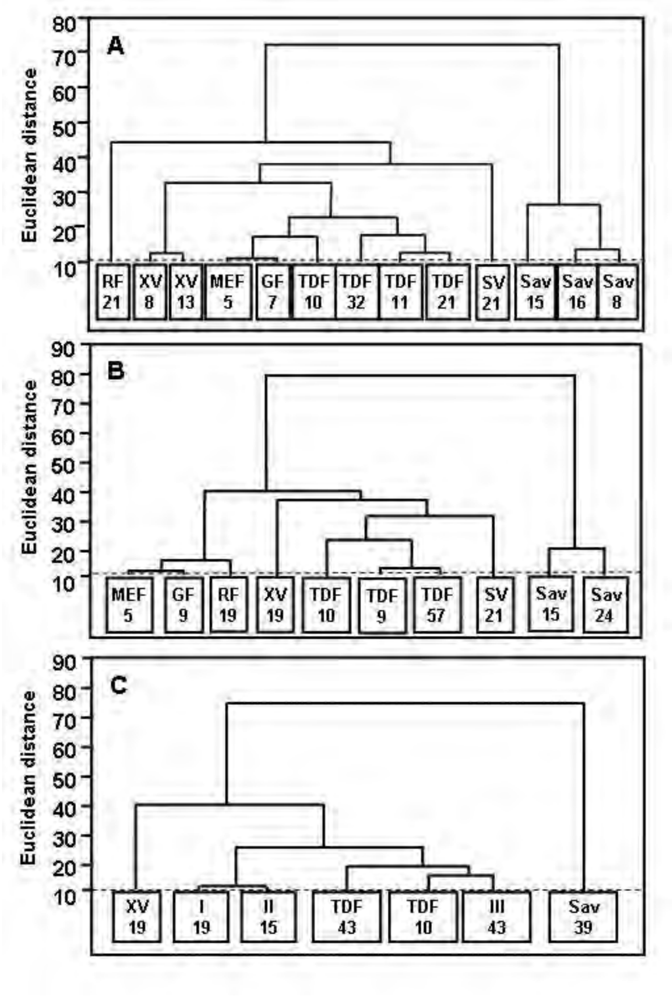

Figure 2. Dendrograms displaying affinities based on floristic structure among 188 vegetation samples (100 m2) from Nizanda, Mexico. The classifications were performed with Ward's method and Euclidean distances, based on binary data (presence/absence) matrices. (a) species-based, (b) genus-based, (c) family-based classifications. GF – gallery forest, MEF – mountain evergreen forest, RF – Riparian forest, Sav – savannah, SV – secondary vegetation, TDF – tropical dry forest, XV – xerophytic vegetation (including xerophytic scrub and TDF on exposed limestone bedrock). In c, Roman numeral I indicates a cluster containing MEF and RF samples, Roman numeral II is a cluster including GF plus TDF, and Roman numeral III indicates a cluster of TDF plus SV.

The third most distinct group in the species level classification (linkage distance ca. 37) was formed by samples dominated by short (<6 m), deciduous, spiny legumes commonly found in old fallows, which had been previously classified in the initial vegetation classification as spiny scrub (Pérez-García et al 2001). This group composed of secondary vegetation plots was not very consistent at higher taxonomic levels. In turn, xerophytic vegetation samples (i.e., xerophytic scrub plus TDF on exposed limestone bedrock; Pérez-García and Meave 2004) formed a very consistent group across taxonomic levels, and was particularly distinct at the family level classification (Figure 2c).

Based on the results of the classification analyses, only the following floristic sets will be hereafter considered: gallery forest (GF), mountain evergreen forest (MEF), riparian forest (RF), savannah, tropical dry forest (TDF), and xerophytic vegetation (XV; including xerophytic scrub and TDF on exposed limestone bedrock). In addition, the rich ensemble of ruderal species typical of open areas such as roadsides and crop fields were included in a single category named secondary vegetation (SV). Finally, a small group of species associated to water bodies, mainly in open, sunlit sites, was classified as aquatic and sub-aquatic vegetation (AV).

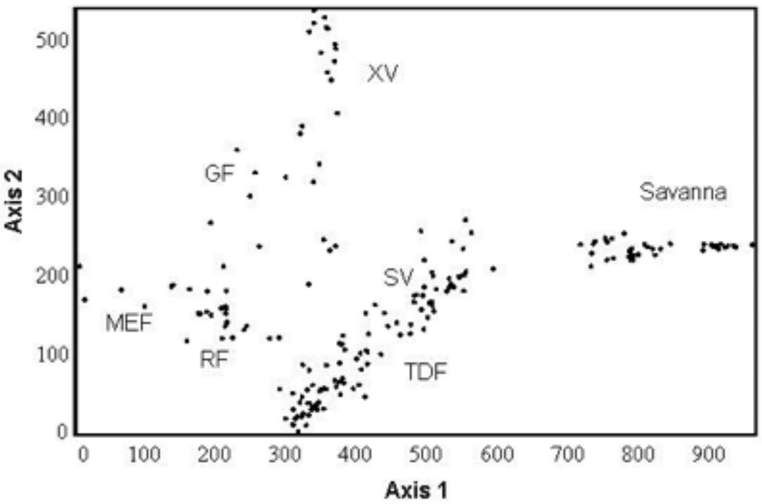

Figure 3. Species-based detrented correspondence analysis (DCA) ordination of 188 vegetation samples (100-m2 plots) from Nizanda, Mexico. GF – Gallery forest, MEF – mountain evergreen forest, RF – riparian forest, TDF – tropical dry forest, Sav – savannah, SV – secondary vegetation, XV – xerophytic vegetation (including xerophytic scrub and TDF on exposed limestone bedrock).

Floristics by Vegetation Types

Floristic richness and composition varied considerably among communities. No single species occurred in all of them. The most widely distributed species was *Croton yucatanensis*, which appeared in five out of the eight floristic sets ultimately recognized, despite being a scarce taxon in the region. Nineteen species (2% of the flora) that occurred in four vegetation types ranked second regarding distribution width, and 80 species were recorded in three communities.

TDF was the vegetation type hosting the largest floristic diversity in Nizanda at all taxonomic levels (82 families, 283 genera and 424 species). This community was followed by the two mesophytic forests (RF and MEF) also at all taxonomic levels. Interestingly, in spite of being the second most extended community in our study area, the savannah was characterized by much smaller family diversity (this community ranked third in species richness but sixth in family richness), but not at the genus and species levels.

Overall, the species distribution patterns by family were similar between TDF and RF, but this was not the case for the remaining vegetation types (savannah, MEF and XV, Figure 4). By using TDF as a reference for comparing such patterns by vegetation type, the dissimilarities in species richness by family between them can be better perceived. Because of such differences, family patterns in the regional flora were not identical to any of those observed in individual vegetation types. For example, with 32 grass species, Poaceae is the largest family in savannah, but it is second on the general list, whereas this family occupied the ninth position in TDF. A similar situation was observed for Orchidaceae, whose largest diversity was recorded in MEF and XV, and that ranked fourth on the regional list despite its low diversity in TDF. This implies that a family ranking high in the regional flora did not necessarily have a high position in every vegetation type.

Biological Spectra

The growth form spectrum for the entire flora showed that, with slightly more than one-fourth of the species (248 species; 26.9%), forbs were the most numerous ensemble, with trees being the second one (223 species; 24.2%). Shrubs (170; 18.4%) and climbers (159;

17.2%) occupied the third and fourth positions (Figure 5a). Phanerophytes were by far the most abundant category in the life-form spectrum for the regional flora (52%), followed by hemicryptophytes (14.9%) and chamaephytes (14.4%; Figure 5b). In terms of growth type, herbs (428 species) were slightly more diverse than woody plants (409). These two categories together accounted for >90% of all species. Inversely, suffruticose, parasites and succulent plants represented each <5% of the flora (Figure 5c). Regarding the growth-habit spectrum, the most different vegetation types were MEF and VX. The epiphytes for MEF, and both epiphytes and lithophytes were better represented in XV than in all other vegetation types (Figure 5d). The categories to which each species belong are shown in Electronic Supplementary Material 2.

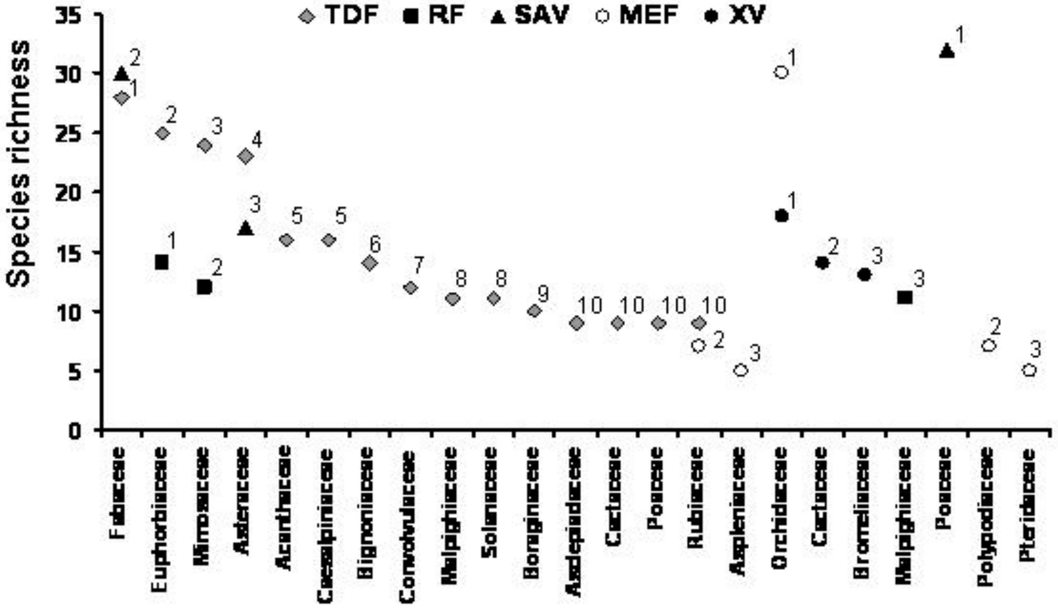

Figure 4. Species richness in the families with the highest numbers of species in each of the five most diverse vegetation types of Nizanda, Mexico. The numbers above the symbols indicate the ranks of the top ten (in tropical dry forest; TDF) or the top three (in other vegetation types) richest families. MEF – mountain evergreen forest, RF – Riparian forest, Sav – savannah, XV – xerophytic vegetation.

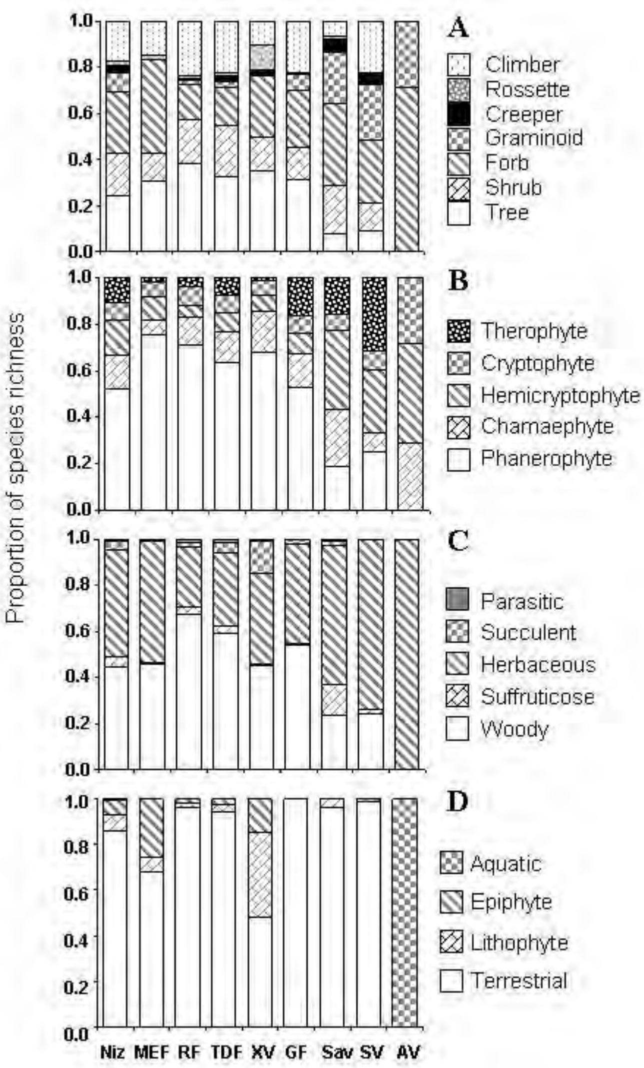

Figure 5. Biological spectra of the species in Nizanda, Mexico, for the entire flora (Niz) and by vegetation type (MEF – mountain evergreen forest, RF – riparian forest, TDF – tropical dry forest, XV – xerophytic, vegetation, GF – gallery forest, Sav – savannah, SV – secondary vegetation, AV – aquatic and semi-aquatic vegetation). (a) growth form; (b) life form, according to Raunkiaer's criteria; (c) growth type; (d) growth habit.

Discussion

Regional Floristics

The new efforts of botanical exploration in Nizanda resulted in an increase equivalent to one-fourth in the number of species of the previously published checklist. Some of these species represented new records for the region or even for the entire state, as exemplified by *Leochilus scriptus* (new record for Oaxaca), *Quassia amara* and *Rinorea hummelii*, all of them typical of very humid habitats. Even further, a few collected specimens of the genera *Chysis* and *Catopsis* apparently represent new species to science, and they are marked as *Chysis* sp. and *Catopsis* aff. *nutan*s. The known richness of *Ipomoea* and *Tillandsia* in Nizanda may still increase in the future. For example, the epiphytic habit of *Tillandsia* species makes it difficult to collect them, particularly in the mountain evergreen forest (MEF). Also, the number of *Acalypha*, *Piper* and *Peperomia* species may continue to increase as the determination process makes further progress.

The addition of nine families to the current checklist represents an increase of ca. 7.6% for a taxonomic category considered to be very stable (Villaseñor et al 2005), although each one of these families contributed only with one or two species. This finding undoubtedly reflects a biological fact, as such family-level additions resulted mainly from collections made in the community developing at the climatically most different site. It is also related, however, to an insufficient taxonomic knowledge; this is the case for the families recently encountered and listed for the tropical dry forests (TDF).

The majority of Nizanda's most diverse families are typical of dry tropical habitats, but they do not always occupy the same prominent places in the floras (Gentry 1995, Lott and Atkinson 2002; 2006, Trejo and Dirzo 2002, Salas-Morales et al 2003). Similarly, the most species-rich genera occurring at Nizanda, namely *Ipomoea*, *Croton* and *Tillandsia*, are common throughout the Neotropics (Torres-Colín 1989; 2004, Gentry 1995, Trejo 2005). However, the absence from this group of the very diverse genera *Cassia* s. lat. (including *Senna*), a genus that is more diversified in southeastern Mexico and other neotropical areas, and *Euphorbia*, which is more diverse in Chamela (Gentry 1995, Lott and Atkinson 2002, 2006), is remarkable.

Vegetation Types in Nizanda

The classification analyses showed that the grouping of samples is consistent with most vegetation types previously recognized for the region based on physiognomic attributes

(Pérez-García et al 2001). In terms of floristic composition, the savannah emerged as the most distinct vegetation type. Savannah establishes on habitats with very shallow soils where fire is a recurring disturbance factor. Fire is probably responsible for the uniqueness of this community at Nizanda, as it has been reported for other localities (Pausas and Bradstock 2007). Conversely xerophytic vegetation (XV), which also thrives on sites with shallow soils – or even with no soil – hosts many epiphytic and lithophytic species, as well as many succulent plants, which are virtually absent from the savannah. Besides, in XV not a single grass species is present, unlike savannahs where 32 species of this family were recorded and where one of them (*Trachypogon spicatus*) accounts for 80% of dominance (López-Olmedo et al 2006).

The classification and ordination analyses provided numeric arguments that supplemented our field observations, and emphasized the need of reclassifying Nizanda's plant communities. Physiognomy and composition play supplementary roles, as similar physiognomies may be associated to substantially different compositions. This was the case of tropical dry forests (TDF) on more developed soils and TDF on bare limestone bedrock, as the latter turned out to be more akin in its floristic composition to the xerophytic scrub (Pérez-García and Meave 2004). The family level classification revealed overall larger similarities between samples when compared to both the species and genus-based classifications. Thus, it is noteworthy that even at this higher taxonomic level some groups kept a clearly distinct identity, as was the case of savannah and XV samples. The high frequencies of Polygalaceae, Oxalidaceae, Turneraceae and Caesalpiniaceae appear to be responsible for the strong grouping of savannah samples, whereas Bromeliaceae, Cactaceae, Commelinaceae and Agavaceae may be accountable for the well differentiated position of XV.

In comparing species richness by family among the five richest vegetation types we found that their distributions were not coincident, possibly reflecting phylogenetic constraints in their abilities to colonize different environments. This is suggested by the large diversities in families whose species have high humidity requirements, such as epiphytes in the Orchidaceae family, ferns of the Polypodiaceae, Aspleniaceae, Pteridaceae and Thelypteridaceae families, and palms of the *Chamaedorea* genus (Arecaceae) in MEF.

Similar situations have been reported for other systems worldwide (Grubb et al 1963, Bhattarai and Vetaas 2003).

Biological Spectra

Assigning each species to a single category in all four biological spectra classifications caused some problems. For one, this process is an oversimplification of the enormous plant form diversity of this rich tropical flora. Also, biological spectra for the regional flora fail to represent species' relative abundances and therefore they may not be accurate indicators of a landscape's vegetation. Notwithstanding, the resulting biological spectra allowed us to identify which categories had the most species.

The flora of Nizanda is dominated by phanerophytes. The prevalence of this life form suggests that the environment is not particularly unfavourable for plant growth and survival in this region. Yet with Nizanda being a region dominated by forest vegetation, it is remarkable that herbs are the most diverse component of the flora, although the difference with woody plants is very small. Moreover, the lack of permanent water bodies in the region is reflected in a very low representation of strictly aquatic or subaquatic species. Several riparian species were classified as terrestrial rather than as aquatic or semi-aquatic, although they always live on the border of water courses but actually grow on land. Species typical of riparian vegetation develop along humidity gradients and thus it is difficult to set limits in classifying them.

The regional growth-form spectrum was not matched by any of the communities taken individually. Considering that TDF contributes with the largest species richness to the regional flora, biological spectra for this community tended to mirror the regional ones, but this was not always so, as exemplified by forb richness (Figure 5a). The large contribution of savannah to forb and graminoid herb richness contrasts with the pattern found for the TDF; additionally, its life-form spectrum is very different from that reported for a Brazilian *cerrado* (Batalha and Martins 2004).

In the structurally complex MEF, the lack of graminoid and creeping herbs is noticeable, whilst forbs had the largest representation. This pattern may change in the future, especially for the categories that were absent, but the abundance of epiphytic forbs may be considered to be a true biological trait typical of this community. Contrastingly, in the riparian forests, both epiphytic and understorey forbs were poorly represented.

The savannah and the SV had the most similar life-form spectra, because in them all categories were most evenly distributed. However, the differences between these two communities in terms of richness of chamaephytes (larger in savannah) and therophytes (larger in SV) are evident. The comparison of growth-form spectra also reveals important differences, because SV climbers were much more numerous, whereas forbs prevailed in savannahs. It is frustrating that biological spectra in Nizanda's flora can only be compared against a handful of studies, simply because they are not available or because they do not report comparable species classifications (i.e., Burke 2001, Matallana et al 2005, Zhu et al 2005, Çakan and Karataş 2006). Unfortunately, floristic research is being increasingly excluded from many research funding and publication priorities.

Biogeographical Affinities

The alien component growing in the wild (22 species) only represents 2.4% of Nizanda's flora. This figure is similar to the proportion represented by the alien flowering plants of Mexico (2.7%; 618 alien among 22,968 native species; Villaseñor and Espinosa-García 2004). In Nizanda, Poaceae (59 species in total) was the family with the most alien species, with a little more than half of all non-native species. This family was distantly followed by Legumes (Casalpiniaceae, Fabaeae, and Mimosaceae), which are an extremely diverse group (128 species in total, i.e., more than doubling richness of Poaceae), but having only two aliens (both Caesalpiniaceae). Interestingly, this pattern is similar to that observed countrywide, as Mexican Poaceae include the most alien species in Mexico (171 species), with legumes being the second family on the list with 57 alien species (Villaseñor and Espinosa-Garcia 2004). It has been argued that this pattern is a consequence of the introductions of grasses used as fodder for cattle (Villaseñor and Espinosa-Garcia 2004). It is noteworthy that several legumes occurring typically in disturbed environments of Nizanda are believed to be native to the region (*Acacia cochliacantha*, *A. farnesiana*, *Mimosa acantholoba* var. *eurycarpa*, *M. tenuiflora*, among others; Lebrija-Trejos 2004, Lebrija-Trejos et al 2008), whereas most grasses present in the secondary vegetation are alien species (López-Olmedo et al 2007).

The different approaches used for the biogeographical analysis of the flora of Nizanda demonstrate that the Isthmus of Tehuantepec region has acted as a biological corridor for the thermophilous floras of the two major oceanic watersheds of southern North America. Nevertheless, it also became clear that it has functioned as a natural barrier for species with a Mesoamerican distribution (southern Mexico to Central America) whose geographical ranges do not include any region north of the Isthmus, and to a lesser extent, providing a southern limit for species typical of central and northern Mexico, as previously suggested (Peterson et al 1999, Cevallos-Ferriz and González-Torres 2005).

The western coastal lowland region of Mexico has been recognized as a center of diversification for the TDF flora (Gentry 1995) and that this center could reach as far south-east as localities as Zimatán, also in Oaxaca but outside the Isthmus of Tehuantepec (Lott and Atkinson 2002, 2006). The results of this study provide evidence indicating that Nizanda and in general the extreme south-eastern Pacific coast of Mexico is not part of such centre of diversification, given the stronger floristic links with southeastern Mexico and Central America revealed by our results. This idea is also consistent with the large number of species having a northern distributional limit in the Tehuantepec region.

Several issues related to the biogeographical relations of the flora of Nizanda remain unsolved. For example, one may ask whether the floristic ensembles of each plant community may display differing geographical affinities (i.e., Brewer et al 2003). Also, it is unclear whether the various biological groups described here correspond to different biogeographical patterns. Finally, we propose that the endemic component of the seasonally dry flora of the Isthmus of Tehuantepec calls for a thorough re-examination. Among other things, endemism appears to be less important than previously stated (Lorence and García-Mendoza 1989).

Acknowledgements

We are indebted to CONABIO (grant L085), SEMARNAT-CONACYT (2002-C01-0267), PAPIIT-UNAM (IN221503 & IN216007-3), to the colleagues listed in Electronic Supplementary Material 1, and to the people of Nizanda, especially to the Reyes-Manuel Family. Marco A. Romero helped with the management of the databases. P. Guadarrama, I. Sánchez-Gallén, O. Núñez-Castillo and many students from the Faculty of Sciences (UNAM) assisted during field work. This article benefitted greatly from the positive comments of two anonymous reviewers.

