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RESUMEN

En esta investigación se analizaron los factores y los procesos involucrados en la regeneración natural de un bosque mesófilo de montaña en un contexto espacial, con el fin de probar la hipótesis de que los árboles del dosel afectan de forma significativa a la regeneración del bosque debido a dos causas principales: primero, por su potencial modificador de las condiciones ambientales en el sotobosque, y segundo, por su relación con los patrones de dispersión de semillas. En la primera parte de la investigación se describió la estructura espacial de las condiciones microambientales y de la comunidad de plántulas de las especies arbóreas presentes en el sotobosque. Se demostró que la humedad del suelo, la profundidad del mantillo, la apertura de dosel y la radiación solar total están estructuradas espacialmente, como también lo están la densidad, la cobertura y la riqueza de plántulas de las especies arbóreas. La profundidad del mantillo fue la única variable ambiental con la que se relacionaron espacialmente las variables estructurales de la comunidad de plántulas y con las que fue posible hacer predicciones de la distribución espacial de la comunidad de plántulas. Las distancias de autocorrelación para ambos conjuntos de variables fueron muy parecidas, lo que sugiere que hay un tercer factor involucrado y que los afecta a ambos. El diámetro promedio de las copas de los árboles del dosel fue muy similar a esta distancia de autocorrelación, lo que llevó a proponer que la identidad taxonómica de estos individuos podría ser la causa subyacente de la estructuración espacial de las variables ambientales y por lo tanto de la comunidad de plántulas. En la segunda parte de la investigación, la cual se enfocó en cuatro especies del dosel (*Cornus disciflora*, *Chiranthodendron pentadactylon*, *Quercus laurina* y *Oreopanax xalapensis*), se analizó esta hipótesis y se demostró que la identidad específica de los árboles del dosel sí afecta diferencialmente, aunque de manera difusa, las condiciones del sotobosque, y que la comunidad de plántulas sólo es afectada negativamente por *Chiranthodendron pentadactylon* debido a la mayor profundidad de mantillo debajo de sus copas. Finalmente, mediante un enfoque de vecindario (modelos basados en la distribución espacial de los adultos, su área basal y la distancia a las semillas o plántulas) se evaluaron, para las mismas cuatro especies, los patrones de distribución de las semillas de la lluvia y del banco de semillas con respecto a sus conespecíficos, y de las plántulas con respecto a un vecindario conespecífico y heteroespecífico. En general, la distribución de semillas parece ser afectada más por la distancia a los árboles adultos que por su biomasa (área basal), aunque la relación puede ser inversa o directa dependiendo de la especie. La distribución de las plántulas dependió de la presencia de los individuos adultos en términos de área basal y de la naturaleza conespecífica o heteroespecífica del vecindario. Este análisis mostró una tendencia general hacia un reemplazo heteroespecífico mediado al parecer por factores bióticos como la depredación (efecto Janzen-Connell). Este estudio confirma la noción de que los mecanismos que subyacen los procesos implicados en la regeneración natural son complejos y espacialmente explícitos y que, al menos en parte, resultan de la interacción de los patrones de distribución de semillas con los factores bióticos y abióticos relacionados con la distribución de los individuos del dosel. La omisión del componente espacial en el estudio de la regeneración natural impide comprender la estructuración de la comunidad en su totalidad, pues esto sería equivalente a tratar de dibujar a las especies y a los factores que las afectan sobre “un único” punto en el espacio.

ABSTRACT

In this study the factors and processes involved in the natural regeneration of a cloud forest were examined in a spatial context, with the aim of testing the hypothesis that canopy trees are capable of driving forest regeneration owing to two main causes: first, because of their potential to modify understory environmental conditions, and secondly, due to their relationship with seed dispersal patterns. In the first part of this investigation the spatial structure of the micro-environmental conditions and of the sapling community of tree species occurring in the understory were described. It was demonstrated that soil moisture, litter depth, canopy openness and total solar radiation are spatially structured, as also are tree sapling density, cover and species richness. Litter depth was the only environmental variable with which the structural variables of the sapling community were spatially related, and with which it was possible to make predictions on the spatial distribution of the sapling community. Autocorrelation distances for both sets of variables were very similar, suggesting the existence of a third factor involved and affecting both variable groups. Mean canopy tree crown diameter was very similar to this autocorrelation distance, which uncovered the possibility that the taxonomic identity of these individuals may be the underlying cause of the spatial structuring of the environmental variables, and ultimately of the spatial structuring of the sapling community. In the second part of this investigation, which focused on four canopy species (*Cornus disciflora*, *Chiranthodendron pentadactylon*, *Quercus laurina* and *Oreopanax xalapensis*), this hypothesis was analyzed and it was demonstrated that the specific identity of canopy trees do affect differentially, albeit diffusely, the understory conditions, and that the sapling community is affected negatively only by *Chiranthodendron pentadactylon* owing to a greater litter depth beneath its canopies. Finally, through a neighborhood approach (models based on the spatial distribution of adult trees, their basal basal areas and their distances to seeds or saplings), dispersion patterns of seeds in the seed rain and in the seed bank were assessed for the same four species relative to the position of their conspecifics, and of saplings relative to conspecific and heterospecific neighborhoods. Overall, distributions of seeds appears to be more strongly affected by the distance to adult trees than by the amount of their biomass (as measured through basal area), although such relationship may be positive or negative, depending on the species. Sapling distribution depended on the presence of adult individuals in terms of basal area, and of the conspecific or heterospecific nature of the neighborhood. This analysis showed a general trend towards a heterospecific replacement, which in turn appears to be also driven by abiotic factors like predation (Janzen-Connell effect). This study confirms the notion that the mechanisms driving the natural regeneration process are complex and spatially explicit, and that they result at least in part from the interplay of seed spatial patterns with the abiotic and biotic factors related with the spatial distribution of canopy trees. Ignoring the spatial component in the study of the natural regeneration of a forest prevents a full understanding of the structuring of a community, since that approach would be equivalent to trying to draw all species and the factors affecting them on a “single” point in space.

CAPÍTULO I

INTRODUCCIÓN GENERAL

CAPÍTULO I. INTRODUCCIÓN GENERAL

1.1 Diversidad, heterogeneidad ambiental y regeneración natural

El proceso de regeneración natural, es decir, el fenómeno por medio del cual los árboles muertos en un bosque son reemplazados por individuos nuevos, es uno de los factores determinantes de la manera en que se ensamblan las especies en una comunidad arbórea. La regeneración natural en los bosques tropicales ha sido estudiada en el contexto del reemplazo heteroespecífico en busca de los mecanismos que mantienen la diversidad (Martínez-Ramos 1994, Nicotra *et al*. 1999, Bellingham y Tanner 2000, Webb y Peart 2000, Harms *et al.* 2001). Las hipótesis opuestas acerca de cómo sucede este reemplazo son: (1) que el establecimiento de cada especie está definido por sus atributos propios y por las condiciones ambientales (Grubb 1977), o (2) que el reclutamiento de las especies se da de forma aleatoria (Hurtt y Pacala 1995, Hubbell 2001, Busing y Brokaw 2002). Una hipótesis alternativa a éstas es la del reclutamiento limitado, la cual argumenta la posibilidad de que especies poco competitivas sean capaces de ocupar y acaparar micrositios disponibles debido a las limitaciones en el arribo de propágulos de las otras especies (Beckage y Clark 2003, Münzbergová y Herben 2005, Veldtman 2005, Moore y Elmendorf 2006).

El análisis de estas hipótesis relacionadas con el reemplazo de especies que forman una comunidad vegetal a través del tiempo suele hacerse por medio del estudio de la dinámica de la vegetación, haciendo particular énfasis en el contexto de la heterogeneidad ambiental. La dinámica espacio-temporal del conjunto de árboles del dosel de un bosque es responsable de una gran parte de la heterogeneidad ambiental medible en dicho bosque, y ésta a su vez influye de manera importante en la dinámica numérica de las plántulas (Hurtt y Pacala 1995, Aiba *et al*. 2004, Queenborough *et al*. 2007). El efecto de la heterogeneidad ambiental sobre el establecimiento, el crecimiento y la supervivencia de las plántulas ha sido evaluado ampliamente (Nicotra *et al*. 1999, Bellingham y Tanner 2000, Beckage *et al*. 2003, Snyder y Chesson 2003). El reclutamiento de plántulas de especies arbóreas en los bosques se caracteriza por una acentuada variación temporal y espacial que resulta de una gama amplia de procesos, los cuales incluyen la variación temporal en la producción de semillas entre poblaciones (Sork 1993, Frey *et al*. 2007, Norden *et al*. 2007), la fuerte agregación en la dispersión de semillas (Hubbell 1979, Augspurger 1983, Hughes y Fahey 1998, Houle y Payette 1990), la variación espacial y temporal en los patrones de forrajeo de animales dispersores y consumidores (Shupp 1988, Shupp *et al*. 1989), así como la variación de las condiciones climáticas y microclimáticas que afectan a la germinación de semillas y la supervivencia temprana de los individuos recién reclutados (Nicotra *et al*. 1999, Enoki y Abe 2004). A pesar de la diversidad de enfoques en el estudio del reclutamiento de plántulas, llama la atención el hecho de que se ha puesto poca atención en los efectos de esta heterogeneidad espacio-temporal en la distribución de los recursos y de los individuos de las diferentes especies, a pesar de que se reconoce que el entendimiento de dicha heterogeneidad es central en la teoría ecológica (Pacala 1997, Dieckmann *et al*. 2002, LePage *et al*. 2000, Veldtman 2005, Getzin *et al*. 2008).

1.2. Regeneración natural: implicaciones de la estructura espacial

El desarrollo de las plantas en sus diferentes estadios del ciclo de vida es función, entre otras cosas, de la densidad y del patrón espacial de los nuevos individuos reclutados y de los preestablecidos (Schupp 1995, Stoll y Weiner 2000). Numerosos estudios han encontrado que en escalas pequeñas (e.g., en parcelas de una hectárea) las especies arbóreas muestran algún grado de agregación, es decir, no se distribuyen aleatoriamente en el espacio (Hubbell 1979, Armesto *et al*. 1986, Forget *et al*. 1999, Hubbell *et al*. 1999, Itoh *et al*. 1997, Nicotra *et al*. 1999, Condit *et al*. 2000, Maestre *et al*. 2003) y que la distribución de los recursos y la densidad de nuevos individuos muestran autocorrelación espacial (Legendre y Legendre 2000, Le Page *et al*. 2000, Lawrence *et al*. 2007). El patrón actual de distribución de las plántulas de los árboles es el resultado de los procesos de regeneración que han sucedido en ese lugar en el pasado más allá de la vida de estas plántulas (e.g. de los árboles parentales que dieron lugar a dichas plántulas). El análisis de la distribución de las plántulas en el contexto de la estructura espacial puede aportar información sobre los requerimientos particulares de las especies durante la regeneración (Itoh *et al*. 1997, Forget *et al*. 1999, Hubbell *et al*. 1999, Nicotra *et al*. 1999, Baraloto y Couteron 2010) y sobre los procesos que generan la estructura espacial a diferentes escalas, que en última instancia determinan el conjunto local de especies (Le Page *et al*. 2000, Gratzer *et al.* 2004). Por ejemplo, qué tan frecuentemente algunos individuos crecen cerca de otros de su especie o de otra especie depende tanto de la abundancia relativa del taxón como de procesos que presentan patrones espaciales particulares (Stoll y Newbery 2005, Comita y Hubbell 2009).