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CAPÍTULO 4

β-diversity and vegetation structure as influenced by slope aspect and altitude in a seasonally dry tropical landscape

José Alberto Gallardo-Cruz, Eduardo A. Pérez-García and Jorge A. Meave

Landscape Ecology (2009), 24: 473-482

Topography is a major driver of insolation distribution and hydrologic processes across a landscape (Nichols et al 1998, Yeakley et al 2000, Pierce et al 2005, Suzaki et al 2005). Patterns of incoming solar radiation cause shifts in available energy and water balance conditions, which in turn are responsible for major changes in vegetation structure and diversity (e.g. Armesto and Martínez 1978, Franklin et al 2000, Martínez-Yrizar et al 2000, Urban et al 2000; Vogiatzakis et al 2003; Hietel et al 2004).

In analyzing topography-related vegetation regional patterns, ecologists often overlook the fact that insolation regimes are not exclusively linked to local terrain features such as altitude and surface orientation, i.e. inclination and aspect (Daubenmire 1968, Pianka 2000, Ricklefs and Miller 2000), but that it also depends upon the latitudinal position on the earth of the mountain under study (Holland and Steyn 1975, Stoutjesdijk and Barkman 1992). Perhaps for this reason it is difficult to generalize the effect of slope aspect on plant communities of tropical regions. At mid- and high latitudes, slopes facing the Equator receive more radiation than slopes facing its closest Pole. Therefore, the former tend to be warmer and consequently drier than the latter. This observation had led to broad generalisations, as exemplified by the statement that "...south slopes are the most suitable habitat for northern-hemisphere organisms with southern distributions, and North slope for organisms with a northern distribution" (Stoutjesdijk and Barkman 1992, p 77). Unlike such predictions related to the geographic distribution of species, it is more difficult to make equivalent generalisations regarding vegetation development. This is so because the vegetational asymmetry is highly dependent upon the regional climate; for example, the observation that vegetation is better developed on the north slope in relatively dry regions of the northern hemisphere (Beaty and Taylor 2001, Sternberg and Shoshany 2001) may not be applicable in areas that do not experience water limitations (Sharma and Baduni 2000).

The radiation balance should be equal between the north- and south-facing slopes of a symmetric mountain located right on the equator, whereas in mountains located between the Equator and the Tropics of Cancer and Capricorn, both slopes receive direct insolation but during periods of very variable lengths throughout the year (Walter 1973). Particularly, in seasonally dry regions of tropical latitudes of the northern hemisphere, the longest exposure of south-facing slopes to direct solar radiation usually coincides with the unfavourable period of low precipitation, a combination that results in a large water stress in plants. A different situation appears to take place in north-facing slopes, as they may be more suitable for plant growth because the season of higher energy for photosynthesis is synchronic with the period of positive water balance of the year. Thus, in these regions one may expect differences in floristic composition between slopes, along with better-developed vegetation on the slope facing North.

Altitude, the second major component of topography, introduces further complexity into this scheme (Rahbek 1995). Numerous studies analysing altitudinal gradients in tropical mountains have established the magnitude of vegetational changes in response to environmental heterogeneity along this axis (e.g. Lieberman et al 1996; Lovett 1999, Grytnes and Vetaas 2002, Grytnes and Beaman 2006), but they have also shown the difficulty to predict the individual behaviour of each environmental factor with altitude (Bruijnzeel and Veneklaas 1998). Water availability on the earth's surface is related to altitude as a result of two processes. For one, evapotranspiration rates decrease with altitude as a result of the corresponding temperature reduction (Stoutjesdijk and Barkman 1992, Lüttge 1997, Bruijnzeel and Veneklaas 1998). In addition, gravity-driven runoff causes a larger moisture accumulation in the lower topographic positions (e.g. Clark et al 1999). Despite the vast number of studies analysing separately vegetation responses to either slope aspect or altitude (e.g. Cantlon 1953, Vázquez-G and Givnish 1998), the combined effects of these two factors has not been sufficiently examined.

The latitudinal position of southern Mexico (~16-20° N) determines a large seasonality in the prevailing climatic regimes, as well as a potential strong differentiation in energy balance between north- and south-facing slopes. Coincidently, the seasonally dry tropical forest of this region harbours a very large plant diversity of ~ 5,000 species (Salas-Morales et al 2003; Villaseñor 2003; Lott and Atkinson 2006). The extensive orographic features of this part of the country (Ferrusquía-Villafranca, 1993) have been suggested to contribute to a large diversity by promoting a regional large species turnover, i.e. a large β-diversity (Gentry 1988, Givnish 1999, Trejo and Dirzo, 2002; Pérez-García et al 2005; Trejo 2005). However, the potential contribution of topography-related environmental factors to this diversity within a landscape has not yet been investigated. Also, no quantitative evaluations of potential energy balances over a terrain surface are available for this region.

In this study we aimed at three goals: (1) to calculate and compare potential energy incomes between slopes of contrasting aspect based on terrain geometry derived from a digital elevation model (DEM), (2) to examine vegetation structure variability in response to slope aspect and altitude, and (3) to relate variations in α- and β-diversity to topography-based environmental heterogeneity.

Methods

Study area

In the Nizanda region (Oaxaca State, Mexico), Mt. Cerro Verde (16°39’48.1” N, 94°59’50.8” W) stands out amid a landscape of low altitude hills (~ 150-250 m). This calcareous elevation covers an area of ca. 3.5 km^2 and its oblong shape allows distinguishing two main slopes, one facing southwest (hereafter referred to as S), and the other facing northeast (hereafter referred to as N). Along its central ridges altitude ranges between 460 and 500 m a.s.l. (Figure 1). The regional climate is tropical sub-humid (Aw_0) with a mean annual temperature of ca. 26°C and mean total annual precipitation of ca 900 mm (Lebrija-Trejos et al in press). Rainfall concentrates from May to October, with a harsh dry season extending from November to April (Pérez-García et al 2001). At Nizanda, the sun is on the zenith at noon on May 7 and August 6; the period between these dates corresponds to the first half of the rainy season. The prevailing high-speed Trade Winds blowing from the North represent an additional important environmental factor affecting the area.

Edaphic conditions on Mt. Cerro Verde change abruptly from relatively deeper soil to areas of exposed rock. Below the 430 m contour, the seasonally dry tropical forest (SDTF) established on deeper soil dominates both slopes. This forest was described by Gallardo-Cruz et al (2005) as having a low stature (mean height = 9.0 m), a dense canopy (mean cover = 45,000 m^2/ha), and a large basal area (53 m^2/ha).

Modeling potential energy income

As measurements of solar radiation are difficult to obtain, we modeled and mapped the spatial and temporal variability of yearly potential energy income by using the DEM available for the region (30 × 30 m grid). This modeling was performed with SOLEI-32 (Mészároš and Miklánek 2006), which calculates potential energy income considering the shadowing of surrounding topography, in addition to slope features and geographical position. We calculated daily potential energy income for a year on a 15-min period basis for each of the plots used for vegetation sampling (see next section).

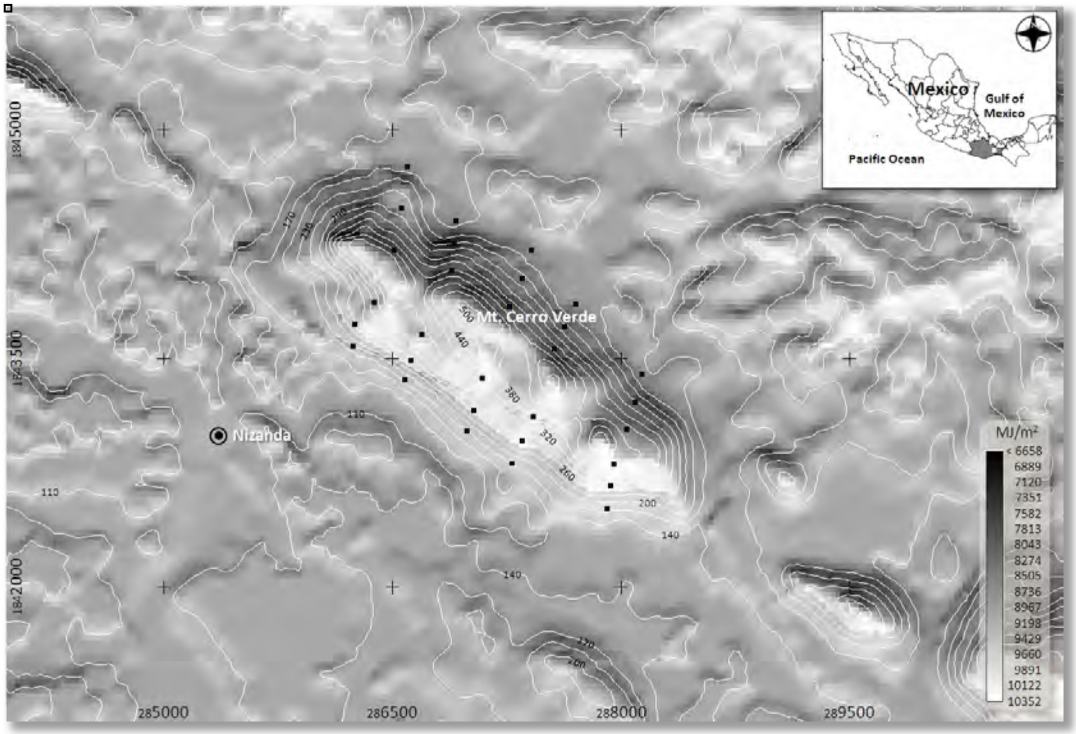

Figure 1. Location (UTM zone 15) and 30 m contour lines of Mt. Cerro Verde and surroundings (Oaxaca), Mexico. The shading indicates yearly potential energy income (MJ/m^2) derived from the SOLEI-32 model using a DEM (30 × 30 m grid). Black squares denote positions of plots for vegetation sampling (not at scale).

Vegetation sampling

The SDTF at Mt. Cerro Verde was surveyed by using 30 plots in total. The units were equally distributed among three altitudinal belts defined on both slopes (N and S); their altitudinal ranges were 130-230 m for the low belt (l), 231-330 m for the mid belt (m), and 331-430 m for the high belt (h). The combination of the three altitudinal belts and the two main orientations produced six environmental groups (Nl, Nm, Nh, Sl, Sm, Sh), represented by five vegetation samples each. There were no significant differences between these groups in slope angle and percent surface of exposed rock (Kruskal-Wallis, $P > 0.6$).

Plants rooted within the plots were classified into two groups: the upper stratum, which included plants with DBH ≥ 1 cm, and the lower stratum, composed of plants with DBH < 1 cm, but ≥ 30 cm high. Sampling of the upper stratum was based on 100 m^2 plots (10 × 10 m), whereas for the lower stratum it was done in five 4-m^2 subplots (2 × 2 m) located at the centre and the corners of the main plot. For the analysis, all structural values obtained for this stratum were extrapolated to a 100-m^2 area. Also, some analyses were repeated for the subset of canopy trees measuring ≥ 15 cm DBH. The taxonomic identity for each sampled individual was recorded, along with measurements of its total height and two crown diameters; for plants in the upper stratum their DBH and number of stems was also recorded. Taxonomic nomenclature followed Pérez-García et al (2001).

Data analysis

Cover, density and basal area were computed through conventional procedures (Mueller-Dombois and Ellenberg 1974; Barbour et al 1999). The proportion of multiple-stemmed trees per plot was expressed as the percent ratio between the number of such trees and the number of plants in the upper stratum. Calculation of mean height was done for two groups: "total mean height" was based on all elements in the upper stratum, and "upper mean height" included the tallest 10 percent of the trees from the same stratum.

Plant diversity by plot was assessed through three diversity indices: (1) dominance Simpson's index:

$$D = \sum \left(\frac{n_i[n_i - 1]}{N[N - 1]} \right)$$

where n_i = the number of individuals in the ith species and N = the total number of individuals; (2) Shannon's information index:

$$H' = -\sum p_i \ln p_i$$

where p_i is the proportion of individuals found in the ith species; and (3) the α-diversity index, which is a parameter of Fisher's log series model (Magurran 2004). The behaviour of this latter parameter has proven to be a good predictor of the number of species represented by a single individual, and was read from Hayek and Buzas' (1997) table using the number of species and the total number of individuals.

All structural, diversity and energy income data were compared between the six environmental groups through a two-way analyses of variance, using slope aspect and altitude as independent variables. When applied to percentages or discrete data these were arc-sine or square-root transformed, respectively (Sokal and Rohlf 1995). If the parametric assumptions were not met, Kruskal-Wallis rank ANOVAs were used. Whenever any of these were significant, pairwise comparisons were performed with Tukey's HSD tests.

Assessment of β-diversity was done in two ways. First, Whittaker's (1960, 1972) β-diversity index was calculated for groups defined by slope aspect (N = 15; S = 15), by altitudinal belt (l = 10; m = 10; h = 10), by the six environmental groups (each with 5 plots), and for the entire set of plots together, as follows:

$$\beta_W = \gamma/\alpha$$

where γ = total number of species recorded for the respective set of plots, and α = mean species richness by plot. Second, individual plots and environmental groups were classified using Ward's method and squared Euclidian distances. Both classifications were based on matrices containing presence-absence data for species. Statistical and classification analyses were performed using STATISTICA 6.0 (StatSoft Inc 1998).

Results

Potential energy income

On average, each point of the study area receives in a year a potential energy of 9036 MJ/m^2 (Figure 1). Based on the calculations performed for the 30 sampling points on Mt. Cerro Verde, a significant spatial difference was observed between slopes (Figure 2): mean energy annual income on the S slope is about 20% larger than on the N slope (9735 MJ/m^2 vs 8138 MJ/m^2). Inversely, potential energy income in a year did not differ significantly between the three altitudinal belts of each major slope, even though a decreasing trend was observed for the N slope, as the value for Nl (8518 MJ/m^2) was about 7% larger than the estimated values for Nm and Nh. In addition to this spatial variation, the temporal behaviour of potential energy income throughout the year differed greatly between the two slopes (Figure 3). When these temporal changes were overlapped with mean total annual precipitation for the period 1949–2006, an interesting pattern emerged. At the beginning and the end of the year, when there is no precipitation in the region, potential energy is high on the S slope. After the onset on the rainy season, the first precipitation peak is synchronic with the moment when potential energy peaks on the N slope (mid July). Later on, a subsequent precipitation maximum roughly coincides with a second peak in potential energy on the S slope (mid- September).

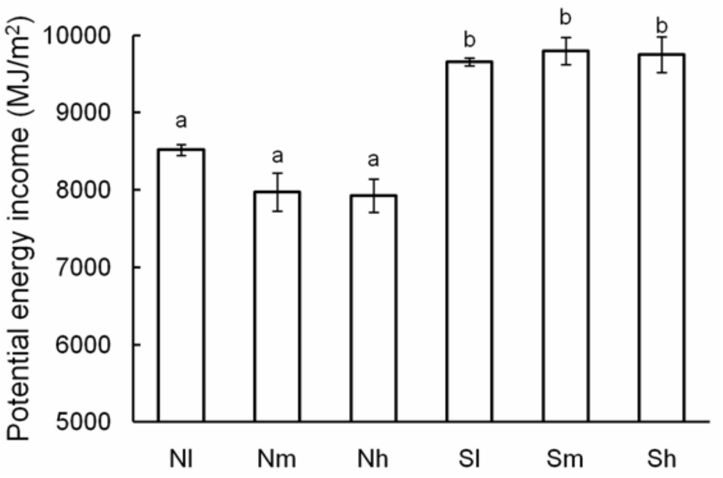

Figure 2. Mean (± 1 SE) potential energy income in a year across the six environmental groups defined on Mt. Cerro Verde (Oaxaca, Mexico). Different letters indicate significant differences according to Tukey's test ($P < 0.05$)

Vegetation structure and diversity

In total, 2619 individuals were recorded (upper stratum, 1478 individuals; lower stratum, 1141), which comprised 197 species. These were distributed among 52 families of Magnoliophyta; 146 of them were encountered in the upper stratum and 145 in the lower one (an appendix with distributions of species across environmental groups is available upon request).

Mean values for vegetation structure variables (total canopy = upper + lower strata) across the six environmental groups are shown in figure 4. Neither aspect nor altitude significantly affected cover for any individual stratum (not shown) or for the two of them combined. However, when the analysis for this variable was performed for the group of largest canopy trees (DBH ≥ 15 cm), altitude had a significant effect ($F = 5.863$; df = 2; $P < 0.01$); pairwise comparisons showed significant differences between the m- and the h-belts (Tukey's HSD test; $P < 0.05$), which averaged (± 1 SE) 189.0 ± 24.7 m^2/ 100 m^2 and 88.7 ± 14.7 m^2/ 100 m^2, respectively.

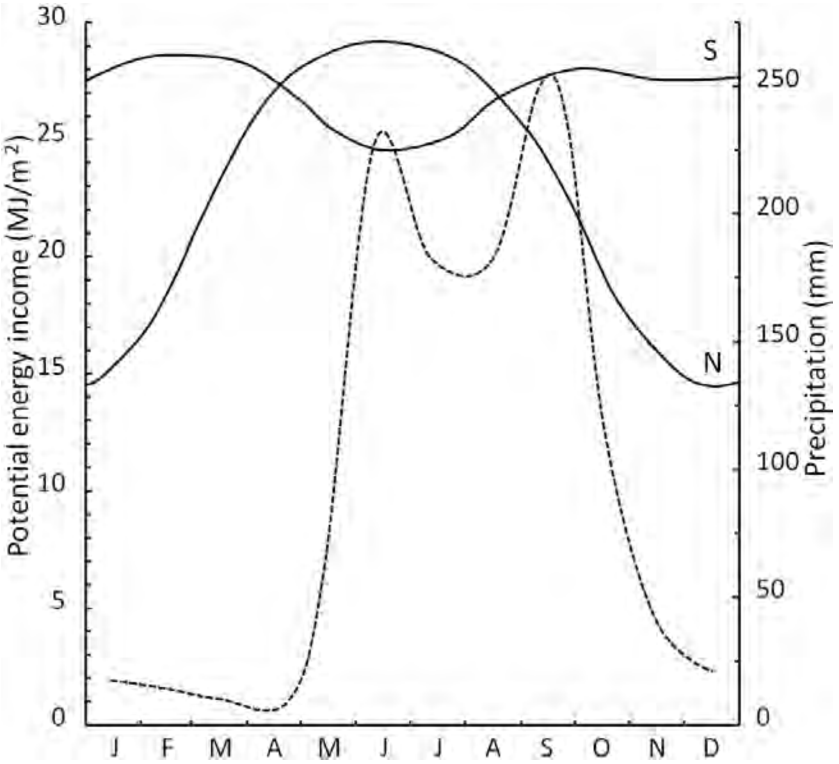

Figure 3. Seasonal behaviour of daily potential energy income (MJ/m^2) in the two major slopes of Mt. Cerro Verde throughout the year (left axis), and regional average of total annual precipitation for the period 1949-2006 (right axis). N = north-facing slope; S = south-facing slope

Over again, neither aspect nor altitude significantly affected density, basal area, proportion of multiple-stemmed trees, total height and upper height, measured for any plant group. The same result was obtained for basal area, even after excluding from the analysis one big individual of *Beaucarnea recurvata* (DBH = 183 cm) with the purpose of reducing the variance. No species occurred within all 30 plots. Excepting for Sl, mean plot richness by environmental group was around 30 species (Table 1). No significant differences were found for any of the diversity or dominance indices related to aspect or altitude. However, some diversity attributes differed considerably between environmental groups. Cumulative species richness was minimum in the l-belt of both slopes (Nl, 75 species; Sl, 83), and maximum in Sm (91). Dominance within groups was generally low; mean Simpson's index peaked in Nl and Sh. According to Fisher's α, singletons always represented at least 25% of mean species richness per plot. Shannon's mean values ranged from 2.67 in Nl to 2.88 in Nm and Sm, with little variation among groups (Table 1).

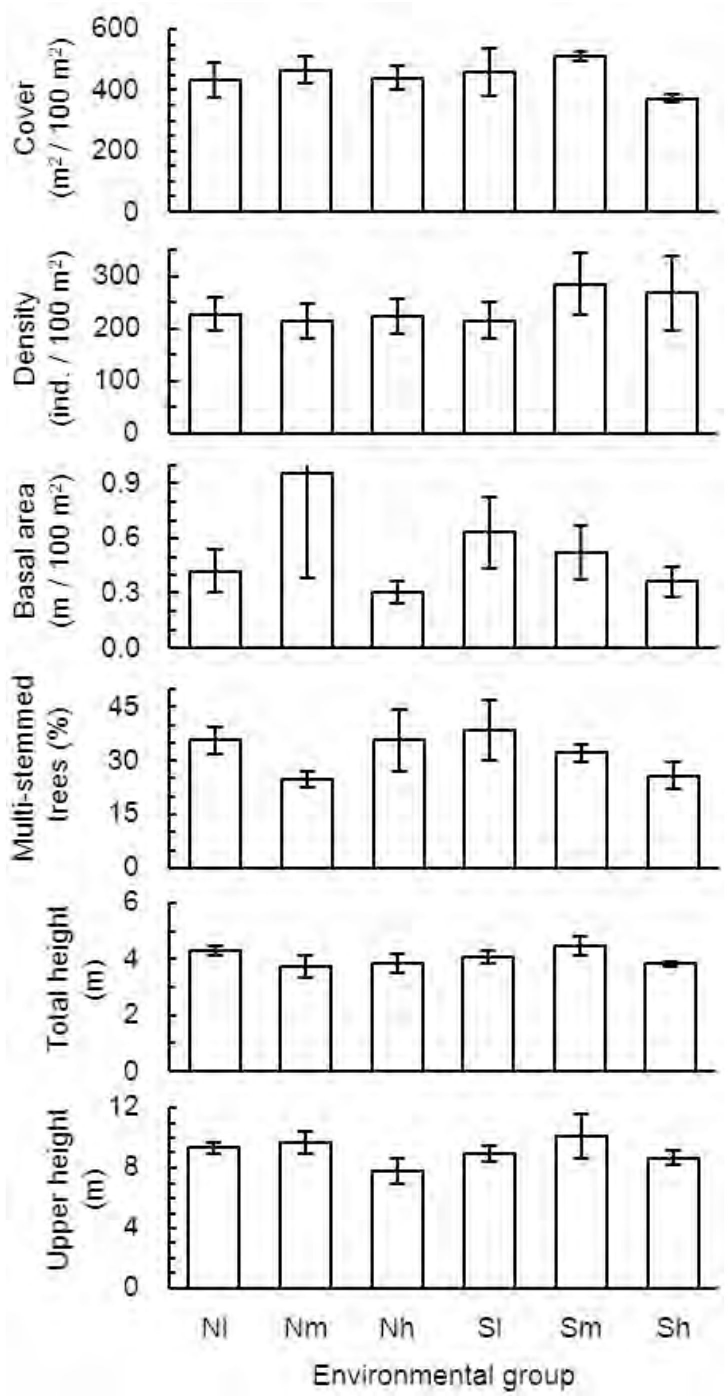

Figure 4. Mean (± 1 SE) structural values across the six environmental groups (Nl, Nm, Nh, Sl, Sm, Sh) evaluated for the SDTF community on Mt. Cerro Verde

Table 1. Mean (± 1 SE) diversity indices values for the six environmental groups (Nl, Nm, Nh, Sl, Sm, Sh) located at Mt. Cerro Verde (Oaxaca), Mexico

Group	Species richness	Simpson's	α	Shannon's
Nl	30.6 ± 2.25	0.12 ± 0.02	9.74 ± 0.97	2.67 ± 0.14
Nm	30.4 ± 2.90	0.07 ± 0.01	9.84 ± 0.89	2.88 ± 0.09
Nh	31.0 ± 3.51	0.08 ± 0.01	9.87 ± 1.06	2.85 ± 0.11
Sl	26.0 ± 1.90	0.09 ± 0.01	8.12 ± 0.95	2.71 ± 0.05
Sm	31.4 ± 1.54	0.08 ± 0.01	9.56 ± 1.74	2.88 ± 0.06
Sh	30.6 ± 2.16	0.11 ± 0.03	9.69 ± 1.31	2.73 ± 0.20

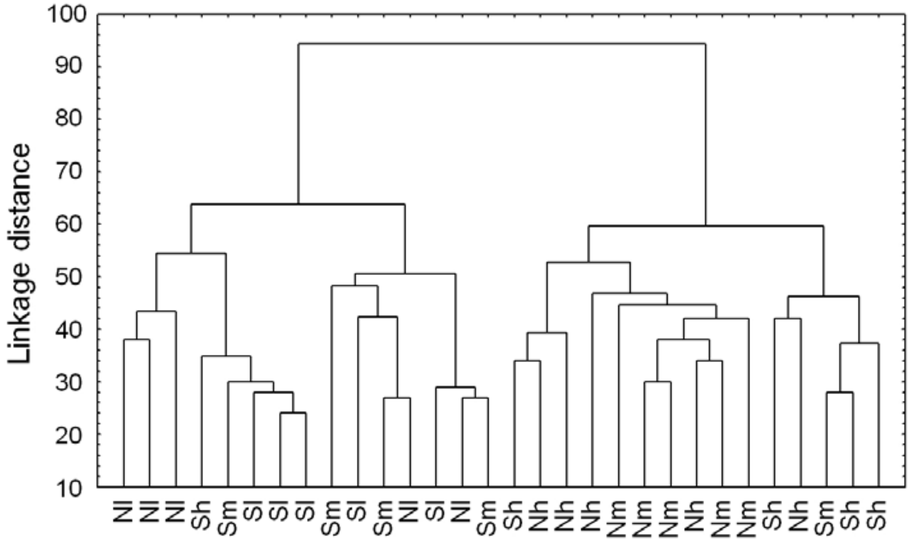

Figure 5. Dendrogram (Ward's method; squared Euclidian distances) for 30 SDTF samples from Mt. Cerro Verde. The classification was based on binary (presence-absence) data for species. The environmental group (Nl, Nm, Nh, Sl, Sm, Sh) of each sample is indicated

The value of Whittaker's β-diversity index for the entire system was 5.46. This figure was larger than all values calculated for any other data subset: values for this index were 3.95 and 3.67 for N and S slopes, respectively, and 3.02 for belt l, 3.30 for m, and 3.15 for h. Variation for this index across groups was small, ranging from a low of 1.71 in Nl, through Sh = 1.77, Sl = 1.88, Sm = 1.89, Nh = 1.90, to a high of 1.92 in Nm.

According to the classification analysis, two sets of plots could be clearly distinguished at a linkage distance of 80 (Figure 5). The first one, located on the left part of the dendrogram, was composed of all plots from belt l, plus four from group Sm, and one from Sh. The other set included the remaining samples from belt h, all from Nm, and one from Sm.

Discussion

The calculation of potential energy income in this landscape confirmed the between-group environmental differentiation regarding slope aspect. Interestingly, the considerable difference in energy income between the two major slopes of Mt. Cerro Verde was not only spatial, as also a temporal component of this differentiation was identified. In this seasonally dry tropical region, water is only available for plant growth during a very short time of the year. The lack of a continuous cloud cover throughout the year in this region (García 2004) minimizes the possible buffering effect of cloudiness on the radiation balance (Stoutjesdijk and Barkman 1992). Thus the coincidence of the rainy season with periods of high energy for photosynthesis is critical in determining vegetation features in the different landscape components.

Unlike the strong spatio-temporal pattern of total energy income, no equivalent differentiation was observed between altitudinal belts within each slope. Therefore, environmental changes linked to altitude on Mt. Cerro Verde could be rather associated to changes in temperature, and consequently in evapotranspiration, along the altitudinal gradient (Lüttge 1997).

Both the spatial and temporal components of potential energy income- and altitudinal-related heterogeneity were matched by an array of differing responses in vegetation diversity and structural attributes. The calculated values for Whittaker's β-diversity index for the six environmental groups were relatively small, ranging from 1.71 to 1.92, reflecting a floristic homogeneity when the environment is held constant. However, building in any factor of environmental heterogeneity into the index (namely slope aspect or altitude), produced a disproportionate increase in its values, clearly indicating that these sources of heterogeneity cause considerable spatial floristic turnover. The index calculated for the entire system, which combined thoroughly the effects of the two factors analysed, reached a value almost three times as large as those for individual environmental groups. This result explains why on Mt. Cerro Verde it was possible to totalize a large number of recorded species (194 in 3,000 m^2), despite a relatively low mean richness by group (85.5 species/500 m^2).

The classification of sampling plots led to the separation of two major clusters. Surprisingly, despite being quite homogeneous, they did not correspond completely to the mount's two major slopes, as one could have expected from the strong spatial energy-based differentiation. While those plots from the intermediate altitude were split apart according to their orientation in an almost identical fashion between both clusters, all plots from the low altitude belt were grouped together in one cluster, as so did all plots but one from the high belt in the other one. This indicates that floristic differentiation is not simply produced by the environmental differences between the two slopes, but also that there is an important variation linked to altitude. The separation of the plots from extreme altitudinal belts in the classification analysis suggests that the altitudinal environmental variation is capable of generating as much floristic differentiation as slope aspect.

The fact that mid-altitude plots from the S slope were grouped together with all plots from the low belt and that mid altitude plots from the N slope were in the same group as the high altitude plots deserves further attention. This result implies an asymmetry between the two slopes of the mountain regarding the rates of floristic change associated to altitude; this rate is larger in the lower half of the N slope, whereas it is higher in the upper half of the S slope. Moreover, the overall floristic change is stronger on the N slope, as seen in the respective values of Whittaker's β-diversity index. Although it is difficult to explain the causes behind this asymmetry, it seems to be related to the fact that total annual potential energy income varied more on the N than on the S slope.

Unlike the evidence for floristic differentiation on Mt. Cerro Verde so far discussed, this study also showed that this variation is not reflected in all vegetation attributes. The analysis of the response of α-diversity to environmental heterogeneity did not produce significant differences in species richness between any combination of plots. The only interesting trend was that groups Nl and Sl had the lowest cumulative richness (83 and 75 species, respectively), whereas the highest richness corresponded to Sm (91). Although not significant, this trend is noticeable because it coincides with findings of other studies in suggesting that community's diversity does not necessarily decrease monotonically with altitude (Fernández-Palacios 1992; Rahbek 1995; Grytnes 2003). Similarly, structural variables were homogenous on the mountain, as cover of canopy trees (DBH ≥ 15 cm) was the only variable significantly affected by altitude. At the highest zones of Mt. Cerro Verde slopes are steep and soils very shallow, all of which considerably limits plant growth (Gallardo-Cruz et al 2005). Moreover, wind turbulence typical of the upper reaches of the mountains (Huggett 1995, Beniston 2000), which on this mountain is particularly strong due to the high speed of the Trade Winds in this region (Romero-Centeno et al 2003), may cause significant reductions in plant cover due to the shear force of the wind (Grace 1981).

The homogeneity in structure and α-diversity contrasts with reported patterns for other SDTF communities (Martínez-Yrízar et al 2000; Balvanera et al 2002, Maass et al 2002). Indeed, the lack of significant trends in vegetation structure associated to slope aspect is contrary to the classic model of slope effect on community structure, for which ample support exists in the literature from temperate and polar regions of the Earth (e.g. Stoutjesdijk and Barkman 1992, Olivero and Hix 1998; Pianka 2000).

An important implication of this result is that at this spatial scale vegetation structure and composition appear to have independent responses to the environment. While the compositional variation may be more strongly linked to the spatial heterogeneity, vegetation structure and α-diversity could be rather shaped by its temporal component. It has been suggested that a given vegetation attribute may be caused be different environmental drivers (Walter 1973; Stoutjesdijk & Barkman 1992; Haslett 1997). This seems to be the case of Mt. Cerro Verde. In this region we identified two likely peaks of primary productivity, each given by the temporal coincidence of a period of high potential energy income with high water availability (see Figure 3). However, the specific timing of these periods is such that each one benefits more the vegetation on one slope at a time. Although the yearly balance of potential energy is clearly larger on the S slope, the balance restricted to the growing period may not differ between slopes. Thus the only net effect may be a temporal lag in physiological activity on the S slope that could be seen as a phenological between-slope asynchrony that ultimately is not capable of producing differences in structure and α-diversity. This possibility remains to be investigated.

Final remarks

The results of this study demonstrated a differential response of vegetational attributes to environmental heterogeneity along a short altitudinal gradient and between two contrasting orientations. The structure did not show significant changes linked to the environmental gradients, but altitude and slope aspect did affect species composition. Our results suggest that the classic model of slope aspect effect on vegetation needs reconsideration. In particular, incorporating the temporal component of environmental heterogeneity, a factor traditionally absent in analyses of topography-related vegetation variability, may be critical in examining vegetation heterogeneity in tropical landscapes.

Acknowledgments

We are grateful to A. Martínez-Yrízar and P. Balvanera for commenting on a previous draft of this manuscript, and to the people on Nizanda for its hospitality and support. L. Ochoa-Ochoa assisted in the field and M. Romero-Romero helped in database management. This study received financial support from CONACyT-SEMARNAT (2002-C01-0267) and PAPIIT-UNAM (IN-221503).

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CAPÍTULO 5

Spatial structure of plant communities in a complex tropical landscape: implications for β-diversity

José Alberto Gallardo-Cruz, Jorge A. Meave, Eduardo A. Pérez-García and José Luis Hernández-Stefanoni

Community Ecology (2010), 11: 202-210

Spatial structuring is an essential property of any community and ecosystem (Kareiva 1994, Tilman 1994, Legendre et al 2002). Therefore, it is surprising that this trait has not yet been fully incorporated into the theoretical background of ecology (Legendre 1993, Legendre and Legendre 1998, Dale and Fortin 2002). This situation is changing rapidly, however, and there is an increasing number of ecologists paying attention to this topic, turning it into a paradigm in the research agenda of community ecology (Dormann et al 2007). The current tendency to overlook spatial structure has restricted the possibility to detect the various potential interrelations between the distribution of the communities and the spatial configuration of the terrain on which they occur, and to test the effect of space as an explanatory variable (Fortin and Dale 2005). In complex landscapes such spatial configuration may not be obvious at first glance, as it may be partially concealed by the own variability of the plant cover, which usually responds also to other factors not related to space.

Understanding the underlying causes of community composition and its spatial variation (β-diversity) remains a major goal in community ecology (Koleff et al 2003, Legendre et al 2005, Bacaro and Ricotta 2007, Tuomisto and Ruokolainen 2008, Jankowski et al 2009). Broadly defined, β-diversity is no more than the quantitative expression of species turnover across space (Whittaker 1972, Magurran 2004). Common interpretations of this component of community diversity are related to ecological processes operating at the community level, such as dispersal, intra- and interspecific competition (including competitive exclusion), as well as facilitative interactions (Hubbell 2001, Condit et al 2002, Laliberté et al 2009). A second set of explanations are related to environmental gradients and the responses of individual species and communities to subtle but continuous variations in the physical environment (Whittaker 1975, Balvanera et al 2002, Gallardo-Cruz et al 2009). Recently, both types of explanations of β-diversity have been framed within a landscape context -and its inherent spatial structure-, opening the possibility to examine a range of community responses to the environment within a single area (He et al 2009, Laliberté et al 2009).

Tuomisto and Ruokolainen (2006, 2008) claimed that spatial analysis is a correct way to examine the variation of β-diversity in a community. This approach allows identifying the links between those processes that are inherent to the landscape and the way in which plant communities become spatially organised. In turn, this analytical approach may potentially shed light on those ecological processes driving community organisation, such as dispersal and niche specialisation (Hubbell 2001, Tilman and Lehman 2001).

With the increasing availability of spatially referenced information on biodiversity, the Mantel test and its derivatives have become essential tools for the analysis of the spatial structure of biological phenomena, as they incorporate multiple spatially structured variables (Fortin and Gurevitch 2001, Dale and Fortin 2002, Perry et al 2002). A heuristic development of this analysis is the construction of correlograms organised by distance classes (Oden and Sokal 1986). The characteristic forms of correlograms are known to be associated with certain types of spatial structures, thus the assessment of their shapes provides sufficient and adequate information to compare spatial patterns between data sets (Sokal 1979, Legendre and Fortin 1989, Legendre and Legendre 1998). More recently, Uuemaa et al (2008) and Mander et al (2009) provided evidence that correlogram structure is also strongly associated to the landscape's spatial configuration.

In a landscape containing various communities with different spatial arrangements, spatial analyses enable the testing of hypotheses related to the causes of these patterns (Legendre and Fortin 1989, Legendre and Legendre 1998). This is particularly relevant in the case of tropical species-rich communities (Laliberté et al 2009), as each of the numerous species that they host acts as a response variable, is capable of sensing the environment individually across space, and thus is likely to display a spatial structure.

The goal of this study was to analyse the degree of spatial dependency of β-diversity in four communities that occur in a tropical complex landscape in southern Mexico. Our approach was to investigate community level spatial patterns through Mantel tests and correlograms using two sets of distance classes (i.e. conducting a two-scale analysis), and in this way to examine the spatial structure of floristic composition, i.e. β-diversity spatial variation, in the context of the observed spatial configuration of the landscape. Because the studied communities appeared to have distinctive landscape configurations, ranging from strongly insular through linear to continuous distributions, we expected that their floristic assemblages would display different spatial structures (Legendre and Fortin 1989).

Methods

Landscape location and description

The studied landscape is centred in the village of Nizanda, Oaxaca State, in the seasonally dry tropical region of Mexico's southern Pacific watershed (Figure 1). It covers an area of ca. 64 km^2 and includes an altitudinal range from 100 to 700 m. Earlier compositional and physiognomic analyses of the vegetation indicated the existence of four major plant community types in the landscape (Pérez-García et al 2001, 2010): tropical dry forest (Gallardo-Cruz et al 2005, 2009), xerophytic vegetation (a combination of xerophytic scrub and tropical dry forest on a rocky, nutrient and water-limited substrate; Pérez-García and Meave 2004, Pérez-García et al 2009), grass-dominated savanna (López-Olmedo et al 2006, 2007), and subdeciduous forest (Lebrija-Trejos 2001). Among these communities, the tropical dry forest has the largest total richness, with 425 known species; this figure strongly contrasts with the relatively poor xerophytic vegetation (135 species), whereas the remaining two communites are intermediate in species richness (savanna, 188 species; subdeciduous forest, 264 species). In spite of the detailed floristic and structural information provided by this previous work, it failed to provide precise information on the spatial arrangements of these community types, despite evident differences between them in this regard.

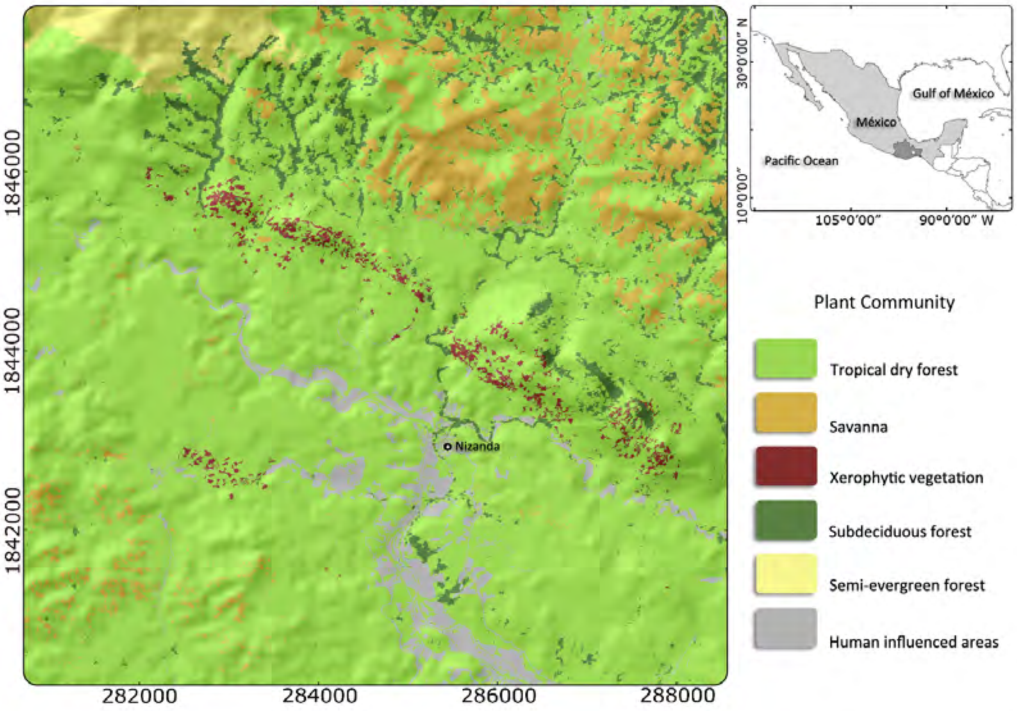

Figure 1. Location (UTM zone 15n) of the studied landscape around the village of Nizanda, Oaxaca State, southern Mexico, and object-oriented classification of a Quickbird satellite image showing community types and human-influenced areas devoid of natural vegetation.

As some of these communities evidently occupied small areas relative to the others, we ensured the remote detection of all of them by using a high-resolution satellite image (pansharpened Quickbird, 60 × 60 cm pixels) for describing their spatial arrangement. Accordingly, we chose to perform an object-oriented classification (Blaschke and Strobl 2001) using Definiens Professional 5.0 (Definiens 2006). Our aim was to detect the four above-mentioned communities while distinguishing them from those areas where human activities have resulted in the clearing of the natural vegetation and the opening of the terrain for agriculture and cattle raising. The underlying paradigm of any object-oriented classification is that groups of pixels may reveal emergent properties that allow the identification of meaningful objects that are likely to be overlooked when using the classic per-pixel clustering procedures in high-resolution imagery. Image objects to be classified were created using the multiresolution segmentation algorithm, setting scale parameter to 50, ands giving equal weights to the red, green, blue and IR bands; as composition of homogeneity criteria we used colour = 0.9, and compactness = 0.5. The classification was based on the textural, shape, colour, and NDVI properties of the analysed objects (Blaschke and Hay 2001). NDVI was particularly useful in eliminating topography-related shadows on the very-high resolution image (Schowengerdt 2007). Further details of this classification procedure can be found in Benz et al (2004).

Field sampling and measurement of β-diversity

We applied a stratified-sampling procedure to account for the differences in the areas covered by each community. The adscription of each plot to a community type was primarily based on physiognomic and floristic criteria (Pérez-García et al 2010), whilst its correct belonging to each class derived from the image classification was verified. In geolocating the 10 × 10 m sampling units, areas affected by human activities were avoided (including early successional forest stands). The final set contained 165 systematically placed plots distributed as follows: 93 in tropical dry forest, 21 in xerophytic vegetation, 23 in savanna, and 28 in subdeciduous forest. A careful inspection of each plot allowed us to assemble a list of all vascular plant species occurring in them. We then constructed a matrix containing presence/absence data for 500 species that were reliably determined to species level; species lacking determination to this taxonomic level were left out to guarantee trustable calculation. Estimates of β-diversity were based on a second matrix of between-plot ecological distances measured by means of the classical Sørensen (presence/absence) similarity index (Magurran 2004):

$$C_S = \frac{2a}{2a+b+c}$$

where a is the total number of species present in both samples, b the number of species exclusive to sample 1, and c the number of species exclusive to sample 2. C_S ranges from 0 to 1, with 1 indicating two identical samples, i.e. no turnover (or no beta diversity) between them, while a value of 0 represents maximum beta diversity between two samples (i.e. no shared species).

Overall β-diversity for each community type was obtained by calculating a mean Sørensen index for all pair-wise comparisons involving sites from the same community. Global (landscape-level) β-diversity was also calculated after combining the information for all plots from the four communities.

Spatial analysis

To examine whether spatial distance explained a significant proportion of the variation in the species assemblages we used both Mantel and partial Mantel tests (Mantel 1967; Legendre 2000), by following the zt-software protocol (Bonnet and Van de Peer 2002). A Mantel test estimates the linear relationship between the distance values of two standardized matrices, as follows:

$$r_M = \frac{1}{N-1}\sum_{i=1}^{N}\sum_{j=1}^{N} a_{ij}b_{ij}$$

where r_M is the standardized Mantel statistic and represents the measure of the degree of spatial autocorrelation, a_{ij} is an Euclidean spatial distance matrix between pairs of the N sampling locations, and b_{ij} is a Sørensen's similarity matrix of the species composition among sites. We used similarities to emphasize the distance-related positive floristic relationships between plots; this decision does not affect the calculation of the r_M statistic, as it only changes the sign of the effect (Bonnet and Van de Peer 2002). The r_M values reflect an averaged isotropic intensity of spatial autocorrelation for the examined data set. The null hypothesis states that distances in a matrix A are independent of the distances between the same objects, contained in a second matrix B. We tested this hypothesis (one tailed test) by comparing the observed statistic with the distribution obtained by randomly reordering 10,000 times the elements in one of the matrices.

A partial Mantel test was used to control for the effects of elevational differences between sites. This required the construction of a third matrix of pairwise elevational differences, which were derived from the digital elevation model for the region (30 x 30 m grid resolution). Significance was tested by permutating 10,000 times the residuals of a null model (Legendre 2000). A straightforward interpretation of the r_M values (range: 1 to -1) is as follows: when it takes positive values for a given distance, the compared objects are more similar at that distance than expected at random; conversely, when it takes negative values the compared objects are less similar than random; a value of 0 represents a situation in which distance has no effect on similarity

To further examine the effect and sign of spatial autocorrelation we partitioned the analysis in several distance classes by constructing Mantel correlograms. These correlograms are a multivariate method for examining scales of spatial autocorrelation that are likely to reveal non-linear patterns, as the estimation of spatial autocorrelation is done at several distance classes rather than for the entire dataset. The r_M statistic for each distance class was estimated following the Mantel test procedure described above. We used two scales of distance partitioning (200 m and 500 m). Overall significance of the autocorrelograms was determined by checking whether the correlogram contained at least one significant value at the $\alpha' = \alpha/\nu$ significance level, according to the Bonferroni method for correcting for multiple tests, with $\alpha = 0.05$ and ν = number of Mantel tests considered in the correlogram (Oden 1984).

Results

Landscape configuration

The object oriented classification revealed a highly heterogeneous spatial arrangement of the four focal communities across the landscape (Figure 1). The overall accuracy of the classification based on training areas was 0.93. The largest cover (ca. 70% of the landscape) corresponded to the tropical dry forest; moreover, this community displayed a considerably continuous spatial distribution, and therefore it may be seen as the matrix of the remaining communities. Savanna had the second largest cover (ca. 15%), but this community strongly contrasts with the previous one in that it is markedly discontinuous; savanna patches occur in two major core areas located in the north-eastern and the south-western corners of the landscape. A much smaller area (< 2%) was classified as xerophytic vegetation, a community type also displaying a highly insular distribution associated to limestone outcrops located along an axis with a south-east to north-west orientation. Similarly, a small proportion of the landscape (< 2%) corresponded to subdeciduous forest, which mostly had a linear configuration because of its association to water streams. Completely transformed areas by human activities concentrate near the village of Nizanda and on the floodplains of the major water streams, and their estimated landscape cover was ca. 5%. The classification also showed the existence of an isolated semi-evergreen forest patch in the north-west limit of the landscape; this community was excluded from the analysis due to its inaccessibility and to minimise the potential confounding effect of elevation.