La regeneración de muchas especies leñosas arbóreas y arbustivas presenta un patrón espacial claramente asociado a las plantas ya establecidas (Herrera *et al.* 1994, Rey y Alcántara 2000, Queenborough *et al*. 2007). Este patrón sugiere la existencia de numerosas interacciones protagonizadas por un propágulo dispersado bajo la cobertura de individuos establecidos durante su ciclo de regeneración. Los efectos de los árboles adultos pueden modificar la probabilidad de que las semillas sean atacadas por patógenos y depredadores, disminuyendo la probabilidad de que germinen (Janzen 1970, Clark y Clark 1985, Bustamante y Simonetti 2000, Wenny 2000). Entre los factores bióticos de mayor importancia están la mortalidad densodependiente (por ejemplo, la competencia intra-específica; Webb y Peart 1999, Uriarte *et al*. 2005a) y la cercanía a los individuos parentales (Augspurger 1983, Bustamante y Simonetti 2000, Lambers *et al*. 2002). Estos efectos negativos se maximizan con la cercanía a la planta materna, de manera que la probabilidad de supervivencia suele ser mayor cuando las plántulas se encuentran alejadas de ella (Janzen 1970, Connell 1971, Jansen *et al*. 2008).

La información disponible sobre la existencia de autocorrelación espacial y sobre la variación espacial de las densidades de individuos sugiere que tanto el reemplazo de unos individuos por otros como los mecanismos que intervienen en la regeneración dependen del vecindario biológico y que actúan a una escala local (Hubbell *et al*. 2001, Uriarte *et al*. 2004, Lieberman y Lieberman 2007). La estructura espacial de estos procesos tiene profundas implicaciones para la ecología de las plantas porque estos organismos interactúan principalmente con sus vecinos más cercanos. Tradicionalmente se ha considerado a la proximidad espacial como un sinónimo de competencia entre plantas por los recursos limitantes, básicamente luz, agua y nutrientes. Los efectos competitivos se han evaluado generalmente en términos de las respuestas de crecimiento de los árboles alrededor de sus competidores en función de la distancia entre ellos y su talla (Yeaton y Cody 1976, Stoll *et al*. 1994, Hubbell *et al*. 2001, Uriarte *et al*. 2004, Canham *et al*. 2006). Las interacciones competitivas entre vecinos han sido analizadas en algunos estudios, casi siempre con el fin de poner a prueba la hipótesis de equivalencia competitiva del modelo neutral de interacción de especies en bosques tropicales propuesto por Hubbell (2001); algunos de ellos han revelado la ausencia de equivalencia ecológica entre las especies arbóreas (Uriarte *et al*. 2005b, Massey *et al*. 2006), contrastando con otros resultados que apoyan esta hipótesis (Hubbell 2005, McGill *et al*. 2006, Economo y Keitt 2008). También desde la perspectiva de la competencia entre vecinos se han examinado los efectos de los vecindarios biológicos locales o específicos sobre el crecimiento de las plántulas y los árboles jóvenes; es decir, se ha investigado si los efectos de estos vecindarios (conespecífico o heteroespecífico) pueden tener impactos sobre el crecimiento poblacional en los estadios tempranos de las especies arbóreas (Weiner 1990, Goldberg *et al*. 2001, Uriarte *et al*. 2004, 2005b). En síntesis, la identidad del vecino tiene relevancia por la manera diferencial de competir por los recursos, pero también por la modificación de las condiciones del medio físico inmediato, afectando directamente el proceso de regeneración natural.

1.3. Heterogeneidad ambiental y árboles del dosel: efectos especie-específicos

Los árboles del dosel modifican las condiciones del medio físico-químico a su alrededor. Por ejemplo, la estructura de la comunidad de árboles del dosel determina fuertemente el ambiente lumínico debajo de él (Denslow 1980, Denslow *et al*. 1998, Montgomery y Chazdon 2001, 2002). Un efecto adverso muy importante de los árboles del dosel sobre las etapas tempranas del ciclo de las especies arbóreas es la intercepción de la luz, ya que afecta a la germinación de las semillas y reduce el crecimiento de las plántulas. No obstante, al mismo tiempo puede tener un efecto benéfico sobre las mismas al reducir la pérdida de agua del suelo e impedir el calentamiento excesivo; incluso en ocasiones se puede presentar un efecto de facilitación cuando se incrementa la supervivencia y el crecimiento de las plántulas bajo arbustos y árboles (Gómez-Aparicio *et al*. 2005, Holmgren y Scheffer 2010, Sánchez-Velásquez *et al*. 2011). El beneficio que reciben los propágulos de árboles al crecer junto a los árboles pioneros puede surgir durante el reclutamiento, desde la dispersión y la germinación de las semillas, el establecimiento y la supervivencia de las plántulas, hasta la supervivencia y el crecimiento de los individuos juveniles (Sánchez-Velásquez 2004, Gómez-Aparicio *et al*. 2005).

Los árboles establecidos son capaces de modificar la disponibilidad de agua, las características del mantillo la textura del sustrato, la temperatura ambiental, y en general la calidad del micrositio, incidiendo así sobre el éxito de la germinación de las semillas recién arribadas (Hurtt y Pacala 1995, Schupp 1995, Gray y Spies 1996, Pickett *et al*. 2000, Pearson *et al*. 2003). En particular, el efecto de los árboles del dosel sobre el micrositio de regeneración es complejo, ya que incluye cambios en el microclima (luz, temperatura y humedad), la fertilidad, la humedad y la estructura del suelo (LePage 2000, Becerra *et al*. 2004, Ayres *et al*. 2009, Harrison *et al*. 2010). Estos efectos están asociados a la comunidad de árboles del dosel y varían dependiendo de la especie, debido al tamaño y la forma de la copa, la forma y el tamaño de las hojas (Beaudet *et al*. 2002). El dosel modifica tanto la cantidad como la calidad de la luz que pasa a través de él: cuando la luz (directa y difusa) llega al dosel, es absorbida, reflejada y transmitida en diferentes proporciones. Esta modificación depende de las características propias del dosel como de la uniformidad de la superficie, su ángulo y profundidad, y su nivel de apertura, además de las características de los claros del dosel, como su tamaño, forma y orientación (Grant 1997, Denslow *et al*. 1998, Acevedo *et al*. 2003). Asimismo, depende de la identidad específica de las especies arbóreas dominantes en el dosel, ya que la influencia o modificación de estos factores también dependen de las características propias de cada especie, incluyendo el tamaño y la consistencia de las hojas, la forma de la copa, la densidad del follaje, la altura máxima, etc. (Pickett *et al*. 2000, Ayres *et al*. 2009).

De manera similar, cuando las hojas caen de la copa de los árboles suelen formar un mantillo diferente en el suelo, dependiendo también de en qué grado son caducifolias las especies y de la forma y composición de las hojas de las diferentes especies (Jonard *et al*. 2008). A la escala de la comunidad arbórea existe una fuente interesante de heterogeneidad química debida a la composición del mantillo; las diferentes especies de árboles originan patrones químicos en la hojarasca, con posibles huellas físico-químicas en el suelo mineral más superficial capaces de influir sobre la germinación y el establecimiento de las plántulas (Becerra *et al*. 2004, Kostel-Hughes *et al*. 2005, Makana y Sean 2005, Vivanco *et al*. 2008). La acumulación de mantillo de los árboles también produce un efecto físico directo sobre el reclutamiento. En los micrositios donde el espesor del mantillo es considerable las semillas que germinan en la superficie, especialmente las de tamaño pequeño, enfrentan dificultades para que las primeras raíces de la plántula accedan al suelo mineral y corren gran riesgo de morir desecadas (Vázquez-Yanes *et al*. 1990, Molofsky y Augspurger 1992); asimismo, si se acumula una gran cantidad de hojarasca las plántulas pequeñas pueden sufrir efectos negativos (Facelli 1994, Clark y Clark 1989, Scariot 2000, Gillman y Ogden 2001). Sin embargo, las semillas de tamaño grande pueden verse favorecidas precisamente en los microhábitats con mantillo más profundo (Facelli y Pickett 1991, López-Barrera y González-Espinosa 2001). En momentos diferentes un mismo micrositio puede ser favorable tan sólo para una o algunas de las fases del ciclo de reclutamiento, produciéndose en consecuencia conflictos entre fases (Schupp 1995). La profundidad diferencial del mantillo asociada a semillas de diferentes tamaños contribuye también a una diversificación del micrositio de regeneración (Molofsky y Augspurger 1992, Vázquez-Yanes y Orozco-Segovia 1992, Daws *et al*. 2005). Además de las condiciones ambientales, el mantillo acumulado sobre el suelo mineral también influye sobre las interacciones bióticas entre plántulas y patógenos en el sotobosque (García-Guzmán y Benítez-Malvido 2003, Packer y Clay 2003). La acumulación de mantillo crea condiciones favorables para la proliferación de hongos fitopatógenos que potencialmente pueden afectar a las plántulas y favorecer la infección por la presencia de hojas de algunos individuos del dosel ya infectados (García-Guzmán y Benítez-Malvido 2003). A su vez, el ataque por patógenos incrementa la vulnerabilidad de las plántulas a los ataques de otros agentes bióticos como insectos herbívoros (Benítez-Malvido y Kossmann-Ferraz 1999).

1.4. Estructura espacial: dispersión y reclutamiento

Los árboles del dosel también pueden modificar los patrones espaciales y temporales de la disposición espacial de las semillas tanto durante la dispersión como ella, ya que funcionan como posaderos de dispersores, modifican el comportamiento de los depredadores de semillas, ofrecen refugio a animales acumuladores de las mismas o incluso interceptan semillas cuando éstas se están desplazando (Callaway 1992, Aguiar y Sala 1994, Debussche y Isenmann 1994 Jordano y Schupp 2000, Díaz *et al.* 2003, Gómez *et al.* 2003). La existencia de discordancias espaciales durante el reclutamiento, entre semillas e individuos establecidos, es un fenómeno común en las dinámicas de reclutamiento de especies leñosas y de vital importancia, ya que a largo plazo pueden afectar la persistencia de las especies en el sitio (Herrera *et al.* 1994, Gómez 2004). El estudio de los patrones espaciales de las plántulas podría revelar la importancia potencial de las limitaciones de la dispersión en relación con la estructuración de la comunidad arbórea (Moore *et al*. 2006, Norden *et al*. 2009). La distribución de las plántulas en el terreno podría mostrar autocorrelación espacial, independientemente de la variación del ambiente, lo que suele interpretarse como un indicio de limitaciones en la dispersión o el reclutamiento (Dalling *et al*.

1998, Valencia *et al*. 2004, Freestone *et al*. 2006). Además, la distribución espacial final de las plántulas depende también, entre otras cosas, de la interacción entre la disponibilidad de semillas y la favorabilidad del sustrato (LePage *et al*. 2000, Dalling *et al*. 2002).

La importancia de la limitación en la dispersión de semillas puede ser comprendida mejor si se analiza en el contexto del establecimiento post-dispersión (Muller-Landau *et al*. 2002). Las características que supuestamente favorecen la dispersión de semillas (semillas pequeñas, sincronía reproductiva) suelen ser desfavorables para el establecimiento posterior de las plántulas, porque los micrositios favorables para la emergencia o el establecimiento de individuos de especies con semillas pequeñas son raros (éste es un ejemplo de una disyuntiva —*trade-off*— ampliamente reconocida entre dispersión y establecimiento exitoso (Lusk y Collen 2003, Kneitel y Chase 2004, Tilman 2004), o porque las plántulas son eliminadas por competidores de semillas grandes (disyuntiva competencia-colonización; Turnbull *et al*. 1999). Además, hay evidencias de que la dispersión limitada de las semillas es un factor importante que afecta, junto con los factores, el éxito de reclutamiento post-dispersión, a la distribución espacial de las plántulas (Svenning y Wright 2005, Ehrlen *et al*. 2006, Schoolmaster 2008). Numerosos experimentos de adición artificial de semillas han mostrado que la baja disponibilidad de éstas puede limitar el crecimiento poblacional de muchas especies, particularmente en hábitats sucesionalmente tempranos (Turnbull *et al.* 2000). Recientemente se han desarrollado modelos espacialmente explícitos que permiten simular el reemplazo de las especies basados en la distribución espacial de los individuos y de los recursos (Veltham 2005, Uriarte *et al*. 2005b). Estos modelos consideran la estructura espacial de los recursos, la competencia localizada y las limitaciones de dispersión basándose en la distribución de los individuos (Gratzer *et al*. 2004, Canham y Uriarte 2006, Norden 2009).