β-diversity

At the landscape level, β-diversity measured through the mean Sørensen similarity index was 0.12. This value was notably smaller than the respective means of the four focal community types. Three of them had similar values (savanna 0.41; xerophytic vegetation 0.41; and subdeciduous forests 0.39). In contrast, the tropical dry forest had a 50% smaller β-diversity value (0.20). The difference between the global value calculated for the entire landscape and the community type level values reflects a large floristic differentiation between these communities.

Spatial structure

The Mantel statistic values for the entire data set, i.e. for the four communities combined, were negative, significant, and very similar both for the Mantel (r_M = -0.23, $P < 0.001$) and the partial Mantel test (r_M = -0.19, $P < 0.001$); therefore, elevation was disregarded in subsequent analyses of floristic spatial differentiation between samples. Regarding the different community types there were some important differences. Savanna and tropical dry forest had overall negative and significant values (r_M = -0.75, $P < 0.001$; and r_M = -0.36, $P < 0.001$, respectively). The r_M value for the xerophytic vegetation was also significant, but positive and much smaller (r_M = 0.04, $P < 0.05$). In turn, the value calculated for subdeciduous forest was not significant (r_M = 0.08, n.s.).

The global correlogram showed the existence of a gradually decreasing positive autocorrelation to a spatial range of about 1000 m, with r_M for the first distance class being 0.3 ($P < 0.05$). In the remaining section of the distance range the large majority of values corresponding to the several distance classes were significant but negative, even for those classes with low frequencies (Figure 2).

Figure 3 shows the correlograms for the tropical dry forest, both for the 500 m and 200 m distance classes. The initial r_M value in the correlogram based on 500 m distance classes (Figure 3a) was ca. 0.37 ($P < 0.05$). The positive, decreasing trend went as far as a spatial range of 1500 m; thereafter, there was a 1 km spatial range with r_M values that did not differ significantly from 0. This was followed by a sharp decrease through a spatial range spanning from 3000 to 4000 m, reaching a minimum significant r_M value of -0.2. The Mantel statistic became non significant after the 5500 m class. The overall shape of the correlogram based on 200 m classes (Figure 3b) was practically the same. For example, in both cases positive and negative values were located within the same distance ranges, and the lowest r_M value corresponded to the distance class with the highest frequency (around 4000 m). However, it is important to note that the maximum and minimum values were different (0.34 and -0.14, respectively).

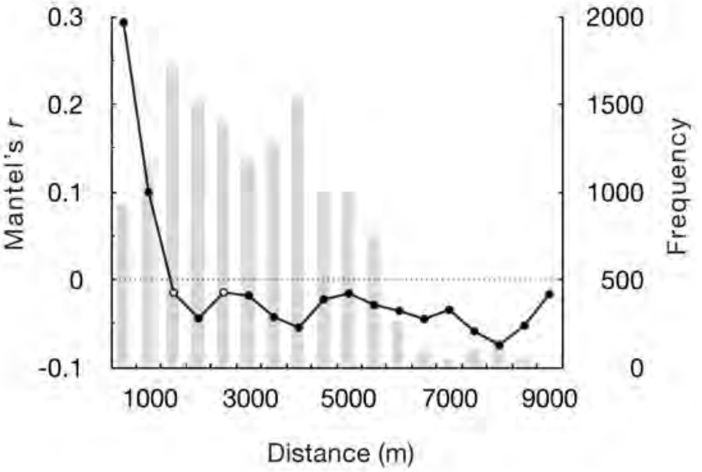

Figure 2. Mantel correlogram showing the relationship between the r_M statistic and distance classes for the four community types combined (tropical dry forest, savanna, xerophytic vegetation, and subdeciduous forest) in the landscape of Nizanda, Oaxaca, Mexico. The histogram shows the frequency distribution of the number of pair-wise comparisons involved in the calculation of r_M for each distance class. Open circles correspond to non-significant r_M values after the Bonferroni correction method ($\alpha' = \alpha/\nu$); black circles are significant ($P < 0.05$).

As in the case of correlograms for the tropical dry forest, the two correlograms based on both distance class partitionings for the savanna had a strong resemblance (Figure 4). In both of them it was clear that there were no r_M values involving distances between 2600 and 3400 m, although minor gaps in the 1800 m, 5200 m, and 6200 m classes were only noticeable in the 200 m class correlogram (Figure 4b). In the correlogram based on 500 m classes (Figure 4a) the initial r_M value was 0.70 ($P < 0.05$). Again, positive values decreased sharply up to a distance range of 1500 m, and then no significant autocorrelation was detected up to a distance range of 2500 m. For the distance classes between 4000 and 6000 m all r_M values were negative, and most of them significant; the minimum r_M value in this region was -0.42. The maximum and minimum significant r_M values in the correlogram for 200 m classes were 0.55 and -0.40, respectively.

The shapes of the two correlograms representing the spatial structure of the xerophytic vegetation differed substantially from those described so far (Figure 5). For example, although the first distance class had a high, positive and significant r_M value, classes representing much larger distances also had significant, positive autocorrelations; in fact, an alternation of significant positive, significant negative, and non significant values was observed throughout the analysed distance range, but this wavy pattern was clearer in the correlogram based on 200 m classes (Figure 5b). Another relevant feature shared by these correlograms is that the largest negative value (i.e. the minimum r_M) was larger than the maximum positive one, but more importantly, that the minima in both correlograms were found in classes corresponding to relatively short distances (1000 m in the 500 m classes correlogram, and 800 m in the 200 m classes correlogram).

The overall trends in spatial autocorrelation reflected by the correlograms for the subdeciduous forest (not shown) were not significant after the Bonferroni correction, indicating that distance does not account for the floristic variation in this community type.

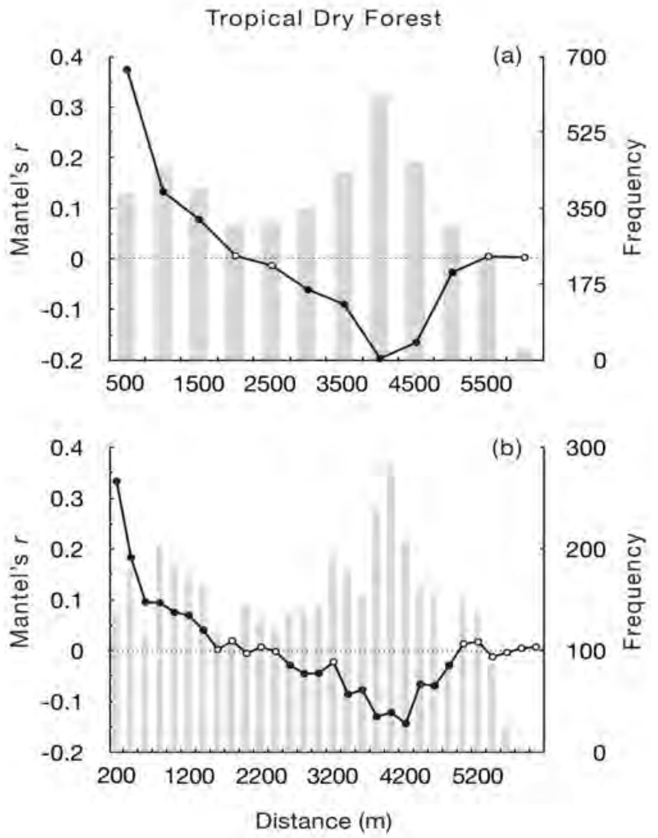

Figure 3. Mantel correlograms showing the relationship between the r_M statistic and distance classes for the tropical dry forest in the landscape of Nizanda, Oaxaca, Mexico. The histograms show the frequency distributions of the number of pair-wise comparisons involved in the calculation of r_M for each distance class. Open circles correspond to non-significant r_M values after the Bonferroni correction method ($\alpha' = \alpha/\nu$); black circles are significant ($P < 0.05$). (a) Correlogram based on 500 m distance classes; (b) Correlogram based on 200 m distance classes.

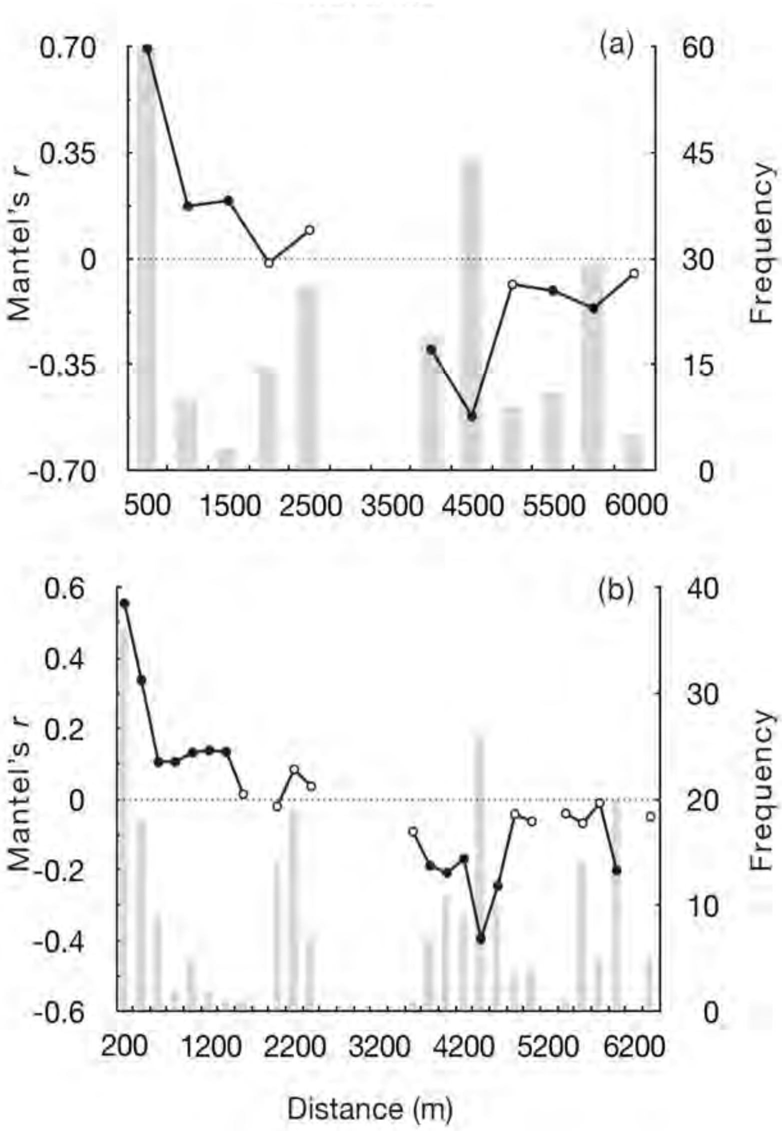

Figure 4. Mantel correlograms showing the relationship between the r_M statistic and distance classes for the savanna in the landscape of Nizanda, Oaxaca, Mexico. The histograms show the frequency distributions of the number of pair-wise comparisons involved in the calculation of r_M for each distance class. Open circles correspond to non-significant r_M values after the Bonferroni correction method ($\alpha' = \alpha/\nu$); black circles are significant ($P < 0.05$). (a) Correlogram based on 500 m distance classes; (b) Correlogram based on 200 m distance classes.

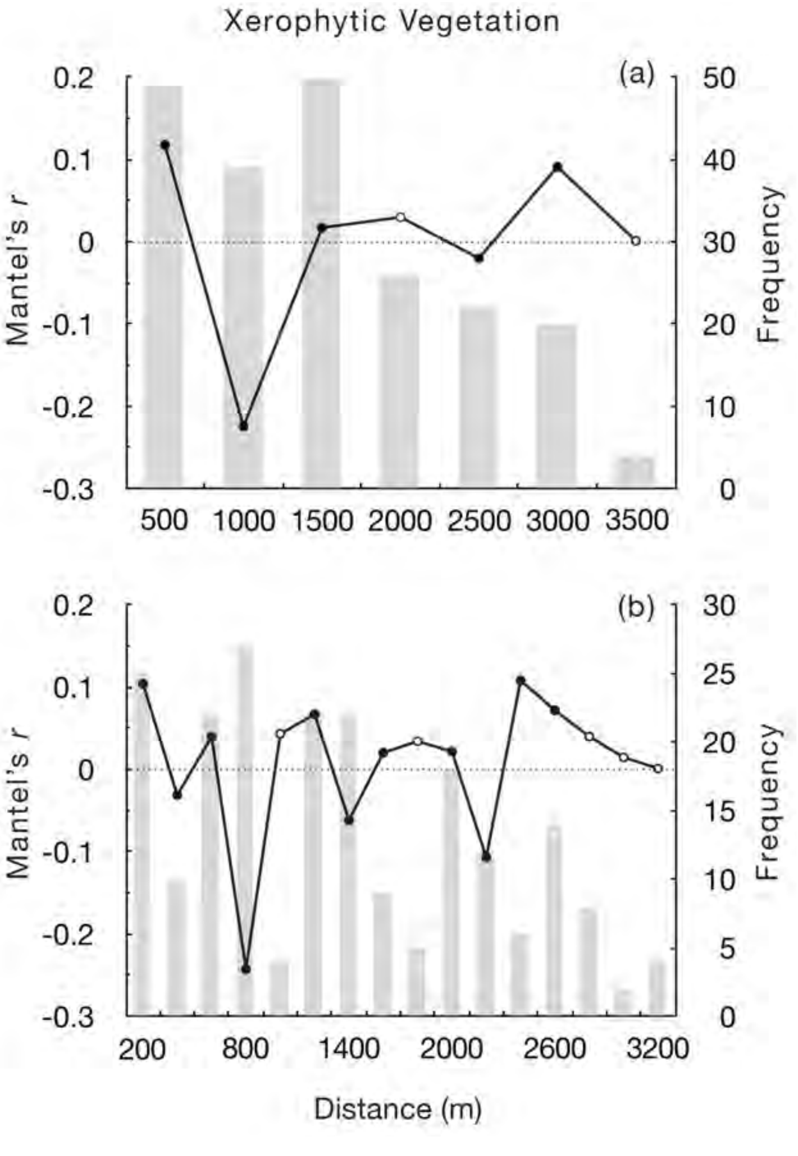

Figure 5. Mantel correlograms showing the relationship between the r_M statistic and distance classes for the xerophytic vegetation in the landscape of Nizanda, Oaxaca, Mexico. The histograms show the frequency distributions of the number of pair-wise comparisons involved in the calculation of r_M for each distance class. Open circles correspond to non-significant r_M values after the Bonferroni correction method ($\alpha' = \alpha/\nu$); black circles are significant ($P < 0.05$). (a) Correlogram based on 500 m distance classes; (b) Correlogram based on 200 m distance classes.

Discussion

The study of spatial autocorrelation in plant communities represents a way to formally approach the spatial structuring of these ecological entities, while searching for the underlying drivers of such structuring (Palmer 2005). Space in itself should not be seen as the ultimate cause of floristic turnover, but it must be rather interpreted as a surrogate of other (often unknown) ecological processes and geographical factors that are spatially structured themselves, such as propagule dispersal, population aggregation, geomorphological processes and the human factor (Mistral et al 2000, Tuomisto et al 2003, Morlon et al 2008), or of non mechanistic processes such as ecological drift (Hubbell 2001), which ultimately are reflected in the community's spatial organization

Our results provide evidence for the role of space as a variable that is capable of explaining (in the statistical sense discussed by Tuomisito and Ruokolainen 2006) much of the variation in community composition (i.e. β-diversity) in all but one community studied by us in the complex landscape of Nizanda. The magnitude of landscape-level β-diversity cannot exclusively be understood based on the number of plant communities in the region, as this would imply a low floristic overlap between them. It is likely that this puzzling situation derives from the fact that the effect of space on the variation of the floristic assemblages of these communities is not homogenous, but that it rather operates in specific ways in each community, even though all of them are part of the same landscape, and are subjected to the same general climatic and historical drivers. In other words, the high floristic turnover does not seem to be dependent on the existence of several communities in the landscape only, but also on a strong internal spatial structuring of each community.

The landscape-level spatial structure, as analysed by Mantel tests and mantel correlogram, is in agreement with the numerous studies that have reported a distance decay similarity for a wide range of ecological communities. However, there are many reasons to believe that his general pattern is concealing a complex of factors operating with variable strengths in each community. An initial attempt to explore the role of environmental heterogeneity in this pattern was achieved through the partial Mantel test, whish showed that elevation play a very minor role in the general autocorrelation. This suggests that the strong spatial structure observed may be actually the result of a complex combination of factors, which may be more readely disentangled by analysing each of the studied commnities separately.

In Nizanda, the tropical dry forest is the community type with the most continuous distribution, and therefore the one likely to bear the stronger connectedness between all covered areas by it. Thus, it is not surprising that its spatial structure is characterised by a monotonic decreasing trend in its floristic autocorrelation, where the effect of space causes a negative autocorrelation beyond 2500 m. For this community we identified a distance of 5 km beyond which space loses relevance. As the ecological conditions appear to be relatively constant throughout all areas occupied by the tropical dry forest, this pattern is not likely to be a result of this community being organised along a linear environmental gradient (Legendre and Fortin 1989). Therefore, a reasonable possibility is that this behaviour is associated to strong spatially autocorrelated dispersal, a process that tends to cause floristic homogenisation at short distances (Hubbell 2001, Condit et al 2002, Tuomisto and Ruokolainen 2006). The shape of the correlogram in the largest distance classes further supports this possibility, as the r_M statistic becomes indistinguishable from 0 instead of remaining negative; the typical shape corresponding to a linear gradient would not include this return to non-significant values (Legendre and Fortin 1989).

The spatial pattern observed for the savanna is essentially the same as for the tropical dry forest, i.e. it also begins with the highest autocorrelation value and shows a decreasing trend thereafter. However, we also found some important differences. First, the existence of two separate core areas of savanna in opposite ends of the studied landscape is reflected in the presence of discontinuities in the Mantel correlogram. Therefore, the left side of the correlogram (small distance classes), where all positive r_M values concentrate, corresponds to comparisons between plots located within the same savanna area, whereas the right side, where the negative values occur, includes comparison of plot pairs located in a different area each. Nonetheless, for this community we failed to identify a distance beyond which spatial correlation is clearly lost: at very large distances some significant negative values were still observed. As in the case of the tropical dry forest, at short distances there appears to exist a homogenising effect, probably associated to dispersal processes (Hubbell 2001). Conversely, the negative autocorrelation displayed by floristic assemblages at long distances seems to implicate a combined effect of distance and ecological differentiation, a possibility suggested earlier by López-Olmedo et al (2007) and Pérez-García et al (2010), based on non-spatially explicit classification analyses. Despite the evidence for the existence of two relatively differentiated floristic assemblages in the savannas, one cannot overlook the fact that β-diversity was smaller in this community than in the tropical dry forest. This may be a reflection of savannas being associated to a more limiting environment than the tropical dry forest (Mistry 2000, Pennington et al 2006), which ultimately may filter more effectively those species capable of establishing and persisting in them.

The spatial structure observed for the xerophytic vegetation was in strong contrast with the structures of the preceding communities. The Mantel correlogram for this community closely matches the shapes of correlograms constructed by Legendre and Fortin (1989) for artificial data sets with bumpy structure. The insular configuration in the landscape of the xerophytic vegetation represents an exogenous source of spatial structuring (Lindo and Winchester 2009). Nevertheless, the peculiar wavy pattern also appears to be related to another important feature of Nizanda's xerophytic vegetation, namely the internal organisation of these habitat islands, which consists in a series of nearly concentric bands corresponding to different facies of the community along a decreasing gradient of soil development (Pérez-García and Meave 2004). Thus, as distance from a given focal point increases, sample pairs belonging to the same and to different facies are alternately compared, so that even at very short distances floristic assemblages can be negatively autocorrelated. Bearing this in mind, the fact that even at large distances no clear loss of spatial autocorrelation (i.e., no distance decay of floristic similarity) was observed, suggests a lack of dispersal limitations among the species of this community. Alternatively, it may also indicate that dispersal limitation plays a minor role compared to the restrictions imposed by a very limiting environment (Palmer 2005), which is reflected in a relatively species-poor, low biomass community. Typical xerophytic vegetation show a high specificity for their environment; for example, in this community there is a larger proportion of endemic taxa), and posses many morphological and physiological adaptations (Pérez-García et al 2009), such as rosette-like form growths and clonality, some of which seem to render them incapable of surviving in the surrounding community types. Pecháčová et al (1999) showed that the prevalence of clonal growth in a montane grassland of Krkonoše, Czech Republic, results in a strong spatially autocorrelated pattern; this finding may be also true for the most xeric facies of our xerophytic vegetation, as this community has the largest incidence of clonal species in the entire landscape of Nizanda (Pérez-García and Meave, 2004).

The absence of spatial structuring in the subdeciduous forest can also be interpreted as a lack of distance decay of similarity in this community. This result casts further doubts on the universal nature of this ecological phenomenon (Soininen et al 2007). In Nizanda, this community type is associated to water streams, which may act as an homogenizing factor, both of the environmental and biological attributes in the riparian zones, which is a widely recognised role played by rivers and water streams worldwide (Naiman and Décamps 1997, Ward et al 2002). Under these conditions, one could expect a wider niche overlap (Nekola and White 1999), leading to the ecological drift predicted by the unified neutral theory proposed by Hubbell (2001). Thus, the reason why this does not take place is the unusually efficient dispersal by water and animals along the riparian corridors.

A further important conclusion of this study is related to the scale at which the spatial analysis is performed. By constructing correlograms for two sets of distance classes (which differ between them by less than one order of magnitude), the observed patterns and therefore the potential conclusions derived from them may differ substantially. Even though we found essentially the same results at both scales for the tropical dry forest and the savanna community types, there is no doubt that we would have missed the essence of the spatial structuring in the xerophytic vegetation, had we used 500 m distance classes only. Therefore, we must emphasise the relevance of using a multiscale approach in future ecological research.

Incorporating a spatial perspective in the analysis of β-diversity proved to be a powerful tool to elucidate the underlying causes of complex biodiversity patterns. Hence, we conclude that by following this approach routinely in their research, community ecologists will make significant progress in understanding and explaining species turnover across space, and the distance decay similarity of diversity, all of which have been elusive issues for a long time.

Acknowledgements

We are greatful to the Reyes-Manuel and Aranjo families of Nizanda for their assistance during field work. Armando Peralta and Marco A. Romero provided technical support in data managing and image analysis, and Rodrigo Gallardo assisted with programming. This study was financially supported by the Universidad Nacional Autónoma de México (PAPIIT programme), the National Council of Science and Techonology (CONACyT-Semarnat and CONACyT-SEP), and the Mexican Biodiversity Commission (CONABIO). This article benefited greatly from constructive comments from Angelina Martínez-Yrízar and Carlos Martorell. J.A. G-C. received a CONACyT grant during his Ph.D. studies at the Posgrado en Ciencias Biológicas, UNAM.

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CAPÍTULO 6

Relating species richness to the structure of continuous landscapes: alternative methodological approaches

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The relation between landscape structure and plant diversity has been a major topic for landscape ecology during the last decades (Gallardo-Cruz and Schindler 2010, Uuemaa et al 2009, Walz 2011). From a theoretical perspective, several species-distribution models have provided useful insights into this relation, for example those based on island biogeography (MacArthur and Wilson 1967), spatial heterogeneity (Tilman and Pacala 1993), dispersal potential (Hubbell 2001), negative conspecific interactions (Connell 1971, Janzen 1970), productivity (Tilman 1982), disturbance (Levin and Paine 1974) and metapopulation theories (Levins and Culver 1971). Interestingly, despite some important differences between these models all of them have a common prediction: a landscape pattern should match an ecological process. The quest for evidence to test this idea has prompted numerous studies all over the world, encompassing a wide array of geographic regions, environments, scales, biomes, taxonomic groups, and naturalness gradients. Despite such ample variety of conditions, the large majority of studies concur in the use of the patch-mosaic landscape paradigm (Forman 1995), deriving their structural data from a classified satellite image.

The use of discrete landscape classes poses severe limitations for predicting patterns of biodiversity in complex systems (Southworth et al 2004, St-Louis et al 2009, Stickler and Southwoorth 2008). Under this view landscape properties within a class are presumed to be homogeneous and consequently may not capture important characteristics for species with heterogeneous distributions (Pameirim 1988). In highly heterogeneous systems image classification errors can be transferred into the composition and configuration of landscape attributes (Wagner and Fortin 2005). Moreover, in ecosystems with broad ecotones the arbitrary delineation of boundaries between landscape classes may lead to a flawed image classification. Also, the classification scheme does not necessarily reproduce the spatial organization of the ecological requirements of the species under study.

For these reasons, some recent studies have emphasized the importance of understanding the pattern of gradients in a landscape, i.e. the gradual changes of landscape attributes across the surface (Cihlar 2000, McGarigal and Cushman 2005). In this regard at least two methods have been put forward. The first one produces a continuous representation of the landscape starting from a classified image; this representation is expected to reflect the species' perception of landscape structure. This idea is grounded on the principle that organisms sense spatial variation of the landscape structure as gradients rather than as discrete mosaics. Therefore, instead of analyzing an overall landscape pattern the method quantifies the local landscape patterns, emulating the way in which the species may experience it through the use of a moving-window approach (McGarigal and Cushman 2005). In turn, the second method analyzes local patterns in the spatial variation of pixels (i.e. texture) found in raw unclassified imagery (Marquez 2008, Petrou and García-Sevilla 2006); these local patterns are indicative of the landscape's complexity according to the principle that links vegetation heterogeneity with the spatial variability of its remotely sensed signal (Farina 2006, Malhi and Román-Cuesta 2008, Rocchini et al 2010, Rocchini et al 2004)

Though the notion that gradual variation is pervasive in natural landscapes is accepted, the question remains as to whether which of these two methodological approaches is more powerful to relate landscape structure and plant diversity, and what the implications would be of using either one to advance our understanding of the diversity-landscape relation. In this paper we attempt to provide a comprehensive answer to these questions not only by comparing the results produced by these two approaches, but also by incorporating into the analysis of this relationship additional relevant sources of variation, namely evolutionary constraints (taxonomy), convergent ecological responses (growth form), spatial scale (extent), and space (i.e. autocorrelation patterns). We did this in a highly complex semi-natural landscape, with a very high plant diversity (Pérez-García et al. 2010).

First, we related landscape structure, derived from both methods, with six sets of plant species: all species, legume species, legume trees, legume shrubs, legume forbs and legume climbers. This procedure allowed us to distinguish potential landscape associations determined by taxonomic affinities or growth form. Second, we examined the effect of changing scale (i.e. extent) on the shape and strength taken by this relationship for the above-mentioned groups (Storch and Gaston 2004, Storch et al 2007); to this end, we used two window sizes to describe both highly localized and medium range landscape variations. Finally, we measured the spatial dependence of species richness of the same plant groups in the study landscape (Dormann et al 2007, Fortin and Dale 2005). This final step allowed us to assess the relative contributions of space and landscape descriptors to the spatial distributions of species using spatial variables and variance-partitioning methods. The relative contributions of these two factors has been seldom assessed in studies relating landscape structure and species richness; while the potential of space to explain a considerable proportion of species diversity variation is presently well known (Legendre 1993, Legendre and Legendre 1998), this has been neglected by those studies that have ascribe the totality of species variability to landscape descriptors.

Methods

Study area

The study focused on the seasonally dry tropical landscape of Nizanda (Mexico; 16° 39.49' N, 95° 0.66' W; Figure 1). This landscape covers an area of 64 km^2 and ranges in elevation from 100 to 700 m a.s.l. Mean annual temperature is 26°C and the total average annual rainfall is 900 mm, mainly concentrated between May and October. Five plant communities display an intricate spatial arrangement across the landscape: tropical dry forest (TDF), savanna (SAV), sub-deciduous forest (SDF), semi-evergreen forest (SEF) and xerophytic (XER) (Gallardo-Cruz et al 2005, Gallardo-Cruz et al 2009, Lebrija-Trejos 2001, López-Olmedo et al 2007, López-Olmedo et al 2006, Pérez-García and Meave 2004, Pérez-García et al 2009). These communities vary considerably in extent, the TDF having the largest area. Therefore, this may be seen as the matrix of the remaining communities (Gallardo-Cruz et al 2010). According to the Index of Naturalness proposed by Machado (2004), this landscape may be classified as a category 8, sub-natural system.

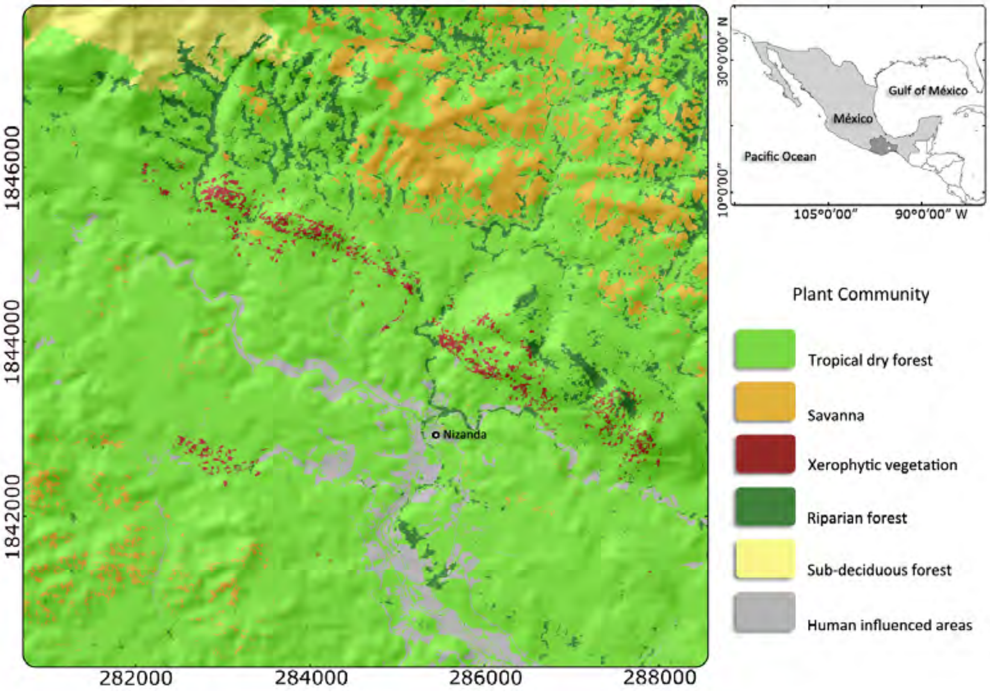

Figure 1. Location (UTM zone 15n) of the studied landscape around the village of Nizanda, Oaxaca State, southern Mexico, and object-oriented classification of a Quickbird satellite image showing community types and human-influenced areas.

Diversity sampling

The survey was based on a stratified random design in which each plant community was randomly sampled in proportion to its area. The number of plots by plant community was adjusted to provide an adequate representation of species richness based on species accumulation curves (Gallardo-Cruz et al 2010). The final set contained 250 plots (10 × 10 m) distributed as follows: 116 in TDF, 47 in SAV, 38 in XER, 26 in SEF and 23 in SDF. All plots were located on the ground with a GPS unit, avoiding areas affected by human activities. Within each plot the taxonomic identity of all plants was recorded following (Pérez-García et al 2001). Based on this information, we constructed six species-richness sets: total species, legume species, legume trees, legume shrubs, legume forbs and legume climbers. We paid particular attention to legumes because of its large richness in the area, its wide distribution across plant communities and its general prevalence in tropical dry landscapes (Pérez-García et al 2012). These variables were tested for normality and homoscedasticity.

Remotely sensed data and image processing

Considering that some of the plant communities occupy very small areas across the landscape (Gallardo-Cruz et al 2010), we maximized the detection of their properties by using a high-resolution satellite image (Quickbird; pixel size = 2.6 m). The scene was acquired at the end of the rainy season to reduce cloud cover and to ensure the presence of foliage in the plants. This image was geometrically and atmospherically corrected to surface reflectance following Krause (2005). The resulting image served as basis to calculate the landscape metrics and for the analysis of image texture.

Landscape descriptors: surface metrics

The initial step to compute surface landscape metrics is to identify in the image ecological units homogeneous in structure, function, and disturbance regimes based on the plant communities and land use types present at the site (Forman and Godron 1986, Yoshida and Tanaka 2005). Accordingly, we performed a supervised object-oriented classification

(Blaschke and Hay 2001) using Definiens Professional 5.0 (Definiens 2006). Our aim was to identify the five above-mentioned communities while distinguishing them from those areas where human activities resulted in the clearing of the natural vegetation for agriculture and cattle raising. This classification was based on the shape and color properties of groups of pixels (objects). Additional details of this classification procedure can be found in Benz et al. (2004).

Table 1**.** Abbreviations and description for the 12 surface metrics used in the analysis. *AM: area-weighted mean, which is equal to the sum across all patches in the landscape of the corresponding patch metric values, multiplied by the proportional abundance of the patch. AM metrics provide a landscape-level measure of landscape structure.

Surface metric	Abbreviation	Description
Largest patch index	LPI	Percentage of total landscape area covered by the largest patch.
Shannon's diversity index	SHDI	Quantifies landscape diversity.
Total core area	TCA	Sum of the core areas in the landscape.
Percentage of landscape	Pland	Proportional abundance of each patch type in the landscape
Total edge contrast index	TECI	Measures the contrast along all edges across the landscape.
Area-weighted mean patch size	AreaAM	A relative measure of mean patch size. *
Area-weighted edge contrast Index	EconAM	An area-weighted amount of contrast along the patch perimeter. *
Area-weighted largest patch index	LPIAM	An area-weighted measure of the percentage of total landscape area covered by the largest patch. *
Mean area-weighted proximity index	ProxAM	A relative measure of patch isolation and fragmentation of the corresponding patch type within a specified neighborhood. *
Mean area-weighted similarity index	SimiAM	An area-weighted measure of patch isolation under a landscape mosaic perspective. This index considers the size and proximity of all patches, regardless of class, whose edges are within a specified search radius of the focal patch. *
Perimeter-area ratio	ParaAM	Measures shape complexity. *
Standard deviation of perimeter-area ratio	ParaSD	Measure of absolute variation of shape complexity.

With the categorical map we calculated 12 class- and landscape-level metrics (Table 1) using a moving-window approach in FRAGSTATS (McGarigal et al 2002). In this technique a window moves across the classified image one cell at a time, calculating the selected metric within the window and returning that value to the center cell. In the resultant surface each cell synthesizes the structure of the landscape within the window (McGarigal and Cushman 2005). From these surfaces we extracted the corresponding metric values for the 250 sampling plots. The effect of scale was analyzed using square windows with sides of 400- and 200-m (sensu Goodchild 2001). These geographic ranges were selected because these distances improved the spatial analysis of plant diversity related to autocorrelation patterns in the region (Gallardo-Cruz et al 2010). The same criterion was applied for selecting window sizes for the following section.

Landscape descriptors: image texture

Image texture is the spatial variation of the pixel-values within a digital image (Haralick 1979, Irons 1981, Marquez 2008). This property was analyzed using second-order texture metrics that consider the spatial relations between groups of two neighboring pixels within a given window (Petrou and García-Sevilla 2006). The calculation of second-order metrics involves the construction of Gray-Level Co-occurrence Matrices (GLCMs), which include the co-occurrence probability of pixel values for pairs of pixels in a given direction and distance. To create such matrices we used a spatial distance of one pixel, four directions (0°, 45°, 90°, 135°), and 64 gray levels. A GLCM was built for each direction, and from each matrix a texture measurement was calculated using the four formulas described in Table 2. Finally, the texture measurements of each direction were averaged to obtain a single spatially-invariant texture metric. These metrics were calculated using a moving-window approach for three data layers: the red (RED; 0.63-0.69 µm) and infrared (IR; 0.76-0.90) image channels, and the enhanced vegetation index (EVI):

$$EVI = G\left(\frac{IR - RED}{L + IR + C_1 \times RED - C_2 \times BLUE + L}\right)$$

This index does not saturate under dense canopy conditions and incorporates empirical parameters ($C_1 = 6$, $C_2 = 7.5$) and the BLUE channel for atmospheric correction, and sensitivity minimization of soil background reflectance variation ($G = 2.5$, $L = 1$; Gao et al 2000).

From the 12 resulting texture surfaces (three layers and four metrics) we extracted the value for each of the 250 plots. To analyze the effect of scale the entire procedure was performed using square windows with sides of 400 and 200 m. The entire procedure was programmed in the ENVI+IDL environment (ITT 2008).

Spatial data

The spatial dependence of species richness across the landscape was analyzed using the 'principal coordinates of neighbor matrices' method (PCNM; Borcard and Legendre 2002). PCNM is based on a principal coordinate analysis of a truncated geographical distance matrix between sampling sites. The method creates a set of explanatory spatial variables (i.e. PCNM vectors) with structures at all scales encompassed by the samples data matrix. The steps to generate the PCNM vectors are: (1) create an Euclidean distance matrix based on the between-sites geographical distances, (2) replace in this matrix those distances greater than the largest distance between adjacent sites with an arbitrary large number (Borcard et al 2004), (3) perform a principal coordinate analysis on the modified distance matrix and, (4) retain the principal coordinate axes that correspond to positive eigenvalues. After completion, the method produced 112 PCNM vectors, among which 29 had positive and significant autocorrelation values ($P < 0.001$, Moran's test). These where kept as the set of explanatory PCNM variables to determine their statistical relation with the response (i.e. species richness) variables. The PCNM method was performed using the 'spacemakeR' library in R (Dray et al 2006, R Development Core Team 2010).

Effects on species diversity

Multiple regression and variation partitioning methods were used to analyze the effects of landscape and space on species diversity. The overall procedure involved four stages. First, using multiple regressions we fitted models between a species diversity variable (total species, legume species, legume trees, legume shrubs, legume forbs or legume climbers) and one set of landscape data (either 12 landscape metrics or 12 texture metrics). These models represent the variation explained by landscape data plus the variation explained jointly by landscape data and spatial structure (a + b). Second, a multiple regression model using the selected set of PCNM variables was fit to the dependent variables. This second model represents spatially dependent variation plus the variation explained jointly by landscape data and spatial dependence (b + c). Third, the total amount of variation explained (a + b + c) was calculated by combining the two previous multiple regression models into a global regression model using exclusively significant variables. All multiple regression analyses were implemented using forward selection in SPSS. Finally, variation partitioning was performed to determine the relatively importance of landscape variables (a = (a + b + c) – (b + c)), spatial structure (c = (a + b + c) – (a + b)) and shared variation (b = (a + b + c) – (a) – (c)) on species diversity (Borcard et al 2004).

Table 2. Abbreviations, formulas and descriptions of the four texture metrics derived from the grey-level co-occurrence matrix (GLCM). $P_{i,j}$ is the (i, j) element of the GLCM, and represents the probability of finding the reference pixel value i in combination with a neighbor pixel value j. Note that $\Sigma_{i,j} P_{i,j} = 1$.

Texture metric	Abbreviation and formula	Description
Mean	$\text{MEAN} = \sum_{i,j=0}^{N-1} iP_{i,j}$	Mean of the probability values from the GLCM. It is directly related to the image spectral heterogeneity.
Variance	$\text{VAR} = \sum_{i,j=0}^{N-1} P_{i,j}(i-\text{MEAN})^2$	Measure of the global variation in the image. Large values denote high levels of spectral heterogeneity.
Correlation	$\text{COR} = \sum_{i,j=0}^{N-1} P_{i,j}\left[\frac{(i-\text{MEAN})(j-\text{MEA}}{\text{VAR}}\right.$	Measure of the linear dependency between neighboring pixels.
Second moment	$\text{SM} = \sum_{i,j=0}^{N-1} P_{i,j}^2$	Measure of the order in the image. It is related to the energy required for arranging the elements in the system.

Results

Overall floristic assessment

In the 250 100-m^2 sampling plots distributed across the landscape we recorded a total of 1,001 vascular plant species. Over 10% of them (119 species) were members of Leguminosae, thus confirming the prevalence of this family in tropical dry landscapes. Additional important plant families were Asteraceae with 73 species, Euphorbiaceae (48), Rubiaceae (41), Poaceae (40), Convolvulaceae (32), Bignoniaceae (31), Malpighiaceae (24), Malvaceae (23), Acanthaceae (21), and Polygonaceae (20). The total set of plant taxa encompassed a considerable proportion of undetermined species (54; 5%), but none of them belonged to any of the most speciose families.

The distribution of legumes by growth form was uneven. Nearly half of all legumes were trees (51; 42.9% of all legumes), forbs and shrubs had intermediate representations, with 27 (22.7%) and 20 species (16.8%), respectively, with climbers being the least represented group with 10 species only (8.4%).

Prediction of total plant species richness

The capacity to predict total species richness based on landscape descriptors was very limited, as no single combination of predictive factors produced R^2 values > 0.20 (Figure 2; Table 3). The highest R^2 corresponded to the full models incorporating both landscape and space variables (a+b+c), with the largest R^2 obtained from the use of surface metrics for the 400-m scale (0.161). Individual inputs of the two main factors, namely landscape structure descriptors (a) and space (c), to total variance were relatively small (Figure 2a, b). In the case of landscape structure the largest contribution came from surface metrics for the 400-m scale (0.030), whilst for space the largest value corresponded to texture-based models, also for the 400-m scale (0.098).

The predictive variables retained in the models constructed for the entire flora were not the same for the two spatial scales in the case of surface metrics (Table 3). Conversely, in the case of texture-based models there were two variables common to both models (RED_{VAR} and RED_{SM}) (Table 4).

Prediction of legume species richness

Full models predicting all-legume species richness had a considerably higher predictive capacity, with the resulting R^2 values generally twice as large as the previous ones (Figure 3; Tables 3 and 4). Texture-based models for the two spatial scales had R^2 values > 0.30. In the case of this plant group, texture-based models gained relatively larger contributions from the landscape component and smaller ones from the spatial component compared to models based on surface metrics.

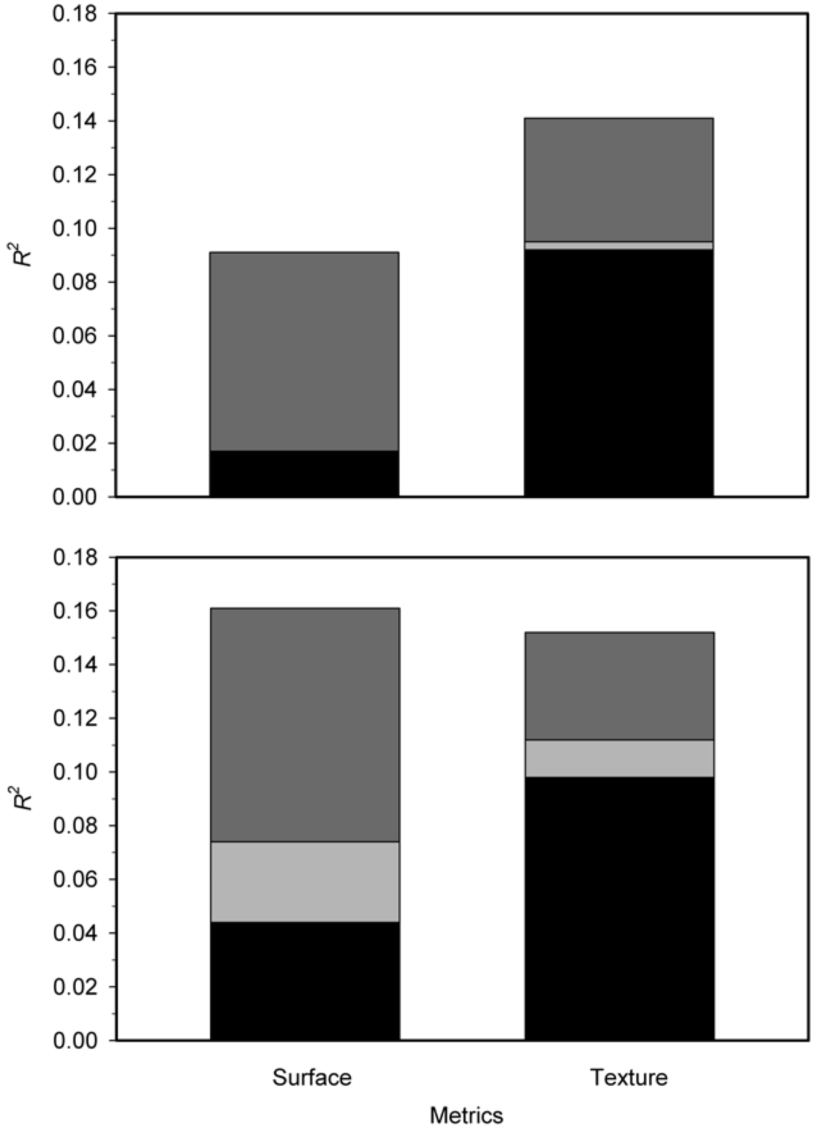

Figure 2. Variation partitioning for full models (a+b+c) predicting all species richness, both based on surface (left bars) and texture (right bars). Bar height indicates total variation (R2) explained by models constructed for the 200-m scale (top), and the 400-m scale (bottom). Different shadings represent the contributions of the different components revealed by variance partitioning: landscape structure (a; light gray), space (b; black), and the shared component (c; dark gray).