1.5. El caso del bosque mesófilo de montaña

Esta revisión pone de manifiesto dos componentes esenciales de la ecología de las comunidades de bosque. En primer lugar, deja ver primero los efectos numerosos y dispares que pueden tener los individuos del dosel sobre la comunidad de plántulas; además, muestra que estos efectos son en gran medida dependientes de la identidad taxonómica. No obstante, llama la atención que apenas en los últimos años los estudios comienzan a examinar la relación entre la dinámica de los individuos adultos y la dinámica de las comunidades pre-adultas con un enfoque espacialmente explícito (Canham y Uriarte 2006, Massey *et al*. 2006, Comita *et al*. 2009). Este tipo de estudios se llevaron a cabo inicialmente en bosques templados y ahora en algunos bosques tropicales (Uriarte *et al*. 2004, Canham y Uriarte 2006, Comita *et al*. 2009), pero aún no se han aplicado en el estudio de la regeneración de los bosques de niebla, bosques nublados o bosques mesófilos de montaña (BMM), como son conocidos en México.

La niebla, característica distintiva del ambiente físico de los BMM, reduce la intensidad de la radiación solar incidente y, en días nublados, disminuye las diferencias entre los claros y los sitios bajo dosel cerrado en la intensidad de la luz recibida, debido a que sólo llega luz difusa (Stadmüller 1987, Bruijnzeel y Proctor 1995, Bruijnzeel y Veneklaas 1998, Acevedo *et al*. 2003). A consecuencia de las temperaturas relativamente bajas, la descomposición de la materia orgánica en los suelos es más lenta que en sitios de tierras bajas tropicales, provocando la acumulación de una capa profunda de mantillo finamente fragmentado y humus que limita fuertemente el crecimiento de las raíces (Bruijnzeel *et al.* 1993, Bruijnzeel y Veneklaas 1998). Por otra parte, los suelos también se caracterizan por sus concentraciones bajas de nutrientes disponibles, particularmente de nitrógeno y fósforo, y por su alto contenido de carbono (Stadmüller 1987, Tanner *et al*. 1990, 1998, Dezzeo *et al*. 1997, Bruijnzeel y Veneklaas 1998, Raich y Khoon 1998). La marcada estacionalidad en la fenología foliar de muchas especies del dosel de estos bosques da lugar a variaciones en el grado de apertura del dosel a lo largo del año, modificando así el ambiente lumínico y los patrones de acumulación de mantillo. Por supuesto, las características particulares del medio físico tienen influencia sobre el proceso de regeneración natural, e incluso algunos estudios han señalado que la humedad del suelo y el mantillo son factores muy importantes en este proceso (Arriaga 1988, 2000, Ortiz-Arrona 1999). Aunado a estas características, el caso de los bosques mesófilos de montaña de México es interesante porque estas comunidades albergan una mezcla compleja de especies arbóreas con distintas afinidades ecológicas, incluyendo taxones de los bosques tropicales de tierras bajas y taxones propios de los bosques templados de altitudes y latitudes altas (Rzedowski 1978, Saldaña-Acosta *et al*. 2008). Esta variación en afinidades ecológicas está relacionada con diferentes morfologías, fenologías foliares y patrones funcionales (*e.g*. Arriaga 1988, Williams-Linera 1997, Saldaña-Acosta *et al*. 2008). Por lo tanto, cabe esperar que estas diferencias entre las especies del dosel en comunidades vegetales de este tipo acentúen los efectos específicos de cada especie sobre la heterogeneidad ambiental del sotobosque, sobre la estructura espacial de los recursos y sobre la disponibilidad de propágulos.

1.6. Planteamiento del problema

Considerando la estructura espacial local —a la escala de una hectárea— de los factores abióticos, de los individuos establecidos y de los propágulos, es razonable argumentar que los individuos del dosel podrían tener un efecto importante sobre el proceso de regeneración natural. Este efecto puede estar relacionado con la modificación del micrositio de establecimiento de las plántulas, por una parte, y con los patrones de dispersión de los propágulos y la posibilidad de la dispersión limitada, por la otra. En este contexto y reconociendo la heterogeneidad espacial a esta escala, y tomando en cuenta además a las características particulares de los BMM, surgió la pregunta central de la presente investigación: *¿cuál es el efecto de los árboles del dosel, de acuerdo con su identidad taxonómica y su distribución espacial, y de la variación ambiental de este efecto a través del tiempo, sobre la estructura espacial de las condiciones microambientales, la plantilla potencial de nuevos individuos y la probabilidad de establecimiento de las plántulas de especies arbóreas en un bosque mesófilo de montaña?*

Esta pregunta se abordó mediante la formulación de objetivos específicos examinados en tres capítulos de resultados cuya interpretación colectiva fue integrada en el último capítulo de discusión general. En la primer parte del estudio (Capítulo II, *Estructura espacial del ambiente abiótico y su asociación con la estructura y la dinámica de la comunidad de plántulas en un bosque mesófilo de montaña*) se examina la estructura espacial de las condiciones ambientales promedio y de la comunidad de plántulas, y se analiza por medio de técnicas de estadística espacial el efecto de la estructura espacial de cinco variables microambientales del sotobosque (humedad y temperatura del suelo, profundidad del mantillo, apertura de dosel y radiación solar total) sobre la estructura espacial de la comunidad de plántulas (densidad y cobertura de plántulas, riqueza de especies, y tasas de reclutamiento y mortalidad); por último, en este capítulo se modela por medio de un procedimiento de simulación condicional la distribución espacial de éstas últimas. En el Capítulo III (*Efecto de la identidad específica de los árboles de dosel sobre el micrositio inmediato y la estructura y la dinámica de la comunidad de plántulas*) se estudia la relevancia de la identidad específica de algunas especies de árboles del dosel y de la variación ambiental estacional como un factor ecológico que influye en el proceso de regeneración, en el contexto del potencial que tienen estos organismos de afectar diferencialmente a la comunidad de plántulas a través de las modificaciones de las condiciones micro-ambientales en el sotobosque. En el Capítulo IV (*Patrones espaciales en la lluvia de semillas, el banco de semillas y en las plántulas en el sotobosque de un bosque mesófilo de montaña: un enfoque de vecindario*), a través de un enfoque de vecindario (modelos basados en individuos) se analiza el efecto de la distribución de los individuos del dosel de cuatro especies sobre la lluvia de semillas, el banco de semillas y las plántulas de las especies arbóreas. Finalmente, mediante la integración de los resultados de cada uno de estos estudios, todos ellos planteados en un contexto espacio-temporal, en el Capítulo V se ofrece una discusión integral sobre la relevancia de los factores y los procesos involucrados en la regeneración natural de un bosque mesófilo de montaña.

CAPÍTULO II

ESTRUCTURA ESPACIAL DEL AMBIENTE ABIÓTICO Y SU ASOCIACIÓN CON LA ESTRUCTURA Y LA DINÁMICA DE LA COMUNIDAD DE PLÁNTULAS EN UN BOSQUE MESÓFILO DE MONTAÑA

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Spatial structure of the abiotic environment and its association with sapling community structure and dynamics in a cloud forest

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Abstract Analyzing the relationship between the spatial structures of environmental variables and of the associated seedling and sapling communities is crucial to understanding the regeneration processes in forest communities. The degree of spatial structuring (i.e., spatial autocorrelation) of environmental and sapling community variables in the cloud forest of Teipan, S Mexico, were analyzed at a 1-ha scale using geostatistical analysis; after fitting semivariogram models for each set of variables, the association between the two sets was examined through cross-variograms. Kriging maps of the sapling community variables (density, cover, species richness, and mortality and recruitment rates) were obtained through conditional simulation method. Canopy openness, total solar radiation, litter depth, soil temperature and soil moisture were spatially structured, as were sapling density, species richness and sapling mortality rate. Mean range in semivariograms for environmental and sapling community variables were 13.14±3.67 and 12.68±5.71 m (±SE), respectively. The spatial structure of litter depth was negatively associated with the spatial structures of sapling density, species richness, and sapling community cover; in turn, the spatial structure of soil moisture was positively associated with the spatial structure of recruitment rate. These associations of the spatial structures of abiotic and sapling community variables suggest that the regeneration processes in this cloud forest is driven by the existence of different microsites, largely characterized by litter depth variations, across which saplings of tree species encounter a range of opportunities for successful establishment and survival.

Keywords Canopy openness · Conditional simulation · Geostatistics · Litter depth · Soil moisture · Total solar radiation

Introduction

Environmental heterogeneity and its effects on seedling establishment and sapling growth and survival in forest communities have been widely examined as a mechanism maintaining community diversity (Welden et al. 1991; Nicotra et al. 1999; Bellingham and Tanner 2000; Webb and Peart 2000; Harms et al. 2001; Montgomery and Chazdon 2001, 2002). However, the dynamics of the seedling and sapling community in the light of the dramatic temporal and spatial variations that result from a wide range of processes is not yet well understood. These processes include the inter-population temporal variation in seed production (Nathan et al. 2000; Dalling et al. 2002; Muller-Landau et al. 2002), the strong spatial aggregation in seed dispersal of some tree species (Augspurger 1983; Hughes and Fahey 1998; Levine and Murrell 2003), the temporal and spatial variation in foraging patterns of herbivorous and seed-dispersing animals (Schupp 1988; Schupp et al. 1989), and the variability in macro- and microclimatic conditions that affect seed germination and early seedling survival (Nicotra et al. 1999; Anderson et al. 2004; Baraloto and Goldberg 2004; Kobe 2006; Abd Latif and Blackburn 2010).

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A certain given distribution pattern of tree saplings is largely the result of the regeneration processes that occurred in that place in the recent past. The analysis of sapling spatial distribution in the context of the environmental heterogeneity is becoming increasingly useful to understand the species-specific requirements during regeneration (Kitajima and Augspurger 1989; Itoh et al. 1997; Forget et al. 1999; Hubbell et al. 1999; Nicotra et al. 1999; Baraloto and Goldberg 2004), which ultimately may determine the community's species assemblage (LePage et al. 2000; Friedenberg 2003; Gratzer et al. 2004). Also, the differential responses of tree species in the early stages of their life cycles to the spatial and temporal structure of the environmental conditions largely determine those sites where new individuals may successfully establish (Busing and Brokaw 2002; Dalling et al. 2002; Gratzer et al. 2004).

A variable is spatially structured when it displays a considerable degree of autocorrelation across a horizontal plane, so that given any value of this variable at any point, the most similar values tend to be recorded either in its close vicinity (positive autocorrelation) or at large distances (negative autocorrelation). The spatial structure of the physico-chemical environment has been suggested to be one of the main contributors to the existence of spatial autocorrelation in the distribution of both populations and communities (Dutilleul and Legendre 1993; Legendre 1993; Legendre and Legendre 1998; Bruckner et al. 1999). Such spatial structure has consequences in community functioning, and therefore attempts to incorporate it in any ecological description and modeling are warranted (Tilman and Kareiva 1997; Gómez-Aparicio et al. 2005a, b; Segurado et al. 2006; González-Megías et al. 2007). Also, by examining the spatial structure of environmental variables, the emerging patterns may shed light on the underlying causes of such structure, which may also be another spatially structured (i.e., autocorrelated) variable or process (Legendre et al. 2002). Recently, the use of geostatistics has become common in analyzing the spatial structure of the plant community or of the abiotic environment (Montgomery and Chazdon 2001; Miller et al. 2002; Poulsen et al. 2006). Less commonly, attempts have been made to assess the association between both structures (Nicotra et al. 1999; Fajardo and McIntire 2007), but to the best of our knowledge, such association has seldom been subjected to a formal analysis (Rathbun and Fei 2006; Damgaard 2008). We claim that this is needed, given that analysis and inferences based only on descriptive procedures to analyze this relationship may be misleading due to sampling variability.