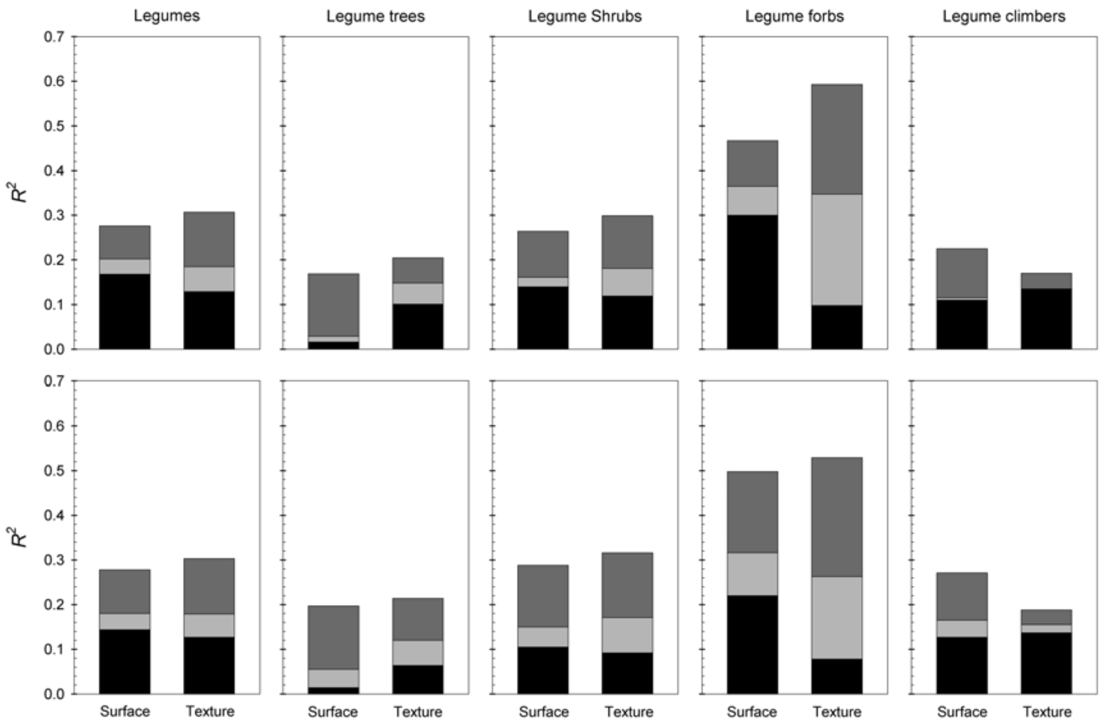

Figure 3. Variation partitioning for full models (a+b+c) predicting species richness in five subsets of legume species (all legumes, legume trees, legume shrubs, legume forbs and legume climbers), both based on surface (left bars) and texture (right bars). Bar height indicates total variation (R^2) explained by models constructed for the 200-m scale (top row), and the 400-m scale (bottom row). Different shadings represent the contributions of the different components revealed by the variance partitioning: landscape structure (a; light gray), space (b; black), and the shared component (c; dark gray).

For the modeling of all-legume species richness based on surface metrics only PARA was retained in the models for both spatial scales. Conversely, four variables were common to the two full texture models (a+b+c), namely IR_{MEAN}, IR_{SM}, RED_{MEAN} and EVI_{MEAN}.

Prediction of legume species richness by growth form

Surface-based and texture-based full models (a+b+c) predicting legume species richness by growth form separately showed a variable behavior, with cases of both larger and smaller R^2 values than full models predicting all-legume species richness (Table 3, 4). Particularly notable was the increase in the predicting ability of models for species richness of forbs, with R^2 values higher that 0.45 for both spatial scales in the case of surface metrics-based models, and higher than 0.50 for both spatial scales regarding texture models. Full models for trees, shrubs and forbs based on surface metrics had higher R^2 values when constructed for the larger scale (400 m), and the same pattern was true for most texture models, excepting the model predicting forb species richness.

The partitioning of full-model R^2 values in their different components for the four groups of legumes revealed that in most cases the contributions of space-related variables accounted for a larger proportion of total explained variance. However, there were three important exceptions to this general trend. These comprised the model predicting legume tree richness based on surface metrics for the 400-m scale, and the models for the two spatial scales constructed to predict legume forb richness using texture. In all of these cases, the contribution of the landscape structure component (a), was always more than twice as large as the spatial component (c) as seen in their R^2 values: 0.041 vs. 0.014 in the case of trees, 0.249 vs. 0.098 in the case of forbs for the 200-m scale based on texture, and 0.185 vs. 0.078 in the case of forbs for the 400-m scale also based on texture.

In modeling forb species richness based on texture the variables included in models constructed for the two spatial scales were $\mathrm{IR_{MEAN}}$, $\mathrm{RED_{MEAN}}$, $\mathrm{RED_{VAR}}$, and $\mathrm{EVI_{MEAN}}$ (Table 4). In turn, the model predicting tree species richness based on surface metrics at the 400 m scale retained LPI, SHDI, AreaAM, LPIAM, and SimiAM (Table 3).

Consistency of variable inclusion in the models

An overall look at Tables 3 and 4 reveals important disparities not only in the identity of landscape variables included in the models for the different plant groups and the two spatial scales, but also in the signs of their coefficients. In fact, no single surface or texture variable was included in all respective 12 models. These inequalities imply relevant differences in the ability of these variables to predict plant species richness in a continuous landscape.

In the case of surface variables, LPI excelled over all others in terms of its relevance, as it was the only one included in more than half of the models (8 models). Next to it, only AreaAM LPIAM, ParaAM and SimiAM appeared in five models. At the opposite end, no model included TCA. A very conspicuous pattern among these variables is that their coefficients are rather inconsistent concerning their signs; a clear example of this is LPI, as this variable had three cases of negative coefficients vs. five cases of positive ones. In this regard, ParaAM was an important exception, as its coefficients were negative in all five models that included this variable. Finally, it was also evident that these variables were highly sensitive to changes in the spatial scale: no single model pair for any plant group included the same or nearly the same variables for the prediction of species richness.

Table 3. Standardized coefficients for linear regression models based on surface metrics for predicting species-diversity in six plant sets (all species, legume species, legume trees, legume shrubs, legume forbs and legume climbers). See Table 1 for abbreviations and description of the twelve surface metrics shown. Values in italics on the first row correspond to R^2 obtained for the full models (a+b+c).

Surface metric	All species		Legume species		Legume trees		Legume shrubs		Legume forbs		Legume climbers	
	Scale 1	Scale 2	Scale 1	Scale 2	Scale 1	Scale 2	Scale 1	Scale 2	Scale 1	Scale 2	Scale 1	Scale 2
	0.091	*0.161*	*0.276*	*0.278*	*0.169*	*0.197*	*0.264*	*0.288*	*0.467*	*0.498*	*0.225*	*0.271*
LPI	-0.263				-0.725	-0.899	0.381	0.358	0.419	0.684	0.156	
SHDI	-0.327				-0.510	-0.526						-0.266
AreaAM			-3.365			3.750	-0.759		-1.097	-3.461		
EconAM				0.185						0.330		
LPIAM			4.542		2.054	-2.789		-0.673		2.128		
TCA												
ParaAM			-0.266	-0.180			-0.261		-0.235	-0.279		
ParaSD		0.175		0.162				0.248				
Pland			-1.302		-1.374							0.190
ProxAM												0.258
SimiAM						0.583	-0.488	-0.667	-0.831	-0.905		
TECI									0.214			0.307

The set of texture variables showed in general a more consistent behavior regarding their inclusion in the different models and the signs of their coefficients relative to surface variables. For example, in this group of variables no one departed largely from all others, as five of them appeared in at least five (but in no more than seven) models ($\mathrm{IR}_{\mathrm{MEAN}}$, $\mathrm{IR}_{\mathrm{SM}}$, $\mathrm{RED}_{\mathrm{MEAN}}$, $\mathrm{RED}_{\mathrm{VAR}}$, $\mathrm{EVI}_{\mathrm{MEAN}}$). More interesting, however, these variables were almost totally consistent in the signs of their coefficients, with the exception of $\mathrm{RED}_{\mathrm{VAR}}$. Furthermore, the spatial scale of analysis had a smaller effect on the models involving texture variables, as there were 12 cases of the same variable being included in the two models predicting species richness of given plant groups for both spatial scales. This pattern was particularly evident in the case of all legumes, and to a lesser extent, of legume forbs.

Table 4. Standardized coefficients for linear regression models based on texture metrics for predicting six species-diversity sets (all species, legume species, legume trees, legume shrubs, legume forbs and legume climbers). See Table 2 for abbreviations, formulas and descriptions of texture metrics. Values in italics on the first row correspond to R^2 obtained for the full models (a+b+c).

Texture metric	All species		Legume species		Legume trees		Legume shrubs		Legume forbs		Legume climbers	
	Scale 1	Scale 2	Scale 1	Scale 2	Scale 1	Scale 2	Scale 1	Scale 2	Scale 1	Scale 2	Scale 1	Scale 2
	0.141	*0.152*	*0.307*	*0.303*	*0.205*	*0.214*	*0.299*	*0.316*	*0.593*	*0.529*	*0.170*	*0.188*
$\mathrm{IR}_{\mathrm{MEAN}}$			1.735	1.346			1.654		2.468	2.193		
$\mathrm{IR}_{\mathrm{VAR}}$		-0.265										-0.135
$\mathrm{IR}_{\mathrm{SM}}$	-0.182		-0.278	-0.807	-0.247	-0.308	-0.254	-0.858				
$\mathrm{IR}_{\mathrm{CORR}}$												
$\mathrm{RED}_{\mathrm{MEAN}}$			-0.869	-0.685	-0.214		-0.727		-1.129	-0.933		
$\mathrm{RED}_{\mathrm{VAR}}$	0.173	0.331				0.197			-0.330	-0.139		
$\mathrm{RED}_{\mathrm{SM}}$	0.169	0.198	0.156			0.311	0.153					
$\mathrm{RED}_{\mathrm{CORR}}$								-0.237		-0.124		
$\mathrm{EVI}_{\mathrm{MEAN}}$			-1.507	-1.147			-1.460		-1.921	-1.709	-0.938	
$\mathrm{EVI}_{\mathrm{VAR}}$												
$\mathrm{EVI}_{\mathrm{SM}}$								0.769	0.555			
$\mathrm{EVI}_{\mathrm{CORR}}$						-0.159		0.186		0.164		

Discussion

It is well known that the largest proportion of the Earth's biota is strongly concentrated in tropical regions, both humid and seasonally dry (Chave 2008). Therefore, any attempt to predict species richness of tropical systems by using surrogates is warranted, particularly considering the large costs in time and money involved in the assessment of such diversity directly on the terrain (Gillespie et al 2005, Gillespie et al 2006, Hernández-Stefanoni 2006, Hernández-Stefanoni et al 2011). Therefore, the relative low predictive capacity of the full-models constructed for the entire flora based on surface and texture variables and for the two spatial scales analyzed seems at first glance disappointing. However, it can be argued that a more realistic view would only expect a higher predictive power in systems characterized by much lower levels of biodiversity (e.g. Moser et al 2002), and that moderate predictive capacities may be the rule with increasing levels of regional diversity, making it unreasonable to expect much higher R^2 values than ours. The base for this reasoning is related to the multitude of individual responses displayed by all species concurring in a given landscape, many of which are not even linear or Gaussian. Simply stated, without such variety of responses, the coexistence of many of those species would be impossible, as predicted by niche differentiation models (Tilman and Pacala 1993, Tilman 1982). The large contribution of fraction c (space) in our variation partitioning exercise provides evidence that many factors affecting the distribution of all species within a landscape were not represented in this analysis.

For decades now, space has increasingly gained recognition among ecologists as a variable that plays an important role in explaining the complex patterns of biological diversity of our planet (Kareiva 1994). This view is strongly supported by our study, as the contribution of space (measured through the PCNM vectors) to total variance, surpassed the contribution ascribable to landscape configuration in 21 out of 24 cases, regardless of the landscape descriptor or the spatial scale used for the analysis. The relative magnitude of the fraction of total variation corresponding to space suggests the existence of some natural process capable of generating the observed spatial structure, even though no explanatory variable is presently available to account for it (Borcard et al 2004, Legendre and Legendre 2000). The measurement of this fraction may become a valuable tool for landscape ecologists for the formulation of new hypotheses about these factors and processes. For example, one could reasonable argue that the species occurring in this landscape are subjected to strong dispersal limitations (Chave and Leigh 2002), but other processes such as individual population dynamics or predator–prey interactions may be involved.

The three cases in which landscape structure accounted for a larger proportion of total variation than space deserve particular attention. In our study this was the case of tree legumes at the 400 m-scale based on surface metrics, and of legume forbs for the two spatial scales based on texture. The first implication of this result is that these two plant groups may be relatively less limited for propagule dispersal than the others. In the case of forbs this is a reasonable interpretation, as small-sized herbaceous plants tend to possess efficient dispersal mechanisms (Baythavong et al 2009, Leishman et al 1995, Soons et al 2005), thus one would not expect these species to have distributional patterns with a strong spatial structure. However, in the case of trees this result seems somewhat counterintuitive, assuming lower dispersal abilities for propagules produced by legume tree species.

Further insight on the drivers of the distribution of these two groups of species across the study landscape may be gained by examining the roles of those variables, either texture in the case of forbs or surface in the case of trees, that were included in those models predicting their respective species richness. In the case of forbs, texture-based models indicate that their species richness is associated with an increasing spectral homogeneity in the system, i.e. negative coefficients for RED_{MEAN}, RED_{VAR}, and EVI_{MEAN}. In other words, forbs richness is highest in large, homogenous regions within the landscape. In our study landscape, such regions correspond with areas covered by savannas and tracts of secondary vegetation, both of which in turn encompass the largest forb richness according to plant inventories (Pérez-García et al 2010).

Unlike forbs, a largest proportion of tree species variation was accounted for by surface rather than by texture metrics. The above-mentioned study showed that although trees are not the most prominent component in the region's flora, they are important constituents of the tropical dry forest (TDF), the xerophytic vegetation (XER) and the subdeciduous forest (SDF), whilst they are virtually absent from savannas and secondary vegetation. Our analysis showed that legume tree richness was negatively associated with two measures of dominance in the landscape (negative coefficients for LPI and LPIAM), but also with a measure of landscape heterogeneity (SHDI), which in theory should be opposite to LPI. These results are inconsistent and therefore difficult to explain. Such inconstant relations between legume tree richness and surface metrics call for caution in using these metrics for the prediction of tropical plant species richness.

An overall examination of the consistencies among the identities and signs of all variables included in the models leads to similar conclusions. Our results showed that surface metrics are highly sensitive to the biological group under examination and to the analyzed spatial scale (i.e. window size); such sensitivity may be a leftover effect of the inability of image classification procedures to capture the internal heterogeneity of landscape patches. Despite the significant attempts to overcome this shortcoming (McGarigal and Cushman 2005), one must bear in mind that these metrics are grounded on an artificial classification of an inherently continuous landscape. In contrast, texture seems to have a more cohesive behavior, and to be more independent of these two factors of analysis. Thus, in attempting to predict species richness more rapidly and accurately, an ecologist may be better off by relying on texture metrics for this purpose.

Several reasons may help explain why texture metrics seem to be better landscape predictors than surface metrics, and why they are better able to predict species richness, at least of one plant group (forbs) examined in this study. We discussed previously the problems that arise when any landscape descriptor is derived from an initial classification procedure of a satellite image. These problems are basically the consequence of treating a landscape whose heterogeneity is intrinsically continuous as a collection of discrete units (Cihlar 2000). Of course, this problem is not equally critical across the entire naturalness gradient, and one may expect anthropic landscapes to be less sensitive to this issue. We acknowledge that surface metrics represent a proposal that recognizes this difficulty as it attempts to cope with the artificial delineation of natural entities within continuous landscapes. Yet classification errors are impossible to avoid. Likewise, our results also demonstrate that the proper selection of the size of the moving window is crucial for the computation of these metrics. For selecting the proper window size, McGarigal and Cushman (2005) suggest that it should reflect the way in which a species (or a process) perceive the landscape. However, what should be done when the response variable pertains to the community level (species richness in our case)?

Of course, our proclivity towards the use of texture metrics does not imply that they are totally problem free. Their major strength is the fact that their derivation does not need an intermediate step (image classification) with its burden of subjectivity. However, the challenge remains to find those metrics that best describe the heterogeneity of the remotely sensed signal. Also, we need to investigate further the effects of multiple factors that may alter the heterogeneity of an image, and ultimately the quantification of the many texture variables that have been described so far (Barbier et al 2010, Couteron et al 2006). Among them, it seems that inclination angle of the scene, topography, season, cloud coverage and other atmospheric conditions should be paid much attention.

Even after considering all these limitations, our study provides sufficient arguments to assert that future efforts to predict species richness in highly diverse tropical systems with a high degree of naturalness, would be more successful if scientists shifted towards the use of the continuous landscape paradigm, as it better matches the nature of these systems.

Acknowledgements

We are greatful to the Reyes-Manuel and Aranjo families of Nizanda for their assistance during field work. Armando Peralta and Marco A. Romero provided technical support in data managing and image analysis. This study was financially supported by the Universidad Nacional Autónoma de México (PAPIIT programme), the National Council of Science and Techonology (CONACyT-Semarnat and CONACyT-SEP), and the Mexican Biodiversity Commission (CONABIO). J.A. G-C. received a CONACyT grant during his Ph.D. studies at the Posgrado en Ciencias Biológicas, UNAM.

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CAPÍTULO 7

Predicting successional forest attributes from space: is the key hidden in image texture?

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PLoS ONE (2012), 7(2): e30506

In the dawn of the 21st century the magnitude of the human footprint on the planet's ecological systems has become undeniable (Hassan et al 2005, Janzen 1998, Lepers et al 2005, Sanderson et al 2002). Although much emphasis has been placed on the effects of industrial activities and their potential contribution to global change through greenhouse gas emissions (Bonan 2008, Fearnside and Laurance 2004, Satterthwaite 2008, Thomson et al 2010), the chronic effects of land clearance for the purpose of food production on the Earth's natural vegetation are likely to be among the most long-lasting human legacies

(Foley et al 2005; 2007, Nelson 2005). Ecologists now acknowledge that the majority of the planet's vegetation during the present century will consist of secondary or successional communities: from now on we will co-exist with secondary forests, use them, and entirely depend on them (Chazdon et al 2009a, Guariguata and Ostertag 2001). The maintenance of terrestrial biodiversity will be possible as long as we are capable of keeping expanses of secondary forests (Chazdon et al 2009b, Dent and Wright 2009), and the regulation of the world's ecosystems will be closely linked to their existence (Chinea and Helmer 2003, Guariguata and Ostertag 2001). Secondary forests have also been identified as important carbon reservoirs and may play a crucial role in mitigating future global warming (Aide et al 2000, Brearley et al 2004, Canadell et al 2007, Castro et al 2003, Ewel 1977, Helmer et al 2008, Jepsen 2006, Kenzo et al 2010, Rhoades et al 2000, Shevliakova et al 2009, Yang et al 2010).

Vegetation ecologists currently struggle in their attempts to distinguish secondary forests from primary vegetation through remote sensing (Arroyo-Mora et al 2005, Carreiras et al 2006, Nelson et al 2000, Tottrup et al 2007, Wunderle et al 2007). More critical, however, is the difficulty in differentiating the various successional stages that secondary forests normally comprise and measure their extent (Castro et al 2003, Helmer et al 2000, Helmer et al 2002, Proisy et al 2007, Sánchez-Azofeifa et al 2009, Vieira et al 2003). As their structure and functions depend on their succesional status, there is a strong need to efficiently evaluate the extent and complexity of secondary vegetation existing in any region and to discern its attributes.

Our success in achieving these goals will depend largely on our ability to estimate accurately the structure and diversity of secondary communities at broad geographic scales. Efforts to assess the extent of secondary vegetation and to distinguish its successional variants through remote sensing have followed several routes. Most studies estimating forest structure and diversity through satellite imagery have exclusively used image spectral features and their derived vegetation indices (Boyd et al 1996, Castro et al 2003, Foody et al 2001, Helmer et al 2000, Lucas et al 1993, Nagendra 2001, Nelson et al 2000, Sader et al 1989, Sohn et al 1999, Steininger 1996; 2000). There are, however, several problems related to this approach; for example, some remotely-sensed vegetation indices face the problem of saturation, i.e. they are unable to discriminate different plant communities beyond a certain biomass or canopy development threshold (Foody et al 2001, Helmer et al 2008, Lu 2005, Nelson et al 2000, Schowengerdt 2007). Moreover, although some studies have succeeded in discriminating forest successional stages accurately, they have been limited to the recognition of few broad stages, which do not reflect the continuous nature of the successional process (Arroyo-Mora et al 2005, Brondizio et al 1996, Helmer et al 2000, Kalacska et al 2004, Kimes et al 1999, Mausel et al 1993, Rignot et al 1997).

Recent theoretical developments in Landscape Ecology have established the link between the structural and compositional complexity of vegetation and the spatial variability of its remotely-sensed signal (Rocchini et al 2010; 2004, Rocchini and Vannini 2010). This spatial variability is directly related to the heterogeneity of the plant community and can be assessed by analyzing the texture of a remotely-sensed image (Barbier et al 2010, Couteron et al 2005, Malhi and Román-Cuesta 2008, Proisy et al 2007). Texture refers to the spatial variation of the elements of which any image is composed (Haralick 1979). Although measures of texture have been commonly used as image descriptors in remote sensing analyses (Fuchs et al 2009, Lu 2005; 2006), the resolution of most sensors currently employed for this purpose has prevented the examination of the internal heterogeneity of plant communities, as the size of commonly-used pixels is too large to detect such small-scale variation (Sarker and Nichol 2011, Vieira et al 2003). This drawback may be overcome by using very-high resolution imagery (VHR; pixels < 10 m), currently available for most of the Earth's surface, as it provides a better match between pixel size and the internal variation of vegetation (Barbier et al 2010, Boyd and Danson 2005, Couteron et al 2005, Hay et al 1996, Kerr and Ostrovsky 2003, Laliberte et al 2004, Malhi and Román-Cuesta 2008, Proisy et al 2007). Therefore, we hypothesized that the textural information contained in VHR images has the potential to reflect the variability of secondary vegetation, allowing us to model the successional process.

The goal of this study was to examine the potential of textural properties of a VHR Quickbird image to model secondary vegetation attributes measured in the field. We wanted to test the power of the texture of remote images to describe and predict vegetation attributes, while identifying those texture attributes with the highest predictive potential. In modeling the relationship between textural and vegetation attributes, we succeeded in producing simple models that can be easily obtained for many regions, and that have a straightforward biological interpretation.

Material and methods

Study area

The study was conducted in the dry tropical region of Nizanda, Oaxaca State, Mexico (16° 39.49’ N, 95° 0.66’ W; Fig. 1). Mean annual temperature is ca. 26°C and the total average annual rainfall is ca. 900 mm, largely concentrated between June and October. The prevailing vegetation matrix is a low-stature (7-10 m) tropical dry forest (Gallardo-Cruz et al 2009, Pérez-García et al 2010). Traditional slash-and-burn agriculture is practiced in the area. Fields are typically cropped for one or two years before being abandoned (Lebrija-Trejos et al 2008), which results in a mosaic of differently-aged fallows spread across the area.

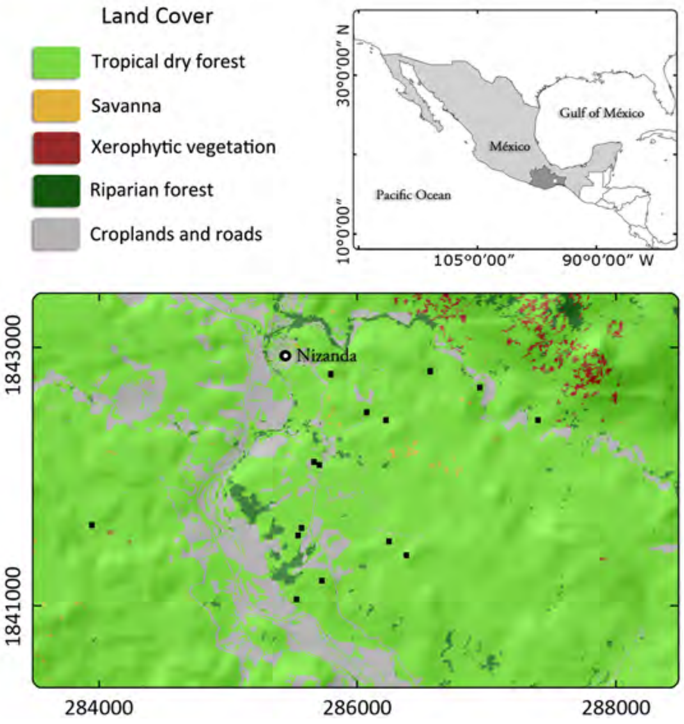

Figure 1. Study area (UTM zone 15n) and location of the secondary plots (■) used for modeling their attributes from the texture derived from a Quickbird satellite image.

Field data

Fourteen 30 × 30 m fallows with time since abandonment (age) ranging from 2 to ca. 60 years, and one mature forest site, were selected from field surveys conducted in 2005. Site age was obtained from interviews with landowners and verified through dendrochronology (Brienen et al 2009). This set of fallows included a large range of environmental and vegetational heterogeneity (Lebrija-Trejos et al 2010; In Press), from sites with a little dense canopy dominated by shrubs of open foliage, to sites with a dense plant cover and a low percentage of bare soil.

The sites were marked and designated as permanent sites in 2003 (Lebrija-Trejos et al 2008; 2010), and detailed structural and floristic information was collected annually. In each fallow, four 20 × 5 m transects (400 m^2, subdivided in four 5 × 5 m quadrats) were established for the sampling of woody and succulent plants. In each transect, all individuals ≥ 5 cm DBH were sampled in the four quadrats; individuals with DBH ≥ 2.5 cm but < 5 cm were sampled in two quadrats, and individuals with ≥ 1 but < 2.5 cm DBH were sampled in one quadrat only. For each individual, DBH and two orthogonal crown diameters (used to calculate crown areas) were measured. Structural variables were obtained by scaling the data to 1 ha. Based on this information, for each plot the $_{\mathrm{T}}$ and $_{\mathrm{U}}$ sets (i.e. Total and Upper, respectively) of structural and diversity attributes were prepared. The $_{\mathrm{T}}$ set included all sampled plants in the plot, whereas the $_{\mathrm{U}}$ set included only those plants that are more likely to be remotely sensed (Kalacska et al 2007). The $_{\mathrm{U}}$ set comprised those plants above the median in the frequency distribution of canopy cover; this subset represented between 50% and 75% of the basal area in a sites. For these two sets we calculated Dn (individuals in the sampled area), CC (the sum of the individual crown areas), BA (the sum of individual basal areas), S (number of species), and *D* and *H*' diversity indices (Magurran 2004). In addition, Hgt was calculated as the average of the heights of eight trees, each the tallest tree in the zones formed by two adjacent quadrats (See Table 1 for a full description of structural and diversity attributes abbreviations).

Image processing

We used a high-resolution Quickbird satellite image (pixel size = 2.6 m) acquired in early December 2005. This date, which corresponds to the beginning of the dry season, was chosen to minimize cloud cover while ensuring the presence of foliage in the plants. The image was geometrically and atmospherically corrected to surface reflectance following Krause (2005).

From the four available bands in this image, we selected the red (RED; 0.63-0.69 µm) and the near infrared (IR; 0.76-0.90 µm) (Nagendra 2001), both of which are known to reflect the condition of vegetation functioning and overall condition. We also estimated two commonly used vegetation indices, namely the normalized difference vegetation index (NDVI) and the enhanced vegetation index (EVI) (Schowengerdt 2007), both derived from the combination of the two bands, as follows:

$$\mathrm{NDVI} = \left(\frac{\mathrm{IR} - \mathrm{RED}}{\mathrm{IR} + \mathrm{RED}}\right)$$

$$\mathrm{EVI} = G\left(\frac{\mathrm{IR} - \mathrm{RED}}{L + \mathrm{IR} + C_1 \times \mathrm{RED} - C_2 \times \mathrm{BLUE} + L}\right)$$

EVI incorporates empirical parameters ($C_1 = 6$, $C_2 = 7.5$) and the blue band (BLUE, 0.45-0.52 µm) for atmospheric correction, and sensitivity minimization of soil background reflectance variation (L = 1). The EVI does not saturate under dense canopy conditions as the NDVI does, and it also appears to be more sensitive to canopy structural characteristics (Gao et al 2000).

Image texture analysis

Image texture refers to the spatial variation and arrangement of the pixels of which any image is composed (Haralick 1979, Petrou and García-Sevilla 2006). Although this property can be extracted through a wide array of methods (Marquez 2008, Petrou and García-Sevilla 2006), we chose to follow a statistical approach for this study. We calculated texture variables known as first-order and second-order measurements. First-order texture measures are statistical properties that do not consider pixel neighbor relationships and are derived from the original image values within a certain window (group of pixels); for this group of texture measures, the spectral variability within the window was assessed by calculating the range and the skewness of the values.

Unlike the textural variables from the first group, second-order measurements consider the spatial relations between groups of two neighboring pixels within the window (Haralick 1979), therefore these measurements were also selected because of their greater potential to reflect the heterogeneity in successional vegetation stands. The calculation of second-order variables involves the construction of Gray-Level Co-occurrence Matrices (GLCMs), which are matrices containing the probabilities of co-occurrence of pixel values for pairs of pixels in a given direction and distance. To construct such matrices we used a spatial distance of one pixel, four directions (0°, 45°, 90°, 135°), and 64 levels of gray. A co-occurrence matrix was constructed for each direction, and from each co-occurrence matrix a specific texture measurement was calculated for the window. The texture measurements of each direction were then averaged to obtain a single spatially-invariant texture value. This procedure was applied for the variables described in Table 1, which correspond to three groups of variables describing the degree of contrast between pixels (homogeneity, contrast, dissimilarity), the regularity in the pixels within a window (entropy, angular second moment), and the statistics derived from the GLCM (mean, variance, correlation).

The ten textural variables (two first-order and eight second-order variables) were calculated for the RED and the IR bands, as well as for the two vegetation indices (NDVI and EVI). We used a moving-window approach with a window size of 15 pixels to match the size of the sampling plots in the field; the central pixel value of this window was extracted from each of the 40 texture layers (four layers and ten variables). The entire procedure was programmed in the ENVI+IDL environment (ITT 2008).

Statistical analysis

We assessed the potential of the 40 texture variables to describe the observed changes in each of the 14 vegetation variables by means of linear models using R (R Development Core Team 2010). In all cases the response variables were log-transformed before model fitting. This procedure guaranteed that the predicted values, when anti-logged to obtain figures in the original scale, would be positive; additionally, such transformation tends to homogenize the residuals, which are usually proportional to the mean in most probability density functions restricted to the positive numbers domain.

Table 1. Texture variables derived from the grey-level co-occurrence matrix (GLCM). The abbreviations, formulas and descriptions of the eight texture variables used to model successional vegetation attributes are presented. $P_{i,j}$ is the (i, j) element of the GLCM, and represents the probability of finding the reference pixel value i in combination with a neighbor pixel value j. Note that $\Sigma_{i,j} P_{i,j} = 1$.

Texture variable	**Formula**	**Description**
Mean	$\text{MEAN}=\sum_{i,j=0}^{N-1} iP_{i,j}$	Mean of the probability values from the GLCM. It is directly related to the image spectral heterogeneity.
Variance	$\text{VAR}=\sum_{i,j=0}^{N-1} P_{i,j}(i-\text{MEAN})^2$	Measure of the global variation in the image. Large values denote high levels of spectral heterogeneity.
Correlation	$\text{COR}=\sum_{i,j=0}^{N-1} P_{i,j}\left[\frac{(i-\text{MEAN})(j-\text{MEAN})}{\text{VAR}}\right]$	Measure of the linear dependency between neighbouring pixels.
Contrast	$\text{CONT}=\sum_{i,j=0}^{N-1} P_{i,j}(i-j)^2$	Quadratic measure of the local variation in the image. High values indicate large differences between neighbouring pixels.
Dissimilarity	$\text{DISS}=\sum_{i,j=0}^{N-1} P_{i,j}\lvert i-j\rvert$	Linear measure of the local variation in the image.
Homogeneity	$\text{HOM}=\sum_{i,j=0}^{N-1} \frac{P_{i,j}}{1+(i-j)^2}$	Measure of the uniformity of tones in the image. A concentration of high values along the GLCM diagonal denotes to a high homogeneity.
Angular second moment	$\text{ASM}=\sum_{i,j=0}^{N-1} P_{i,j}^2$	Measure of the order in the image. It is related to the energy required for arranging the elements in the system.
Entropy	$\text{ENT}=-\sum_{i,j=0}^{N-1} P_{i,j}\ln P_{i,j}$	Measure of the disorder in the image. It is inversely related to ASM.

Assuming that different texture variables provide supplementary information about the remotely-sensed vegetation, we fitted three types of models, depending on whether they included one, two or three texture variables; no interaction was examined due to the limited degrees of freedom. All possible combinations of variables were explored, and for each of the three model types we selected the one having the largest R^2 value. This resulted in three models for each vegetation variable.

Due to the large number of models that were fitted and the small data set, it was expected that large R^2 values would be obtained by chance. To minimize this possibility, we produced null models by randomly sorting the texture- and vegetation-attribute data, fitting the same linear models as above, and selecting those with the largest R^2-values. This procedure was repeated 1,000 times and an empirical distribution of the largest expected R^2 was obtained. We then estimated the P-value associated with each model as the fraction of the simulated R^2 values that were greater than the observed ones. The median of the empirical distribution was used as a measure of the expected magnitude of R^2 under a completely random scenario.

To assess the predictive power of the models, we used leave-two-out cross-validation, i.e. we used a linear model fitted to the data from 13 plots (the calibration data) to predict the vegetation attribute of the remaining two plots (the validation data). We fitted a model for each possible split of the data set into calibration and validation subsets, and calculated the sum of squares between the estimated and observed values of the vegetation variable for the two validation plots. The model with the highest predictive power would be the one with the smallest average sum of squares ($\overline{SS}$) averaged over all the possible splits of the data set. We used a leave-two-out procedure to avoid the problems arising from the more popular leave-one-out approach (Baumann 2003, Browne 2000, Shao 1993), while keeping a sample size as large as possible for the estimation of the four parameters of the most complex models (those based on three texture variables).

The actual values of $\overline{SS}$ cannot be compared between vegetation attributes as they depend on the scale of measurement. A more informative statistic is given by the proportion of the variation of the vegetation attribute that can be predicted by the model. This statistic, expressed as a leave-d-out cross-validation R^2_{CV}, is:

$$R^2_{\mathrm{CV}} = 1 - \frac{\frac{1}{d}\overline{SS}}{\frac{1}{n}\sum_{i=1}^{n}\left(y_i - \bar{y}\right)^2}$$

where y_i is the vegetation attribute for the i^{th} plot, and n is the number of plots. R^2_{CV} ranges from $-\infty$ to 1, where a value of 1 means that a model predicts the validation data perfectly, while a negative value means that a model is over-fitted, because it would make worse predictions than those made by a null model. This statistic is dimensionless, so it can be used for comparing vegetation variables.

Results

Structural and diversity attributes of secondary vegetation

Two sets of structural and diversity attributes were analyzed for each sampled plot (Table 2). For the set named Total ($_{\mathrm{T}}$), which included all sampled plants in the plot, most structural variables exhibited clear increasing trends with successional development. However, this was not the case for stem density (Dn_{T}), which did not show a clear successional pattern, and for the Simpson's index (D_{T}, dominance), which tended to decrease from young to old fallows. Some variables clearly showed stabilizing trends, particularly mean tree height (Hgt) and crown cover (CC_{T}), or non-monotonic responses, as was the case of species richness (S_{T}).

The Upper canopy set ($_{\mathrm{U}}$) was arbitrarily defined as those trees that were above the median of the canopy cover cumulative distribution of each fallow. The proportion of total basal area (BA_{T}) accounted for by this set (BA_{U}) was in general higher (mostly above 60%, and often higher in mid-age fallows), despite the very low number of individuals included in this community's subset (in all cases less than 2% of stem density of the entire community).

Descriptive models of successional vegetation attributes

We constructed three sets of linear models to describe the relationship between 14 vegetation attributes and 40 image texture variables derived from a VHR Quickbird satellite image. These sets differed only in the number of texture variables used in constructing the model, i.e. one (560 models), two (10,920) or three (138,320) variables, as no interaction was examined.

Most of the selected models had relatively high significant R^2 values, and these increased as more variables were included. Among one-variable models, five out of 14 models had $R^2 > 0.80$, and this number increased to 10 and 12 for two- and three-variable models, respectively (Table 3). We measured the performance of these models through the additional variation explained by the best-fit models compared to the median of the random re-arrangements of the data set (null models); this performance decreased with the inclusion of more variables, from 0.37 for models with one variable, to 0.24 and 0.11 in two- and three-variable models, respectively (Fig. 2). Also, the proportion of non-significant best-fit models increased from 0.14, through 0.21 to 0.43 as more variables were included. There were small, non-significant differences (paired t =0.190, P = 0.851) between the R^2 values calculated using the two data sets ($_T$ and $_U$).

BA_T and BA_U were the response variables for which the best descriptive models were obtained (Table 3). For the best two-texture variable models, R^2 values were 0.93 and 0.92 for BA_T and BA_U, respectively. These vegetation attributes had an R^2 value of 0.96 for the best three-texture variable models. Conversely, R^2 for the best descriptive model with one textural variable was 0.82. Unlike most vegetation variables, the best-fit models for density (Dn) had much lower R^2 values, and these did not differ significantly from the values derived from the null model. The same occurred for the best-fit models for Shannon's (*H'*) and Simpson (D) indices, both for the entire community and for the upper canopy, in the case of the three texture-variable models.

Comparison between the three sets of models revealed that the most complex models did not necessarily incorporate the same variables as simpler models (Table 3).

Table 2. Structural and diversity attribute values for 15 plots. Age: years since abandonment of the fallow (M: mature forest), Hgt: height (m), S: species richness, Dn: density (number of individuals in the sampled area), BA: basal area (sum of individual basal areas; m^2/ha), CC: canopy cover (m^2/ha). *H'*: Shannon's diversity index (logits), *D*: Simpson's diversity index (logits). Total set ($_T$) includes all sampled plants, Upper set ($_U$) only those plants above the median of the canopy cover cumulative distribution.

Age	Hgt	S_T	S_U	Dn_T	Dn_U	BA_T	BA_U	CC_T	CC_U	H'_T	H'_U	D'_T	D'_U
2	2.4	7	3	1850	40	1.023	0.808	4996.664	2954.275	1.325	0.518	0.394	0.728
3	2.7	5	4	4850	102	1.756	1.092	13929.704	7424.604	0.538	0.424	0.756	0.815
5	4.6	4	2	4750	66	6.526	3.887	18587.796	10168.898	0.571	0.136	0.734	0.940
7	4.7	6	1	1825	18	6.150	3.438	18949.464	9832.621	1.293	0	0.367	1
9	4.6	19	7	6775	91	11.068	6.341	31597.844	16515.046	1.975	0.954	0.245	0.539
12	6.1	15	5	4100	46	10.201	6.590	28930.809	14945.067	1.835	1.240	0.281	0.325
13	6.6	29	14	6475	82	15.344	10.523	32446.110	16544.336	2.561	1.851	0.139	0.264
18	7.3	17	10	6925	73	14.604	10.672	31694.175	15909.057	1.730	1.469	0.311	0.391
20	7.0	22	8	4425	58	14.234	8.744	29682.050	15220.037	2.250	1.387	0.220	0.358
25	6.4	12	5	3850	45	11.042	7.022	23283.665	12097.390	1.591	0.814	0.323	0.611
32	6.5	21	9	5600	70	15.464	10.401	33259.234	16699.067	2.299	1.404	0.162	0.372
38	6.5	41	28	7725	122	26.040	17.116	36110.813	18559.764	3.055	2.615	0.070	0.120
42	6.8	27	12	5550	99	21.611	11.820	32099.665	16774.770	2.720	1.640	0.093	0.278
60	8.3	36	11	4500	46	21.441	14.374	36176.727	18135.708	2.993	1.614	0.085	0.330
M	7.0	36	17	7675	57	29.641	15.329	42411.829	21630.317	3.019	2.314	0.071	0.147

Most descriptive one-variable models included RED_{VAR} or RED_{MEAN} as the best explanatory variables of the behavior of vegetation variables (See Methods and Table 1 for a full description of texture variables and their abbreviations); $NDVI_{CORR}$ and $NDVI_{SM}$ were important only for Dn_U and Dn_T. For two-variable models, either RED_{VAR} or RED_{MEAN} were retained in six models only, whereas variables incorporating textural information derived from vegetation indices (NDVI and EVI) became prominent. When moving to the set of three textural-variable models, IR_{MEAN} emerged in eight models as capable of making a significant contribution to the descriptive power of the models. Conversely, in this set RED_{MEAN} and other RED-related textural variables became much less important, which indicates their limited descriptive ability in the presence of other textural variables. The signs of the coefficients of the textural variables in the models changed according to the way in which they relate to the different response variables. Within the group of one-variable models, D_T and D_U were the only vegetation variables whose models had positive coefficients associated to the textural variables. This relation is less obvious for two- and three-textural variable models, yet the coefficients of the textural variables still have different sign when involved in the descriptive modeling of dominance as opposed to other vegetation variables.

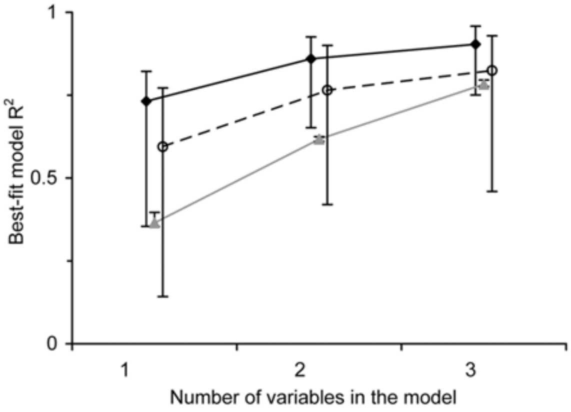

Figure 2. Fraction of the variation in vegetation attributes (median and range) explained by the descriptive (—◆—), predictive (- -○- -) and null (—▲—) models using a different number of textural attributes as explanatory variables. For the descriptive and null models conventional R^2 values are reported, while for the predictive models R^2_{CV} is reported, so the values are not strictly comparable (see Methods for explanation).

Predictive models of successional vegetation attributes

Most (27 out of 28 models) one- or two texture-variable best-fit models predicting vegetation response variables were identical to the respective descriptive models regarding the identity of the explanatory variables (see Table S1). Moreover, Spearman correlations between all possible R^2 and the cross-validation R^2 (R^2_{CV}) pairs of values for each vegetation variable and group of texture variables were very high. These correlations, which were higher for the one texture-variable models, were inversely related to the number of texture variables involved (Table 4). In general, R^2_{CV} values were lower than R^2 values in descriptive models, as low as 25% but more often around 10% lower (Figure 2, Table 4). Despite such reduction, BA_U and BA_T had $R^2_{CV} > 0.90$ in three texture-variable models. As was the case with descriptive models, there were no significant differences between the R^2 values of predictive models developed from the upper canopy and total sets (paired $t = 0.634$, $P = 0.534$).

Departure of predictive models from descriptive ones occurred mostly within the set of three texture-variables models (Figure 3, Table S1). For the new set of predictive models, textural variables derived from the RED band (i.e. RED_{VAR} or RED_{MEAN}) became prominent again among models with high R^2_{CV}.

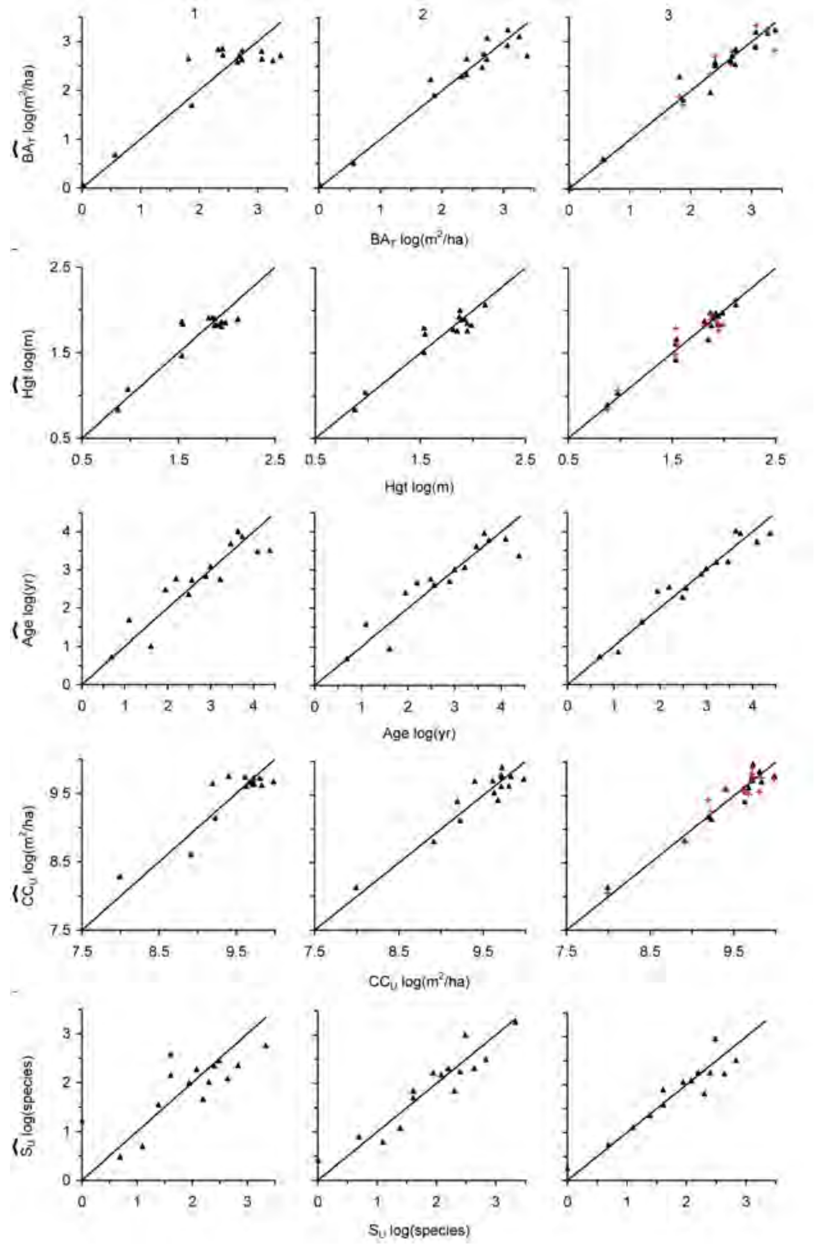

Figure 3. Observed (x-axes) vs. estimated (y-axes) values for the best descriptive (▲) and predictive (+) linear models for vegetation attributes. BA_T: total basal area, Hgt: height, Age: time since abandonment, CC_U: upper canopy cover, and S_U: upper species richness. Digits 1, 2, and 3 refer to the number of textural variables included in the model as explanatory variables.

Table 3. Descriptive linear models for 14 vegetation attributes (VA) as a function of 1, 2 and 3 textural variables (TV) with corresponding R^2, P and R^2_{CV} values. Only those textural variables that were included in at least two models are shown. For the descriptive models conventional R^2 values are reported, while for the predictive models R^2_{CV} is reported, so the values are not strictly comparable (see Methods). P–values calculated from the empirical distribution of the largest expected R^2. The plus (+) and minus (–) symbols denote the sign of the coefficients in the models. Age: years since abandonment, Hgt: height (m), S: species richness, Dn: density, BA: basal area; m^2/ha), CC: canopy cover (m^2/ha). H': Shannon's diversity index (logits), D: Simpson's diversity index (logits). Total set ($_T$) includes all sampled plants, Upper set ($_U$) only those plants above the median of the canopy cover cumulative distribution. IR: near infra-red band, RED: red band, NDVI: Normalized Difference Vegetation Index, EVI: Enhanced Vegetation Index. See Table 4 for the description of textural variables denoted by subindices $_{MEAN}$, $_{VAR}$, $_{ASM}$, $_{CORR}$, $_{DR}$, $_{SKEW}$, $_{DISS}$, and $_{CONT}$.