Cloud forests have attracted the attention of community ecologists for decades given their transitional character between lowland, tropical communities and those forests typical of highland regions with temperate climates (Bruijnzeel and Proctor 1995; Hamilton et al. 1995; Kappelle et al. 1995). In addition to their remarkably large biodiversity (Gentry 1995; Kappelle 1996), they also stand out because of the very specific—albeit heterogeneous—conditions that limit their occurrence (Stadtmüller 1987). Previous work on the natural regeneration in a few cloud forest localities identified soil moisture and litter depth as important environmental variables affecting seedling recruitment (Arriaga 1988, 2000; Ortiz-Arrona 1999). Nonetheless, processes associated with the spatial structure of saplings have not yet been examined in detail. Thus, the goal of this study was to examine through formal statistical analyses the spatial structures of five micro-environmental understorey variables (soil moisture, litter depth, soil temperature, canopy openness and total solar radiation) and their effects on the spatial structure of the sapling community (density, species richness, cover, and recruitment and mortality rates) in a cloud forest of southern Mexico. We achieved this by modeling the effects of environmental variables on both the static and dynamic variables of the sapling community through a linear model that includes a non-independent and spatially correlated random error term.

Materials and methods

Study site

The study was conducted in Santo Tomás Teipan (hereafter Teipan), Oaxaca State, southern Mexico (16°14′–16°16′N, 95°57′–96°00′W; 2,400 ma.s.l.). The climate is considerably seasonal, with rainfall concentrated from May to October; yearly total rainfall average is >1,400 mm, and mean annual temperature is ca. 12.3°C (IG-UNAM 1970; García 2004). Most of the area is covered by a cloud forest which forms part of the communal property of Teipan. The forest surface is ca. 326 ha and ranges in elevation from 2,200 to 2,500 m.

Field survey

Field work was conducted in a 1-ha permanent plot that was initially established in 2002, ca. 1 km N from Teipan, on the lower slope of Mt. Calabazo (Mejía-Domínguez et al. 2004). The lowest point in the plot (the NW corner) has an elevation of 2,300 m. In this permanent plot, the dynamics (survivorship, recruitment and mortality) of the forest canopy (trees with dbh ≥2.5 cm) has been monitored yearly since 2002 (Mejía-Domínguez 2006).

In March 2007, 153 1-m^2 plots were established and permanently marked within the 1-ha plot. These were used to assess sapling community structure and dynamics. More than one-half of these quadrats (100) were systematically placed at the center of 100 m^2 quadrats in which the large plot was divided, and the remaining 53 were placed randomly. Distance between quadrats ranged between 3 and 128 m. All saplings and shrubs $\leq$50 cm high and lacking cotiledonary leaves (i.e., beyond the seedling stage) occurring in the plots were individually tagged, their crown areas (two perpendicular diameters) measured, and their exact locations in the quadrat recorded on a grid to the nearest centimeter, which allowed us to verify the presence/absence of each sapling in subsequent censuses. Thereafter, saplings were surveyed at 3-month intervals (from August to November 2007, and from February to May 2008). At each census, the height of surviving plants was re-measured. Newly recruited saplings fulfilling the inclusion criteria were tagged and measured, and their locations recorded.

In addition to assessing sapling community structure and dynamics, at each census we also measured three soil variables at two opposite corners of each quadrat. These variables were: (1) soil relative moisture, (2) soil temperature (both measured with an Aquaterr T-300), and (3) litter depth (flexometer, to the nearest mm). Concurrently, hemispherical photographs were taken horizontally 1 m above the centre of each quadrat (digital camera Nikon Coolpix 990 with an 8-mm FC-E8 fisheye lens). Percent canopy openness and total solar radiation (hereafter solar radiation) were estimated from the photographs with the GLA software (Gap Light Analyzer; Simon Fraser University, Burnaby, BC, Canada, and the Institute of Ecosystem Studies, Millbrook, NY, USA). From now on, we will collectively refer to these variables as “environmental variables”.

Data analysis

Sapling density was estimated as the number of saplings per 1 m^2 plot, and percent cover of this community (hereafter cover) as percent of area covered by saplings in 1 m^2. The number of species per plot was considered as the species richness. These variables describe the sapling community.

The dynamics of the sapling community was assessed through mortality (M) and recruitment (R) rates, using the following equations (Sheil 1995, Sheil 2001):

$$M = \left\{1 - \left[(N_0 - m)\,/\,N_0\right]^{1/(\Delta t)}\right\} \times 100 \tag{1}$$

$$R = \left\{\left[(N_0 + r)\,/\,N_0\right]^{1/(\Delta t)} - 1\right\} \times 100 \tag{2}$$

where N_0=initial density, m=number of dead saplings, Δt= time period (months), and r=number of recruited saplings. These two variables describe the dynamics of the sapling community.

Geostatistics is a valuable tool for identifying the existence of spatial autocorrelation and understanding the spatial structure of populations and communities (Duncan and Stewart 1991; Liebhold and Gurevitch 2002; Kint et al. 2003; Lawrence et al. 2007; Dormann et al. 2007). Geostatistical methods were used to estimate the spatial association between environmental and sapling community variables. Prior to the analysis, we performed variable transformations, as follows: sapling density was square-root transformed, whereas cover, recruitment and mortality rates, canopy openness and soil moisture were log transformed.

Like all spatial statistical methods, geostatistics is based on the fact that neighboring locations tend to show similar values of the variable under analysis Z. For any two locations s_i, s_j within a study area D, the semivariogram provides a measure of the statistical association between the values of the spatial variable $Z(s_i)$ and $Z(s_j)$ (Bulit et al. 2003). The semivariogram is defined as:

$$\gamma(h) = \frac{1}{2} E\left[Z(s_i) - Z(s_i + h)\right]^2 \tag{3}$$

However, given the impossibility of knowing the true spatial structure of $Z(S_i)$, the semivariogram is estimated by fitting a parametric model to the empirical semivariogram (Goovaerts 1997):

$$\widehat{\gamma}(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} \left[z(x_i) - z(x_i + h)\right]^2 \tag{4}$$

where $\widehat{\gamma}(h)$ estimates the semivariance for all the samples located in space, separated by a distance interval h; $N(h)$ is the total number of sample pairs separated by the distance interval h; $z(x_i)$ is the value of the sample in position x, and $z(x_i+h)$ is the sample value at distance h from x_i.

Most parametric models fitted to the semivariogram have the general form

$$\gamma(h) = C_0 + C_1 f(h; r) \tag{5}$$

where $f(h, r)$ is an increasing function of the distance h, with parameter r. For the so-called “transition models”, C_0+C_1 is the upper bound of the semivariogram, also known as “sill”, and C_0 is the “nugget” effect. C_0+C_1 represents the total variability of the spatial variable Z in the study area D. The range (r) is the distance at which the sill is reached, i.e. it represents the distance at which the spatial association becomes null. Beyond this distance, two values of Z become statistically independent. C_0 indicates the variation between two samples in an infinitely small distance due to natural variability and/or experimental error (Goovaerts 1997; Bulit et al. 2003). For semivariogram models where

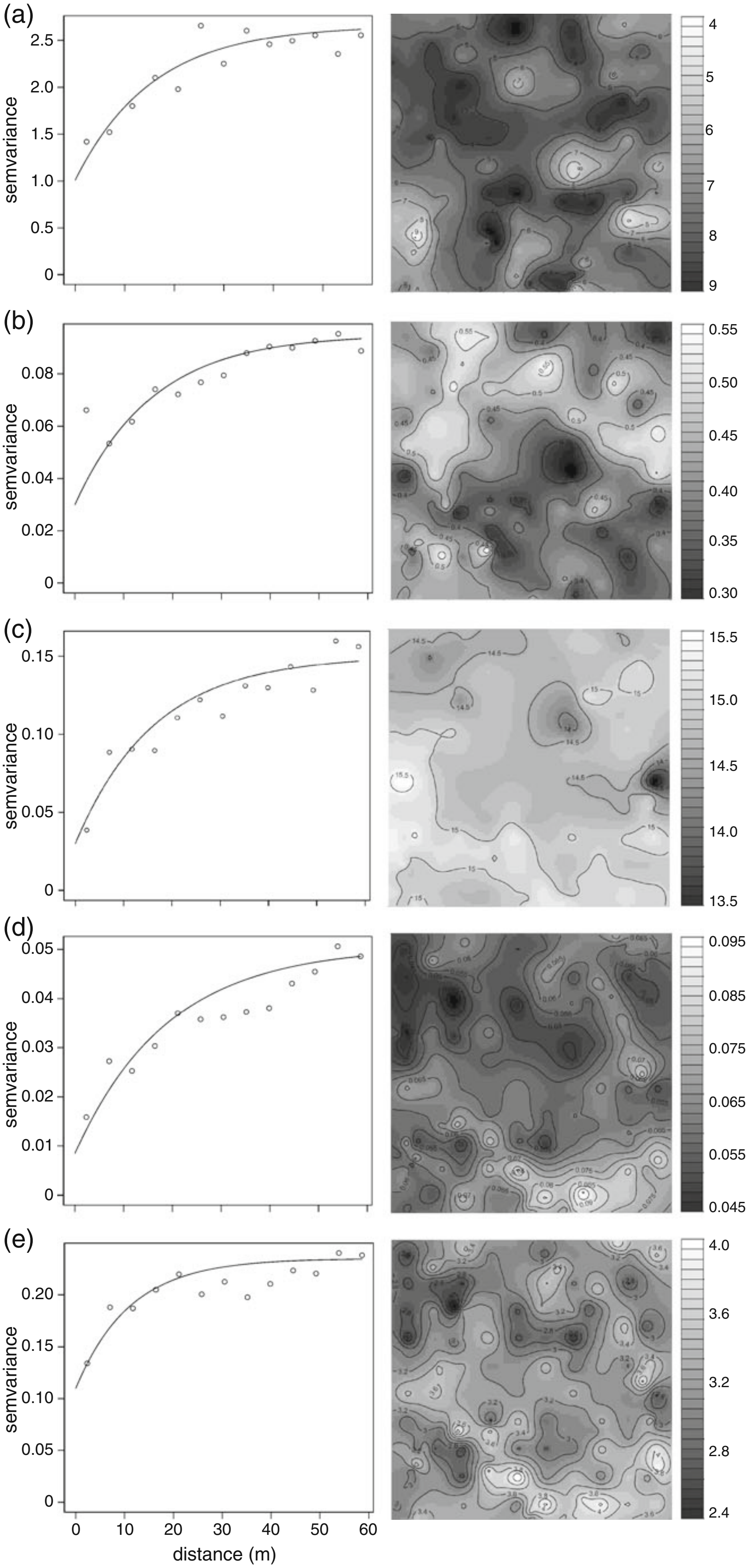


Fig. 1 Semivariograms and distribution maps (100×100 m) showing isoclines of environmental variables (right) of **a** litter depth, **b** soil moisture, **c** soil temperature, **d** canopy openness, and **e** total solar radiation. *Dots* are mean values for all dates; the highest values are shown in *very light gray*

Table 1 Parameter estimates for the variogram models fitted of environmental and biological variables

Variable	Model	Sill (C_0+C)	Range (*r*)	Nugget (C_0)	SSC
Enviromental variables					
May 2007					
LD	Exp	5.59	4.68	2.71	48.48
SM	Exp	0.20	9.77	0.13	65.00
ST	Exp	0.28	9.77	0.05	17.86
CO	Exp	0.18	14.66	0.04	22.22
TSR	Exp	1.24	13.03	0.43	34.68
August 2007					
LD	Exp	4.87	19.02[a]	2.69	55.24
SM	Exp	0.57	11.40[a]	0.27	47.37
ST	Exp	0.19	9.77[a]	0.11	57.89
CO	Exp	0.22	13.03	0.05	22.73
TSR	Exp	1.75	14.66	0.67	38.29
November 2007					
LD	Exp	2.94	11.40[a]	1.39	47.28
SM	Exp	0.26	11.40[a]	0.13	50.00
ST	Exp	0.16	13.03	0.06	37.50
CO	Exp	0.25	19.02	0.06	24.00
TSR	Exp	1.10	12.68	0.57	51.82
February 2008					
LD	Exp	4.37	6.52	3.06	70.02
SM	Exp	0.23	15.85[a]	0.08	34.78
ST	Exp	1.57	19.55[a]	0.00	0.00
CO	Exp	0.07	15.85	0.03	42.86
TSR	Exp	0.20	15.85	0.12	60.00
May 2008					
LD	Exp	5.78	9.77	1.98	34.26
SM	Exp	0.18	11.40	0.07	40.00
ST	Exp	0.32	9.51	0.17	53.13
CO	Exp	0.07	13.03	0.03	46.15
TSR	Exp	0.71	11.40	0.35	49.30
Mean					
LD	Exp	2.58	15.85	1.00	38.76
SM	Exp	0.10	15.85	0.03	31.58
ST	Exp	0.15	16.29	0.03	20.00
CO	Exp	0.05	19.02	0.01	16.83
TSR	Exp	0.24	11.10	0.11	46.81
Seedling community structure and dynamics variables					
May 2007					
N	Exp	5.55	11.40	2.59	46.67
Cov	Nug	–	–	42.19	0
S	Exp	1.61	7.93	0.85	52.80
August 2007					
N	Exp	6.53	17.44	2.47	37.83
Cov	Nug	–	–	42.98	0
S	Exp	1.58	7.93	0.64	40.51
M	Nug	–	–	54.40	0
R	Nug	–	–	8.36	0

Table 1 (continued)

Variable	Model	Sill (C_0+C)	Range (*r*)	Nugget (C_0)	SSC
November 2007					
N	Exp	6.78	15.85	2.38	35.10
Cov	Nug	–	–	44.14	0
S	Exp	1.67	9.51	0.79	47.31
M	Exp	70.78	9.77	24.87	35.14
R	Exp	41.81	9.51	22.60	54.05
February 2008					
N	Exp	7.30	14.27	2.96	40.55
Cov	Nug	–	–	44.69	0
S	Exp	1.78	9.51	0.96	53.93
M	Exp	27.77	26.95	11.39	41.02
R	Nug	–	–	23.96	0
May 2008					
N	Exp	6.48	15.85	2.70	41.67
Cov	Nug	–	–	45.00	0.00
S	Exp	1.69	11.10	0.89	52.66
M	Nug	–	–	29.14	0
R	Exp	14.88	7.93	5.48	36.83
Mean					
N	Exp	6.14	11.10	2.35	38.27
Cov	Nug	–	–	38.51	0
S	Exp	1.57	7.93	0.74	47.13
M	Exp	50.16	5.85[a]	31.18	62.16
R	Nug	–	–	46.36	0

SSC Spatially structured component, Exp exponential model, Nug nugget effect, LD litter depth, SM soil moisture, ST soil temperature, CO canopy openness, TSR total solar radiation

[a] Cases for which the range was calculated with the trimmed mean

the sill is reached asymptotically, *r* represents the effective range, the distance at which 95% of the sill has been reached (Goovaerts 1997).

For a spatial variable *Z*, the spatially structured component (SSC) is defined as the percentage of the total variation of *Z* that is explained by the spatial structure. It is calculated as follows (Bulit et al. 2004):

$$\mathrm{SSC} = (C_0 / C_0 + C) \times 100 \tag{6}$$

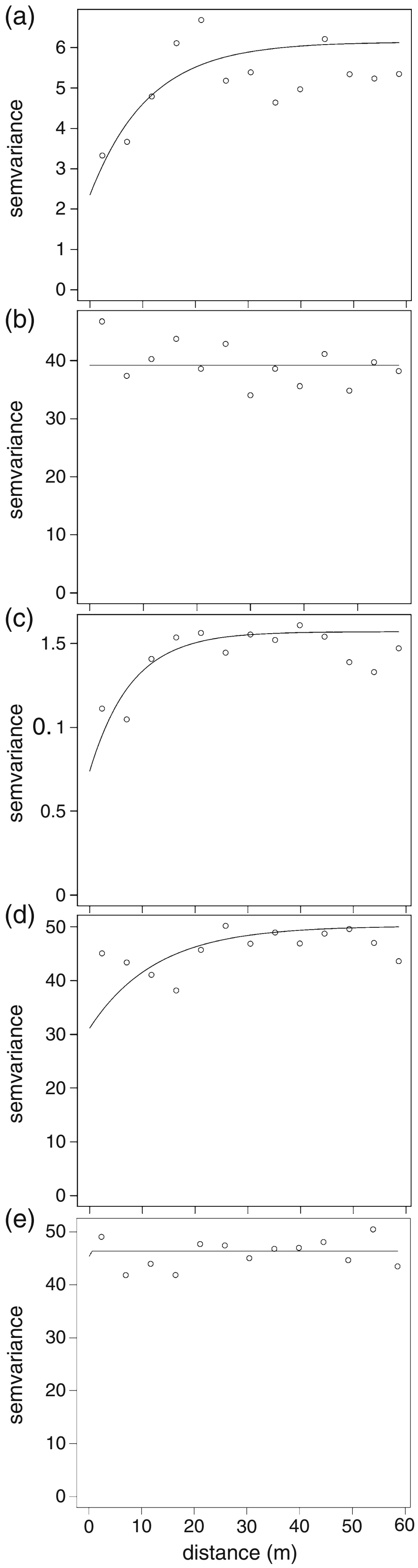
The semivariogram is further utilized for solving the kriging equations, whose solution allows the spatial prediction of the variable *Z* at non-sampled positions, thus enabling the production of distribution and abundance maps of the variable under analysis. This method provides the minimum variance prediction error, which reduces the uncertainty of the estimated values (Bulit et al. 2004).

The analysis of the spatial relationship between pairs of variables is performed through a crossed semivariogram (or correlogram) for two regionalized variables *Z*(*x*) and *Y*(*x*), by calculating, as is done in the simple semivariogram, the variance between the values taken by one variable with respect to the other, at each point located at a given distance *h* (de la Cruz Rot 2006):

$$\gamma_{YZ}(x+h,x) = \gamma_{YZ}(h) = \frac{1}{2}\sum[(Y(x+h) - Y(x))(Z(x+h) - Z(x))] \tag{7}$$

We subjected our data to this analysis to obtain the spatial structure and the relationship between environmental and sapling community variables. The analyses were performed by using the Geo R module of the R package (Ribeiro and Diggle 2001, available online, www.r-project.org/i). Further details of the utilized geostatistical methods are provided in Chilés and Delfiner (1999), Goovaerts (1997), and Bulit et al. (2003). The robustness of the fitted variogram models was assessed through cross-validation. Despite its limitations, this technique allows checking for the effect of changes in the parameters on the predicted values at unsampled locations, as well as comparisons between competing models (Goovaerts 1997).

Fig. 2 Semivariograms of **a** sapling density, **b** cover, **c** species richness, **d** mortality rate, and **e** recruitment rate. *Dots* are mean values for all dates ▶



The association between the environmental and the sapling community variables was tested through the following linear model:

$$\mathbf{Y}(s) = \mathbf{X}\beta + \varepsilon(s) \tag{8}$$

where $\mathbf{X}(n\times 6)$ is a matrix of environmental variable values (covariates), $\boldsymbol{\beta}$ is a vector of regression coefficients, $\mathbf{Y}$ is a column vector with the observed values of the biological variable, and $\varepsilon(s)$ is a zero mean Gaussian random field with exponential spatial covariance:

$$C(h) = \begin{cases} C_0 + C_1 & \textit{if } h \leq 0 \\ C_1 \exp[-r/h] & \text{otherwise} \end{cases} \tag{9}$$

It must be noted that the model formulation considers spatially correlated errors. Also, since the values for the covariates in the entire study area were predicted by kriging, the covariates $\mathbf{X}$ include an error source $\boldsymbol{\delta}$, whose variance is equal to their kriging variance. The error term $\varepsilon(s)$ was not assumed to be independent because we expected *a priori* the existence of a degree of spatial variation not fully explained by the covariates. The coefficients $\boldsymbol{\beta}$ in the linear model provide insight on the strength of the association between sapling community and environmental variables.

We used the spBayes library to fit model (8). Model fitting was done using the spGGT function, and subsequent prediction at new locations was done with the spPredict function. We assumed a N(0, λ) prior for $\boldsymbol{\beta}$, an inverse gamma prior for C_1 and C_0 with parameters (0.5, 0.5) and (3, 1), respectively. The choice of parameters was done trying to cover the range of possible values for C_0 and C_1 according to the empirical semivariograms. We selected a uniform prior for r with parameters $(0, 128)$ to give the range the possibility of being as large as the maximum distance within the study area. Kriging maps were produced on an expanded grid of 40×40 points distributed evenly across the study plot. The values of the environmental variables at each point of the expanded grid were obtained from the corresponding GIS covers of the distribution maps.

Maps of the spatial distribution for the sapling community variables were obtained by using values derived from the following predictive distribution:

$$N\left[x(s_0)'\boldsymbol{\beta} + \gamma'\Sigma^{-1}(\mathbf{Y} - \mathbf{X}\boldsymbol{\beta}), C_1 + C_0 - \gamma'\Sigma^{-1}\gamma\right] \tag{10}$$

where γ is a vector whose entries are the covariance between the sample locations and the point s_0, and Σ is the spatial covariance matrix (Banerjee et al. 2004). These maps were used to compute other maps representing the mean and the spatial 5 and 95% envelope for each sapling community variable (Møller 2003). Also, cross-correlograms were computed to analyze the spatial association between pairs of environmental and plant community variables.

Results

Spatial structures of sapling community and environmental variables

The semivariograms and correlograms, and their respective fits, show that the mean values for all sampling times of litter depth, soil moisture, soil temperature, canopy openness and solar radiation were spatially structured (Fig. 1), as were the individual semivariograms for the same variables for each time period (Table 1). Average range in the semivariograms for environmental variables was 13.14±3.67 m (±SE), with a mean SSC of 69.2%. The distance to which a given environmental variable was autocorrelated varied depending on the period of the year (Table 1). For example, for litter depth (average range=16.29 m), the semivariogram ranges varied between 4.68 and 21.18 m. The average semivariogram range for the sapling community variables was 12.68± 5.71 m (±SE) with a mean SSC of 50.81%. Nevertheless, only sapling density, mortality rate and species richness showed some spatial structure at every census, unlike sapling community cover and recruitment rate, which showed only a "pure nugget effect" (i.e. no spatial autocorrelation; Figs. 2 and 3). Also, the ranges of semivariograms for sapling density, mortality rate and species richness were relatively constant across periods (Table 1).