VA	TV	R^2	P	R^2_{cv}	IR_{MEAN}	RED_{VAR}	RED_{MEAN}	$NDVI_{ASM}$	EVI_{ASM}	IR_{CORR}	RED_{DR}	$NDVI_{SKEW}$	$NDVI_{MEAN}$	EVI_{MEAN}	$NDVI_{DISS}$	RED_{CONT}	IR_{VAR}	EVI_{SKEW}
BA_T	1	0.802	< 0.001	0.755		–												
	2	0.926	< 0.001	0.900		–									+			
	3	0.958	< 0.001	0.907		–	–									+		
BA_U	1	0.784	0.001	0.733		–												
	2	0.916	< 0.001	0.875		–									+			
	3	0.957	< 0.001	0.906					–								–	+
Hgt	1	0.819	0.003	0.772		–												
	2	0.887	0.004	0.841		–												
	3	0.939	0.005	0.861	–				–									+
Age	1	0.822	< 0.001	0.755			–											
	2	0.851	0.001	0.761			–											
	3	0.937	0.001	0.872			–				–					+		
CC_U	1	0.802	0.001	0.629		–												
	2	0.884	0.002	0.777		–						–						
	3	0.931	0.002	0.807	–				–	+								
CC_T	1	0.809	0.003	0.630		–												
	2	0.885	0.003	0.769		–						–						
	3	0.923	0.015	0.797	–				–	+								
S_U	1	0.597	0.028	0.442	–													
	2	0.877	0.005	0.792	–			–										
	3	0.910	0.012	0.849	–			–									+	
S_T	1	0.743	0.001	0.636			–											
	2	0.869	0.002	0.778	–													
	3	0.897	0.036	0.776	–			–				+						
H'_U	1	0.603	0.019	0.464			–											
	2	0.820	0.012	0.721	–			–										
	3	0.881	0.062	0.678	–				–	–								
D'_T	1	0.721	0.002	0.560			+											
	2	0.813	0.009	0.736									–	+				
	3	0.849	0.163	0.732				+					–	+				
D'_U	1	0.573	0.049	0.423			+											
	2	0.774	0.035	0.650	+			+										
	3	0.843	0.178	0.436	+													
H'_T	1	0.674	0.018	0.440			–											
	2	0.751	0.115	0.511						–	–							
	3	0.810	0.329	0.584						–	–							
Dn_U	1	0.513	0.119	0.314														
	2	0.685	0.252	0.497									–					
	3	0.778	0.548	0.379								–	–					
Dn_T	1	0.354	0.530	0.142				–										
	2	0.652	0.360	0.417					–					–				
	3	0.750	0.691	0.459	–	–					+							

Table 4. Spearman's ρ between descriptive R^2 and predictive R^2_{CV} values calculated for all linear models resulting from modeling each vegetation attribute as a function of one, two and three textural variables (TV). Age: years since abandonment of the fallow, Hgt: height (m), S: species richness, Dn: density (number of individuals in the sampled area), BA: basal area (sum of individual basal areas; m^2/ha), CC: canopy cover (m^2/ha). *H*': Shannon's diversity index (logits), *D*: Simpson's diversity index (logits). Total set ($_T$) includes all sampled plants, Upper set ($_U$) only those plants above the median of the canopy cover cumulative distribution. R^2_{CV} : cross-validation R^2 values (see Methods for explanation).

TV	Age	Hgt	S_T	S_U	Dn_T	Dn_U	BA_T	BA_U	CC_T	CC_U	H'_T	H'_U	D'_T	D'_U
1	0.734	0.687	0.928	0.946	0.820	0.481	0.904	0.902	0.862	0.864	0.769	0.952	0.904	0.933
2	0.617	0.610	0.768	0.874	0.624	0.460	0.774	0.753	0.804	0.791	0.612	0.863	0.703	0.854
3	0.592	0.611	0.722	0.815	0.568	0.469	0.751	0.731	0.773	0.779	0.581	0.812	0.658	0.796

Discussion

Predictive potential of satellite image texture

In this study we demonstrate the large potential of image texture for predicting vegetation attributes during tropical forest succession. Texture is an emergent property of satellite images that is related to the neighborhood relationships among pixels (Haralick 1979), and thus it is capable of reflecting the internal organization (i.e. heterogeneity, directionality, entropy) of a region of interest, rather than on its mean properties. This seems to be the reason why the performance of texture-based analyses tends to exceed those based on spectral information in discriminating different successional stages (Barbier et al 2010, Couteron et al 2005, Kuplich et al 2005, Lu 2005, Malhi and Román-Cuesta 2008, Murray et al 2010, Proisy et al 2007, Sarker and Nichol 2011, Wijaya et al 2010). High R^2 values comparable to those obtained by us have been reported by some studies, but only after complex image processing and modeling protocols based on mean canopy reflectance (Helmer et al 2009, Kalacska et al 2007, Liu et al 2008, Nelson et al 2000, Song et al 2007, Steininger 2000). Apparently this complexity has limited the broad application of these procedures, hence motivating the ongoing search for simpler solutions that are useful in a variety of circumstances. The method proposed in this study contrasts by its simplicity: the analysis was performed with a single image, and the models were linear and included few variables. Moreover, textural information can presently be extracted with ease. This simplicity, which becomes an asset in studying secondary vegetation and its attributes, depends on the basic principle that image texture actually reflects the internal heterogeneity of successional vegetation at the proper scale (Sarker and Nichol 2011).

The ability to predict characteristics of secondary vegetation accurately depends on a combination of three relevant methodological aspects, all of which synergically contribute to the high predictive value of the models.

The first aspect is high image resolution. Typically, scholars interested in predicting vegetation attributes from space have used images with pixel size ≥ 30 m (e.g. Arroyo-Mora et al 2005, Gillespie et al 2005, Helmer et al 2009, Kalacska et al 2007, Liu et al 2008). Agricultural fields derived from non-mechanized practices in tropical dry regions often have relatively small sizes (in our study area, the sizes of most successional stands range from 900 to 2,500 m^2); thus a single such large pixel covers just one secondary vegetation stand. Therefore, high spatial resolution is required to detect and analyze the internal spatial variation typical of each secondary stand. Proisy et al (2007) came to a similar conclusion while mapping biomass in successional mangrove communities.

The second aspect was the inclusion of stand-level heterogeneity, an essential feature of successional vegetation. This inclusion was achieved by using a range of image textural attributes, some of which proved to have a very high predictive potential, even though our study also shows that many textural attributes do not have such potential (Table 2 shows nine variables that were included in only one model, in addition to 17 variables that were not included in any of them), in agreement with other studies (Fuchs et al 2009, Sarker and Nichol 2011).

The third aspect was the decision to assess and contrast two large sets of models derived from alternative modeling procedures: one set included a limited number of descriptive models that included all sampling sites, whereas the other consisted of numerous predictive models constructed through leave-two-out cross-validation. The high degree of consistency between the models selected from either procedure confers increased reliability to the results, and implies that constructing descriptive models may suffice for assessing the secondary vegetation in a region. This is a valuable result as the construction of predictive models may require a large computational capacity as well as ample programming and statistical skills.

It is not uncommon for this kind of studies to face a limitation derived from the high cost of obtaining field information for every vegetation stand; thus having a large sample size, which would increase the accuracy in the predictions of the models, may not be feasible. This limitation was a strong motivation for this investigation. One would expect the prediction of vegetation attributes for new plots using our models to be flawed in two cases, neither of which occurred in our study. The first case would be if the models were used to estimate the attributes of plots with ages beyond those used in model fitting (extrapolation). We did not need to extrapolate because our plots represented the broadest possible successional gradient. The second case would be if the model's estimated coefficients were inaccurate due to a small sample size. We avoided this problem by using the leave-two-out cross-validation procedure (Browne 2000). Our high predictive R^2 values confirm that even a model based on a rarified sample was capable of providing reliable estimates for the vegetation attributes of new sites and warrants that our conclusions are not the artificial result of a small sample size.

An unanticipated result from our analysis was the relatively poor performance of models constructed with three texture variables relative to those based on two variables, as the former did not explain much more variation than the latter, and there were no large differences between their predictions and those derived from null models. The minor increases in R^2 associated with three-variable models relative to two-variable models do not compensate for the extra computing time and costs; also, model consistency was directly related to the degree of departure from null models, as demonstrated by the different results obtained when using different modeling procedures.

Despite previous suggestions that forest structure and diversity characteristics is preferably predicted from canopy-reflectance information (Castro et al 2003, Kalacska et al 2007), in our case restricting the analysis to the upper canopy did not necessarily result in a better predictive capacity. In fact, our models predicting BA_T had higher R^2 values than BA_U. In the case of an analysis based on texture of VHR imagery, predicting total community or upper canopy attributes can be done with comparable accuracy.

Even though we were able to demonstrate a high potential of GLCM textural indices to predict successional vegetation attributes, some caution must be exerted in using them.

Like other indices, GLCM face potential important limitations that must be acknowledged. A particularly worrisome one is the fact that texture may be sensitive to image sun-view acquisition conditions (Barbier et al 2010). Recently, Barbier et al. (Barbier et al 2011) proposed a mitigation method for FOTO (Fourier Transform Textural Ordination) indices that seems promising, albeit expensive and not totally straightforward. Further research is required aimed to develop a similar procedure to GLCM indices.

The significance of image textural information

Understanding why some textural attributes are more useful than others in predicting vegetation properties, and therefore why they were repeatedly incorporated into the models, is important for a number of reasons. From a practical perspective this knowledge will orient future efforts to assess secondary vegetation by guiding researchers as to which variables they should focus on. Also, this information will provide a firmer ground for theoretical inquiry, as it represents an efficient way to identify relevant biological properties of the vegetation system and its spatially explicit spectral expression.

In this study it became clear that the three textural attributes that excelled in their predictive capabilities were IR_{MEAN}, RED_{VAR} and RED_{MEAN} (Table 2), which indicates that in the context of texture, the predictive potential of the raw information contained in these bands exceeds that of NDVI and EVI, both based on RED and IR (Schowengerdt 2007). This implies that in calculating these indices the relevant spatial information that reflects the internal heterogeneity is lost. Under an approach centered on the examination of the internal heterogeneity of successional stands such loss of information is crucial at this scale of analysis, as objects that are not well differentiated spectrally can be finely discerned (Castro et al 2003).

One finding that deserves particular attention is the inverse relationship between satellite-sensed heterogeneity, in particular the mean and the variance of textural variables, and ground-level vegetation development (i.e. stand age and other vegetation attributes). Large mean values obtained from a grey level co-occurrence matrix (GLCM) denote high levels of between-pixel spectral heterogeneity. Likewise, large GLCM variances indicate that such changes are highly variable regardless of the mean change. Therefore, although the inverse texture/vegetation relationship may seem counterintuitive and even contradictory to some recent findings reported in the literature (Foody and Cutler 2006, Gould 2006, Levin et al 2007, Palmer et al 2002), the explanation might lie in comprehending what the satellite actually perceives. One conceivable explanation is that the pixels corresponding to an early successional stand not only contain the reflectance properties of the plants, but also the spectral properties of the substrate on which they grow. If this interpretation is correct, it follows that textural attributes should show decreasing trends as vegetation structure becomes more complex and covers the soil. Thus the internal heterogeneity of a mature successional stand would be mostly related to the differences between less contrasting reflectance properties of the plants.

Our research is in agreement with other studies that have shown texture of satellite imagery to be closely related to the heterogeneity of the vegetation stand (Couteron et al 2005, Malhi and Román-Cuesta 2008). For example, Frazer et al. (Frazer et al 2005) reported that LiDAR-derived indices such as lacunarity (the degree to which an object departs from a geometric pattern) are sensitive to canopy structure attributes. Despite the obvious ability of GLCM indices to reflect community-level attributes (e.g. total basal area, stand age), it is not yet clear how they relate to individual-level or other finer-scale traits (e.g. crown size). Thus, a promising line of future research will consist in finding out how these textural metrics relate to fine-scale vegetation and overall stand properties.

Potential applications of image-texture-based modeling

The application of the method described here may produce important information related to two of the most relevant threats to biosphere integrity: climate change and biodiversity loss (Díaz et al 2006, Dirzo and Raven 2003, Thomas et al 2004, Walther et al 2002). Basal area, the vegetation variable that was best predicted from image textural attributes, is strongly correlated with the standing biomass of a forest community (Slik et al 2010), and thus to carbon storage (Brown 1997). Carbon sequestration rates may also be obtained by considering stand age (Sánchez-Azofeifa et al 2009), another variable accurately predicted from image texture. Therefore, by applying this procedure, it should be possible to assess and map with high confidence the spatial distribution of the potential carbon storage and sequestration in regions dominated by secondary vegetation in different stages of development.

Biodiversity conservation is one of the major goals of tropical ecologists nowadays (Barlow et al 2007, Brodie et al 2010, Putz et al 2001). Several efforts have been made recently to assess the possibility that local floras and faunas may persist in regions where native vegetation has undergone major transformations (Chazdon et al 2009b, Daily et al 2001, Mayfield and Daily 2005, Perfecto and Vandermeer 2008). Therefore, the possibility to predict species richness is of utmost importance. Our results show that species richness can be predicted with a precision close to 80%. This figure implies the existence of a relationship between the occurrence of different species in the terrain and the information sensed by a satellite. At present this topic is receiving much attention from researchers (Hernández-Stefanoni et al 2011, Kerr and Ostrovsky 2003, Rocchini and Vannini 2010, Turner et al 2003), and our analysis opens new avenues to pursue it.

Canopy cover and vegetation height were also well predicted by our models. Again, there are several potential applications of this result. For example, information on canopy cover in a region dominated by secondary vegetation may help in assessing the potential soil erosion due to the kinetic energy of rainfall (Brandt 1988, Marques et al 2007, van Dijk et al 2002). Similarly, it will provide information that can be used to assess habitat quality for a regional fauna, particularly for those animals whose survival depends on a closed canopy (Bélisle et al 2001, Harvey et al 2006, Trzcinski et al 1999).

Concluding remarks

Analyzing the extent and complexity of secondary vegetation by recognizing the spatial variation of its spectral information opens new and attractive research avenues; these differ substantially from previous efforts to study secondary vegetation that have been primarily based on the examination of spectral reflectance properties. Overall, the procedure is potentially usable in any in successional plant community whose development involves large changes in heterogeneity through time. The current availability of VHR imagery, together with increasing computing capabilities, make it possible to develop faster and more efficient ways to assess the amount and condition of secondary vegetation in increasingly human-impacted regions world-wide based on this approach.

Acknowledgments

Armando Peralta provided support in image processing. JAGC and EJG thank the Graduate Program in Biological Sciences of the Universidad Nacional Autónoma de México for providing continuous support during their PhD studies. Thanks to Trudy Kavanagh for revision and edition of the manuscript. We warmly thank the people of Nizanda for their hospitality, permission to work on their land and assistance during fieldwork.

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CAPÍTULO 8

Discusión general

Un hecho evidente para cualquier observador es que no todas las especies se encuentran en todos los sitios. Esto es particularmente notorio al estudiar los patrones en la distribución de especies en el paisaje de Nizanda (Capítulo 3). Visto a la distancia dicho paisaje está compuesto por ocho comunidades vegetales que se entremezclan en el terreno (i.e. bosque de galería, bosque de montaña siempreverde, bosque ribereño, sabana, bosque tropical seco, vegetación xerofítica, vegetación acuática y vegetación secundaría). Pero al acercarse, no sólo lo intrincado de la cubierta vegetal llama la atención. Sobre todo, el hecho de que cada comunidad esté representada por contingentes florísticos particulares es notorio, a pesar de que la distancia que las separa en ocasiones no rebasa las decenas de metros.

La distribución preferencial de las especies de plantas en determinadas porciones del paisaje se opone a las teorías que suponen una distribución aleatoria de las especies en una región. Históricamente, el contraste entre estas dos visiones ha generado fuertes debates académicos que han buscado entender si los ensambles comunitarios se dan por procesos azarosos o deterministas (Capítulo 2). En principio, los cambios abruptos en la composición de especies sugieren la existencia de factores ambientales que ordenan a las comunidades vegetales de la región de Nizanda. El cambio más notable ocurre en las zonas de contacto entre el bosque tropical seco (BTC) y la sabana, donde es común observar un remplazo comunitario completo en menos de un metro de distancia. Sin embargo, el recambio en la composición de especies también puede darse en forma gradual. Por ejemplo, a simple vista se nota que en la parte baja de los cerros el BTC cambia en respuesta al incremento en la disponibilidad de agua. Esta observación motivó la exploración detallada de los efectos de las variaciones topográficas sobre la composición de especies en dicha comunidad.

El componente topográfico resultó ser una de las fuentes de estructuración más importantes del paisaje debido a las modificaciones en los patrones espaciales y temporales de insolación que genera (Capítulo 4). Las variaciones espaciales en el balance energético modelado se vinculan con los cambios en la composición florística del BTC. Esto contribuye al aumento del acervo de especies, y explica en parte la elevada diversidad de especies de esta comunidad. Por su parte, la variación temporal en la radiación conlleva a una homogeneización en la riqueza y en la estructura de la vegetación que mantiene la unidad funcional de la comunidad.

Es importante resaltar que la gran mayoría de los estudios que abordan el efecto de la orientación sobre algún proceso ecológico han dado por sentado la existencia de una asimetría energética espacial entre las laderas de una formación topográfica. Sin embargo, la posición latitudinal del sitio de estudio determina si dicha asimetría en realidad existe. Así, mientras una montaña ubicada por arriba del trópico de cáncer presenta un fuerte desbalance energético entre las laderas norte y sur, una montaña equivalente ubicada en el ecuador no muestra ninguna variación espacial entre laderas en términos de la cantidad de radiación captada. Por ello, la modelación de la radiación potencial en el paisaje de Nizanda incorporó tanto las variaciones topográficas como las latitudinales, demostrando la utilidad de incorporar este tipo de variables en el estudio de la relación entre las propiedades del paisaje y la diversidad vegetal en una región altamente compleja.

Aun en ausencia de variaciones ambientales el recambio de especies (i.e. diversidad-β) puede ocurrir en una comunidad y expresarse en la estructura espacial de sus componentes (Capítulo 5). Esta investigación dejó ver que el espacio es otra fuente importante de estructuración ya que explica mucha de la variación en la composición de la comunidad. No obstante, también evidenció que el efecto del espacio no es homogéneo, sino que opera de manera diferencial en cada comunidad a pesar de que todas están sometidas a los mismos reguladores climáticos e históricos regionales.

El espacio no debiera ser visto como la causa del recambio florístico. En cambio, su estructura (e.g. autocorrelación) sirve como indicador indirecto de otros procesos espacialmente estructurados. Estos pueden ser ecológicos, geomorfológicos o no mecanisísticos, y en última instancia expresan la organización espacial de la comunidad (Mistral et al 2000, Hubbell 2001, Tuomisto et al 2003, Morlon et al 2008). Por ejemplo, la estructura espacial del BTC y de la sabana se asocia con procesos de dispersión espacialmente autocorrelacionados. En contraste, la estructura espacial de la vegetación xerofítica denota la existencia de islas de hábitat que restringen la distribución de las especies de esta comunidad en el paisaje.

A partir de los resultados derivados del análisis espacial se debe hacer hincapié en la importancia de utilizar un enfoque multiescalar en la investigación ecológica del futuro. Si este estudio hubiera optado por estudiar sólo la escala más gruesa se hubiera pasado de largo la esencia de la estructuración espacial de la vegetación xerófila, y la capacidad de construir hipótesis que la explicaran. La principal justificación para realizar un estudio multiescalar radica en la imposibilidad de conocer a priori la escala a la que ocurre un proceso ecológico determinado. En el caso de una comunidad esto es aun más crítico, ya que se trata de un contingente de especies cuyas expresiones individuales podrían darse en tantas escalas como número de especies contenga.

Desde su origen la ecología del paisaje ha trabajado bajo el supuesto de que los elementos de un paisaje constituyen unidades ecológicas homogéneas en estructura y función (Capítulo 1; Forman y Godron 1986, Yoshida y Tanaka 2005). Un problema inherente a dicha epistemología es el reconocimiento y la delimitación de las unidades de análisis, sobre todo después de haber encontrado evidencia de que en el paisaje operan procesos que generan transiciones graduales al interior y entre las comunidades vegetales (Capítulos 3, 4 y 5; Burnett y Blaschke 2003, Ivits et al 2005). Por ello, este proyecto analizó la relación entre la riqueza de especies y los atributos paisajísticos comparando dos metodologías contrastantes (Capítulo 6). Una vez más los resultados dejaron ver la importancia de emplear múltiples escalas de análisis en los estudios ecológicos. Además, arrojaron suficiente evidencia como para afirmar que el futuro de la investigación en ecología del paisaje y los esfuerzos para predecir la riqueza de especies, tendrían más éxito si se adopta el uso del paradigma del paisaje continuo en los sistemas muy diversos donde no se distinguen con facilidad los límites entre sus elementos.

En este sentido, las medidas que mejor describen la heterogeneidad del paisaje son las métricas de textura, que cuantifican la organización y la variación de los pixeles de una imagen satelital. La principal fortaleza de estas métricas radica en que su cálculo no involucra el paso intermedio de la clasificación de la imagen con la subjetividad que eso acarrea. A pesar de esto, el desafío sigue siendo identificar los mejores indicadores que describan la heterogeneidad de la señal digital y su posible vinculación con un proceso biológico. Además, en un futuro cercano será necesario investigar más a fondo los efectos de múltiples factores que puedan alterar la heterogeneidad de una imagen comparando el sinfín de las variables de textura descritas hasta el momento (Couteron et al 2006, Barbier et al 2010) .

Aun cuando se desconocen muchas de las propiedades de las métricas de textura, el futuro de la modelación de los atributos vegetacionales y paisajísticos basado en ellas es promisorio. En 1976 Levin identificó a los procesos sucesionales como una de las tres principales fuentes generadoras de patrones en un paisaje. Sin embargo, distinguir en campo o con percepción remota las variaciones graduales asociadas con los cambios de fase ha sido sumamente complejo (Helmer et al 2000, Helmer et al 2002, Castro et al 2003, Vieira et al 2003, Proisy et al 2007, Sánchez-Azofeifa et al 2009). En este estudio se demostró que es posible modelar la diversidad de especies y otros atributos de la vegetación secundaria del BTC a partir de la textura un imagen de alta resolución (Capítulo 7). En general, el procedimiento desarrollado es potencialmente útil para cualquier comunidad vegetal cuyo desarrollo sucesional implique grandes cambios en los niveles de heterogeneidad. Dada la disponibilidad actual de imágenes satelitales de alta resolución, junto con los elevados poderes de cómputo, este enfoque debería facilitar la evaluación rápida del estado de la vegetación secundaria en diversas partes del mundo.

En síntesis, los resultados y las conclusiones derivadas de este proyecto permitieron identificar algunos de los procesos y factores que moldean los patrones de la diversidad de especies en un paisaje altamente complejo. Asimismo, abren la puerta a nuevas rutas de investigación que busquen incorporar variables paisajísticas y de percepción remota en la modelación de la diversidad de especies en extensiones territoriales circunscritas a la mesoescala.

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