Consistent with the spatial structure observed for most of these variables, kriging maps for the mean value of environmental variables displayed some clear spatial patterns. Litter depth reached its highest values (8–9 cm) in the southwest corner (Fig. 1a). Soil moisture was also high in the same area (55%), and generally in the lower (northern) half of the plot (Fig. 1b). Similarly, canopy openness and solar radiation values were higher in the upper (southern) half of the plot, with intermediate values in small sections of the lower part (Fig. 1d, e). Soil temperature showed a more homogenous spatial distribution, although a zone with relatively cooler soil (with values as low as 13.5°C) was evident halfway between the lowest and the highest points of the plot (Fig. 1c).

Association between sapling community and environmental variables

The cross-variograms based on the mean values for the entire study period showed that the environmental variables

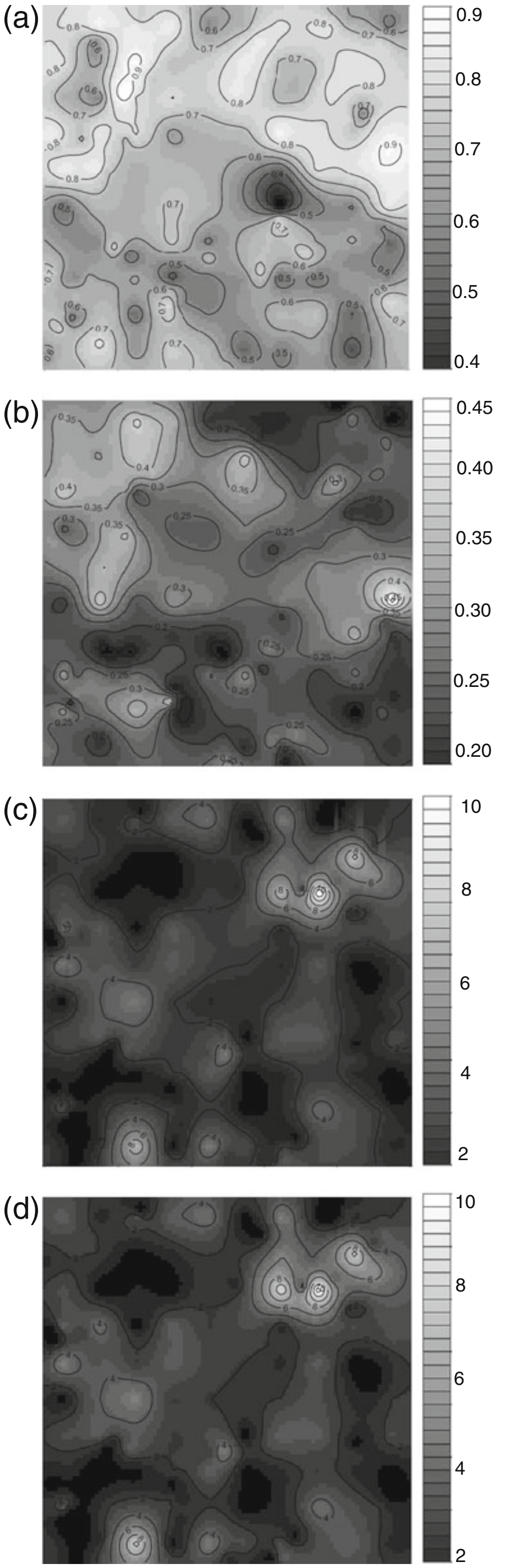


Fig. 3 Distribution maps for **a** soil moisture in August 2007, **b** soil moisture in February 2008, **c** sapling density in August 2007 and **d** sapling density in May 2007

were associated among themselves (Fig. 4a–c), and the same was true for the sapling community variables (Fig. 4d–f). Canopy openness and solar radiation were positively associated with each other, as were solar radiation and soil temperature (Fig. 4a, b). Conversely, solar radiation and soil moisture showed a negative spatial association (Fig. 4c). Cross-variograms between sapling community variables showed positive associations of sapling density with species richness (Fig. 4d), mortality rate (Fig. 4e) and cover (Fig. 4f).

The associations between environmental and sapling community variables show that litter depth was negatively associated with sapling density (Fig. 4g) and species richness (Fig. 4h). Litter depth was negatively associated with cover and mortality rate (not shown). Soil moisture was positively associated with recruitment rate (Fig. 4i). The only significant regressions of sapling community structure and dynamics variables on environmental variables were those involving litter depth (Table 2).

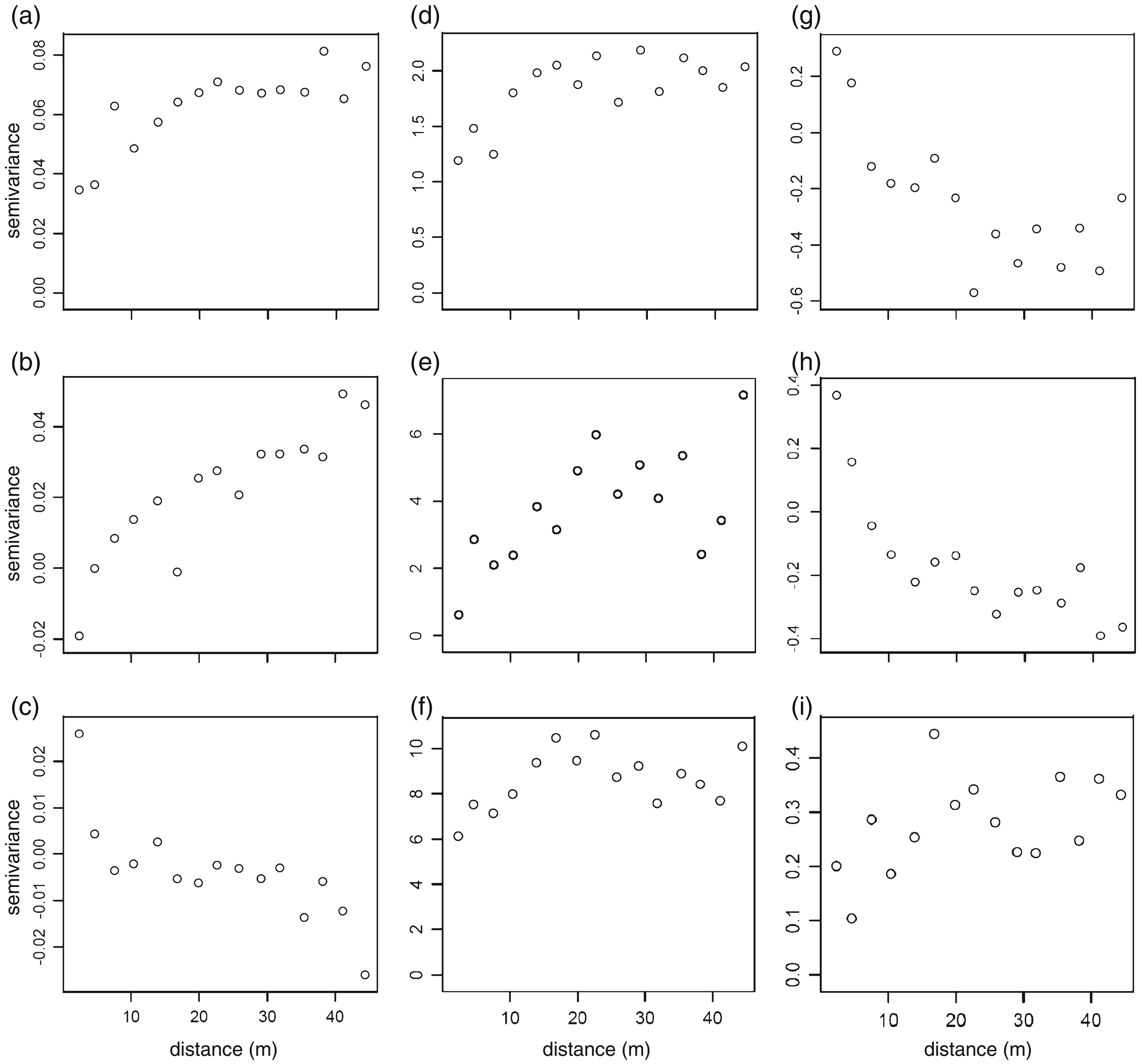


Fig. 4 Cross-variograms for **a** total solar radiation−canopy openness, **b** total solar radiation−soil moisture, **c** total solar radiation−soil temperature, **d** sapling density−species richness, **e** sapling density −mortality rate, **f** sapling density−cover, **g** litter depth−sapling density, **h** litter depth−species richness, **i** soil moisture−recruitment rate

Table 2 Parameters of Bayesian regression models between environmental and community variables

Variable	Parameter	Quantile			P
		5%	50%	95%	
Cov	r	0.24	1.65	2.82	
	C_0	1.74	30.49	43.40	
	C_1	1.23	5.02	39.65	
	Intercept	−12.81	29.91	73.95	0.868
	LD	−1.39	−0.84	−0.29	0.008
	SM	−3.85	−0.96	1.98	0.294
	ST	−4.09	−1.83	0.36	0.090
	CO	−5.00	1.63	8.10	0.664
	TSR	−2.99	−0.07	2.81	0.486
N	r	0.07	0.15	2.34	
	C_0	0.34	0.47	0.61	
	C_1	0.33	0.48	0.68	
	Intercept	−1.64	5.14	12.19	0.891
	LD	−0.17	−0.07	0.02	0.105
	SM	−0.49	−0.03	0.43	0.452
	ST	−0.55	−0.16	0.20	0.238
	CO	−0.86	0.23	1.29	0.634
	TSR	−0.59	−0.15	0.29	0.288
S	r	0.17	1.45	2.76	
	C_0	0.56	0.83	1.14	
	C_1	0.56	0.78	1.14	
	Intercept	−4.39	4.83	13.89	0.804
	LD	−0.24	−0.12	0.00	0.049
	SM	−0.61	−0.01	0.58	0.492
	ST	−0.60	−0.14	0.35	0.327
	CO	−1.13	0.24	1.62	0.611
	TSR	−0.61	0.00	0.59	0.501

LD litter depth, SM soil moisture, ST soil temperature, CO canopy openness, TSR total solar radiation

The predictions produced for the three spatial envelopes used in the conditional simulation of sapling community structure and dynamics were very similar (Fig. 5), indicating that they are robust and thus reliable. Two small areas of higher sapling density were observed in the plot, near the NE and SW corners, respectively, whereas sapling density was very low (0–2 ind. m^{-2}) or intermediate (3–6 ind. m^{-2}) in the remaining areas (Fig. 5a, d, g). Interestingly, zones of intermediate density coincided with those having the highest predicted values of species richness, in the central-left section of the plot (Fig. 5b, e, h). Similarly, for sapling community cover two areas of high values were observed, near the SW corner and in central sections of the plot. Patches with higher litter depth were associated with a lower sapling density, species richness and sapling cover (Figs. 1a and 5d–f).

Discussion

The few studies that have analyzed the spatial autocorrelation of environmental variables in forest communities (Becker and Smith 1990; Walter and Himmier 1996; Trichon et al. 1998; Montgomery and Chazdon 2001; Miller et al. 2002; Poulsen et al. 2006) coincide in concluding the existence of a clear spatial autocorrelation. In addition to the spatial structure of environmental variables, in this study we also demonstrated that the sapling community organization and dynamics are also spatially structured in the cloud forest of Teipan. Despite this overall agreement among studies, there are some important differences between their findings; for example, the distance to which spatial autocorrelation is maintained is highly variable (2.5−21.0 m) and it appears to be specific to different forest types.

Assessing the spatial structure either of environmental or of community variables is simply a first step in the search of the factors driving such patterns, or in the assessment of its consequences for community organization. Factors and processes involved in the spatial structuring of ecological systems are likely to be manifold and system-specific. Previous studies indicated that spatial autocorrelation may be primarily associated with the different architectures and the spatial arrangements of canopy species (Roburn 2003; Gómez et al. 2004). In our study, the spatial associations observed in the cross-variograms between environmental variables are also likely to be influenced by canopy structure, particularly by canopy openness, a variable that was spatially associated with most other environmental variables, with the notable exception of litter depth. Such independent behavior of litter depth and canopy openness suggests, in turn, that other factors play relevant roles regarding litter accumulation and decomposition processes, such as leaf traits (thickness, chemical composition), which are species-specific and thus not necessarily linked to the amount of foliage in the forest canopy. However, it must be noted that we found a temporal concurrence between canopy openness and litter depth, as the increasing litterfall typical of the early dry season was reflected in both larger values of canopy openness and a deeper litter, which may be explained by the strong seasonality in litterfall (Vasconcelos et al. 2008).

This study showed positive spatial associations between sapling density, sapling community cover and species richness, even though the largest values of species richness were recorded in zones with intermediate sapling densities. Interestingly, despite the strong temporal variations in the abiotic environment, sapling density, cover and species richness were considerably constant through time, suggesting that the environmental changes between seasons are not capable of modifying the characteristics of the present

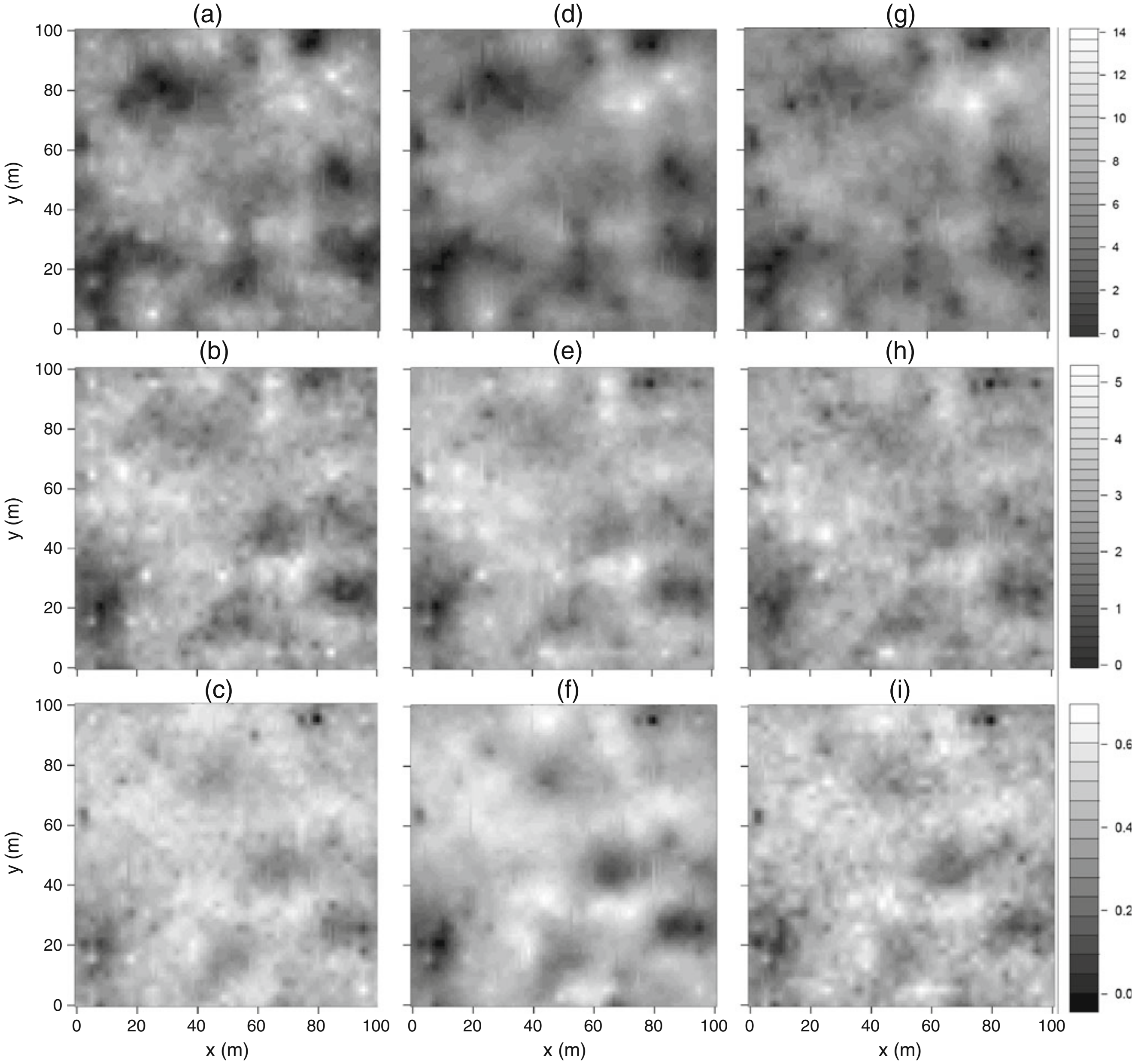


Fig. 5 Distribution maps (100×100 m) of sapling density (**a**, **d**, **g**), species richness (**b**, **e**, **h**) and cover (**c**, **f**, **i**) based on conditional simulation. Lower quantiles (5%) are shown on the *left* (**a**–**c**), mean quantiles (50%) in the *central column* (**d**–**f**), and upper quantiles (95%) on the *right* (**g**–**i**). A scale in *gray shading* (*light* low values, *dark* high values) is given for each variable

sapling community. Conversely, sapling mortality and recruitment rates did show important differences between sampling periods; for example, the largest values of the antagonistic processes of sapling recruitment and mortality were recorded in the late rainy season. It is conceivable that other factors are also involved in this community's dynamics, such as a density-dependent survivorship, or increased pathogen attacks in the most humid time of the year (Harms et al. 2000; Weiner et al. 2001), particularly in common species such as *Oreopanax xalapensis* (Kunth) Decne. & Planch., which forms large and conspicuous sapling banks in this forest.

The estimated mean range in the variograms of environmental variables (13.14±3.67 m) was almost identical to that obtained for the sapling community variables (12.68±5.71 m); this quantitative similarity indicates that the environmental variables affect the sapling community, or alternatively, that both the environment and the saplings are affected or modified by a third factor (or factor group), such as canopy crown size. In this cloud forest, mean crown diameter for upper canopy trees (i.e., with heights >15 m) is 11.2±4.5 m (N. Mejía-Domínguez, unpublished data), and therefore it seems likely that the spatial structure of resources and conditions for sapling establishment, growth and survival are affected by the individual crowns of the upper canopy and the discontinuities between them (Grant 1997; Denslow et al. 1998; LePage et al. 2000; Becerra et al. 2004). The cross-variograms based on mean values show spatial associations between some environmental and understorey (sapling community structure and dynamics) variables. Our results suggest that litter depth has a strong negative effect on sapling density, species richness, and cover, in agreement with previous findings for the sapling community in a similar forest (Ortiz-Arrona 1999). Seeds under litter are deprived of light and seeds resting on its surface cannot root easily, limiting both the number of plants that establish in a given microsite, and the number of species represented in them (Vázquez-Yanes and Orozco-Segovia 1992; Daws et al. 2005). Ortiz-Arrona (1999) reported that soil moisture is related to the regeneration of cloud forest tree species; our data demonstrate that higher soil moisture was spatially associated with a higher recruitment rate. Based on these associations, we conclude that soil moisture and litter depth, the former being in turn affected by solar radiation and the latter being associated to canopy openness, are among the most relevant environmental variables for sapling community structure and dynamics in this forest type.

It could be argued that analyzing sapling community attributes in the light of current understory environmental conditions may be somewhat misleading, as the spatial structure of the sapling community likely reflects the spatial structure of the environment in the past. There are two reasons suggesting that this is not a problem in our forest. First, the size (both height and stem diameter) of canopy trees that are most responsible of the environment under their canopies discards the possibility that these trees were not present at the time of the establishment of the saplings recorded by us, considering the relatively low growth rates observed for these trees (N. Mejía-Domínguez, unpublished data). Secondly, the large permanent plot was first set up in 2002 and has been monitored yearly since. During this 8-year period of continuous observations, some tree deaths were recorded, but the overall forest structure has remained essentially unchanged (Mejía-Domínguez et al. 2004).

Conclusions

Patterns of seed dispersal, which represent the “initial” or potential spatial pattern, together with other biotic interactions and density-dependent phenomena, may also be involved in the spatial structuring of the establishment of new individuals in the sapling community (Dalling et al. 1998, 2002; Jordano et al. 2004; Gómez-Aparicio et al. 2005a, b; Gómez-Aparicio 2008). Regardless of this possibility, our results support the conclusion that the sapling community in the cloud forest of Teipan is spatially structured. Such structure is intimately linked to the spatial structure of the micro-environmental variables operating at the forest floor level, which in turn appear to be mostly associated with the complexity of the upper canopy, including aspects such as tree architecture and species spatial distribution. The association of the spatial structures of the environment and the sapling community strongly suggests that the regeneration processes in this cloud forest are driven by the existence of different microsites, largely characterized by litter depth variations, in which tree saplings encounter differential opportunities for their successful establishment and survival.

The relevance of spatial variation of the abiotic environment on sapling survivorship, as compared to the relatively minor role of temporal variation, has been reported for other forest communities (Gómez-Aparicio et al. 2005a, b). By constructing a robust model of the sapling community variables and their association to environmental variables by means of conditional simulation, we can now conclude that their spatial distributions, although heterogeneous, are not random, but that they rather display a strong correspondence in well-defined patches across space. This fact, along with the mean autocorrelation distance observed for all variables, suggests the existence of a further higher-level factor that dominates the overall relation between the two sets; for our forest, we can hypothesize that understorey conditions and attributes are driven by canopy characteristics, and therefore that the taxonomic identity of canopy individuals plays a significant role in this process.

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CAPÍTULO III

EFECTO DE LA IDENTIDAD ESPECÍFICA DE LOS ÁRBOLES DE DOSEL SOBRE EL MICROSITIO INMEDIATO Y LA ESTRUCTURA Y LA DINÁMICA DE LA COMUNIDAD DE PLÁNTULAS

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Individual Canopy-Tree Species Effects on Their Immediate Understory Microsite and Sapling Community Dynamics

ABSTRACT

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Individual Canopy-Tree Species Effects on Their Immediate Understory Microsite and Sapling Community Dynamics

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ABSTRACT

Canopy trees are largely responsible for the environmental heterogeneity in the understory of tropical and subtropical species-rich forests, which in turn may influence sapling community dynamics. We tested the effect of the specific identity of four cloud forest canopy trees on total solar radiation, canopy openness, soil moisture, litter depth, and soil temperature, as well as on the structure and dynamics of the sapling community growing beneath their canopies. We observed significant effects of the specific identity of canopy trees on most understory microenvironmental variables. Soil moisture was higher and canopy openness lower beneath *Cornus disciflora*. In turn, canopy openness and total solar radiation were higher beneath *Oreopanax xalapensis*, while the lowest soil moisture occurred beneath *Quercus laurina*. Moreover, *Chiranthodendron pentadactylon* was the only species having a positive effect on litter depth under its canopy. In spite of these between-species environmental differences, only *C. pentadactylon* had significant, negative effects on sapling density and species richness, which may be associated to low seed germination and seedling establishment due to an increased litter depth in its vicinity. The relevance of the specific identity of canopy trees for natural regeneration processes and species richness maintenance depends on its potential to differentially affect sapling dynamics through species-specific modifications of microenvironmental conditions.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: canopy openness; cloud forest; forest regeneration; litter depth; sapling density; soil moisture; species richness; specific identity.

NATURAL FOREST REGENERATION IS ONE OF THE DRIVING MECHANISMS influencing community diversity maintenance. Several authors have emphasized the need to examine this process in the context of environmental heterogeneity and heterospecific replacement of individuals (Nicotra *et al*. 1999, Bellingham & Tanner 2000, Webb & Peart 2000, Harms *et al*. 2001). Research that fully incorporates the analysis of such heterogeneity, however, and examines its causes and its role in community diversity maintenance is still scanty (Hutchings *et al*. 2000, Beckage & Clark 2003, Potts *et al*. 2004).

Vegetation structure and composition at present are largely the products of the different processes that take place during forest regeneration (Hartshorn 1980, Runkle 2000). Newly established seedlings and young saplings in a forest understory face a much heterogeneous environment across space (Hurtt & Pacala 1995, Aiba *et al*. 2004, Queenborough *et al*. 2007b). The prevailing microenvironmental conditions during the early life of a canopy tree affect the probability of such tree eventually reaching the canopy or of dying before succeeding (Augspurger 1984, Spies & Turner 1999, Poorter 2007). Many forest dynamics studies that have analyzed environmental heterogeneity have related such variation to the opening of canopy gaps, which often modifies profoundly the understory environment (Grant 1997, Denslow *et al*. 1998, Arriaga 2000, Aiba *et al*. 2004). There is increasing recognition, however, that some features of the community's overstory such as tree density, size, or shape, may also have similar effects (Tremmel & Bazzaz 1993, Montgomery & Chazdon 2001, Acevedo *et al*. 2003). The known effects of canopy trees on the understory microenvironment are complex and include local modifications of light quality and quantity, air temperature and relative humidity, and soil properties including fertility, soil structure, litter characteristics, and water contents (Molofsky & Augspurger 1992, LePage *et al*. 2000, Acevedo *et al*. 2003, Becerra *et al*. 2004, Ayres *et al*. 2009). The overall microenvironmental effects of canopy trees may also differentially limit the germination success of seeds newly arrived in the area (Hurtt & Pacala 1995; Schupp 1995; Gray & Spies 1996; Hubbell *et al*. 1999, 2001; Pearson *et al*. 2003). Studies on the regeneration niches (*sensu* Grubb 1977) of tree species have found large between-species differences in this regard (Webb & Peart 2000, Yamada *et al*. 2006, Queenborough *et al*. 2007a, Russo *et al*. 2008).

The recognition of the specific identity of canopy trees as an ecological factor in the study of forest dynamics offers interesting new perspectives. For example, by using the species of canopy trees as a reference, one may be able to detect more readily the degree of heterogeneity in a forest understory or to assess to what extent this factor interacts with baseline heterogeneity, given the potential of each species to maintain the existing environmental conditions or to transform them, creating new ones (Pickett *et al*. 2000). Also, this approach may help to gain insight on the potential interactions experienced by propagules deposited under the canopies of different species (Hurtt & Pacala 1995, Harms *et al*. 2001). In this context, the case of Mesoamerican cloud forests is particularly interesting, as these communities host complex mixtures of tree species with different ecological affinities, including those with lowland tropical forests and temperate forests of higher altitudes and latitudes (Rzedowski 1978). These varying ecological affinities are related to different morphologies, leaf phenologies, and functional

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patterns (*e.g.*, Arriaga 1988, Williams-Linera 1997, Saldaña-Acosta *et al.* 2008), which further suggests the possibility that the different canopy-tree species could make a significant contribution to the heterogeneity of the regeneration microsites associated to them.

The aim of the present study was to test the hypothesis that the effects of cloud forest canopy trees on the regeneration processes are species-specific due to the differential abilities of the species to shape the regeneration microsites. The specific goals were the following: (1) to analyze the effects of the specific identity of canopy individual trees on total solar radiation, percent canopy openness, percent soil moisture, litter depth, and soil temperature; (2) to assess the effects of the specific identity of trees on seedling community structure and dynamics; and (3) to determine whether the species effect remains the same throughout the year, considering the seasonal variation of the habitat.

MATERIALS AND METHODS

STUDY AREA.—The study was conducted in a cloud forest in Santo Tomás Teipan (hereafter Teipan), Oaxaca state, southern Mexico (16°15′ N; 95°58′ W; 2400 m asl), which occurs across an elevational range from 2200 to 2500 m. Yearly total rainfall in this area ranges between 1400 and 1500 mm, and mean annual temperature is *ca* 12.3°C (Instituto de Geografía, Universidad Nacional Autónoma de México [IG-UNAM] 1970, García 2004). Mean temperature for the coldest month (January) is 8°C, and for the hottest one (May) is 26°C; the highest and lowest temperature extremes recorded in the region are -4°C and 32°C, respectively (IG-UNAM 1990). In Teipan the climate is considerably seasonal, with 96.8 percent of total annual rainfall concentrating between May and October (Mejía-Domínguez *et al.* 2004).

FIELD SURVEY.—Fieldwork was conducted in a 1-ha permanent plot that was first established in 2002, located *ca* 1 km north from Teipan, on the lower slope of Mt. Calabazo (Mejía-Domínguez *et al.* 2004). The lowest elevation in the plot (the NW corner) is 2300 m, and the highest point is 60 m higher. In this plot, the dynamics (survivorship, recruitment, and mortality) of the forest canopy (trees with dbh ≥ 2.5 cm) was monitored yearly between 2002 and 2007.

In May 2007, 153 1-m^2 quadrats were established and permanently marked with metal stakes throughout the large plot. These quadrats were located either in areas under the single influence of the crowns of one of four selected canopy species (listed below), or in areas of mixed canopy influence, where no single-species effect could be identified. Areas under mixed canopies only containing the four focal species in any combination were discarded, *i.e.*, areas of mixed influence always included several of the remaining species forming part of the canopy in this forest (Mejía-Domínguez *et al.* 2004). We produced a map of the 1-ha plot showing potential locations for 1-m^2 quadrats, considering the desired condition, based on crown projections of all canopy trees with heights ≥ 10 m (up to 35 m) measured in the first forest census; in the field we verified that the quadrats met unambiguously the selection criterion. Between-plot independence was maximized by incorporating areas as much as possible located under different individuals and in different sectors of the plot.

The cloud forest of Teipan has a relatively simple vertical structure. Under the largest canopy trees, there is one readily distinguishable subcanopy layer of low trees (5–10 m in height), strongly dominated by two species (*Psychotria galeottiana* and an as yet undescribed *Miconia* species). They occur everywhere together in the 1-ha plot, and show a significant positive association between them (Mejía-Domínguez *et al.* 2004). Their joint occurrence results in a homogenous light attenuation across space. This situation justifies ascribing understory environmental differences mainly to canopy trees (10–35 m in height), which account for *ca* 87 percent of total community crown cover. The relatively little overlap between the crowns of different canopy species enabled us to identify areas that were almost exclusively influenced by a single species.

The selection of canopy species for examining their specific effects (specific identity [SI]) on understory environment and dynamics was based mostly on their relative importance values (RIV) (*i.e.*, the sum of their relative frequencies, densities, and basal areas) in the canopy; additionally, the selection was also based on some physiognomic traits such as leaf form and crown geometry. The following canopy species were chosen: (1) *Cornus disciflora* DC. (Cornaceae), which had the highest RIV in every previous census; (2) *Quercus laurina* Bonpl. (Fagaceae), which always had the second largest RIV and the second largest cover despite a low density; (3) *Oreopanax xalapensis* (Kunth) Decne. & Planch. (Araliaceae), a species ranking sixth in RIV among canopy trees, but first in the understory community; and (4) *Chiranthodendron pentadactylon* Larreat. (Sterculiaceae), a species ranking eighth according to RIV but of interest due to its potential effect on the light environment and litter properties under its crowns, as it is the tree species with the largest leaves in this forest. Hereafter, these species will be referred by their generic epithets only.

The selected species differ in several attributes with potential effects on the environment under their canopies (Table 1). Two of the four species are deciduous (or nearly), whereas the other two are evergreen: *Cornus* remains completely leafless, while *Quercus* retains some of its hard, sclerophyllous leaves during the dry season. The two evergreen species also differ in their phenological behavior, as *Chiranthodendron* sheds leaves continuously throughout the year but *Oreopanax* does not. Moreover, *Quercus* has the deepest crowns, in contrast to the very flat crowns of *Cornus* and *Chiranthodendron*. Leaf size, a trait related both to litter accumulation on the soil and canopy openness, also differs greatly among species, with *Chiranthodendron* and *Oreopanax* having much larger leaves than the other two. The crowns of *Cornus* and *Oreopanax* are evidently more open than those of *Quercus* and *Chiranthodendron*, apparently because of a prevalence of orthotropic branches in the former vs. a larger proportion of plagiotropic branches in the latter, but this architectural trait has not been formally assessed. These differences in crown architecture may not be related to a differential light interception only, but also to the particular proportions of throughflow and stemflow for each species, and consequently their abilities to funnel water into their surrounding soils (Loustau *et al.* 1992, Park & Cameron 2008).

TABLE 1. *Characteristics of the four selected canopy tree species. Shown values are those recorded in a 1-ha plot in Teipan, Mexico. Leaf length includes both leaf blade and petiole.*

Species	Maximum height (m)	Leaf phenology	Mean crown depth (m)	Maximum crown depth (m)	Leaf length (cm)
Cornus disciflora	27	Deciduous	5.5	10.0	4–5
Quercus laurina	35	Subdeciduous	7.0	13.0	6–7
Oreopanax xalapensis	26	Evergreen	5.0	12.5	15–16
Chiranthodendron pentadactylon	26	Evergreen	5.3	10.3	14–15

Every sapling of tree and shrub species with a height ≤ 50 cm and lacking cotiledonary leaves occurring in the 153 plots was individually marked with aluminum tags, and its height (to stem apex) and cover (two perpendicular diameters) were measured. Additionally, their exact location in the quadrat was recorded on a grid to the nearest centimeter; this information was used in subsequent surveys to verify the fate of each plant. Subsequently, seedlings were surveyed at 3 mo intervals (August and November 2007, and February and May 2008) until data for an entire yearly cycle were gathered. Newly recruited saplings, *i.e.*, those already fulfilling the inclusion criteria, were tagged and measured, and their locations noted.

In addition to assessing seedling community structure and dynamics, at each census we also measured three soil variables in each quadrat (the first two at a depth of 20 cm): (a) percent relative soil moisture (Aquaterr T-300, Aquaterr Instruments and Automation LLC, Costa Mesa, California, USA), (b) soil temperature (Aquaterr T-300), and (c) litter depth (flexometer, to the nearest mm). Concurrently, hemispherical photographs were taken horizontally 1 m above the ground at the center of each quadrat (Nikon Coolpix 990 digital camera and an 8-mm FC-E8 fisheye lens); percent canopy openness and total solar radiation for 3-mo periods were estimated from the photographs with the gap light analyzer (GLA) software (Frazer *et al.* 1999). Photographs were taken near ground level because we were interested in characterizing the light environment of the understory, where seedling establishment and initial sapling growth occurs, but not in potential differences at other heights through the forest profile that could not be perceived by such small plants.

DATA ANALYSIS.—In order to discard potential site-specific effects unrelated to the main investigated factor (SI), we used a generalized linear model (GLM) and an analysis of deviance to test for differences in slope inclination (arcsine transformed) between quadrats associated to the different specific identities.

Sapling density was estimated as the number of saplings per 1-m^2 quadrat, and percent cover of this community (hereafter referred to simply as cover) as the percentage of area (m^2) covered by saplings in the same area. Species richness was defined as the number of species per quadrat. We assessed seedling community dynamics by estimating mortality (*M*) and recruitment (*R*) rates with the following equations (Sheil 1995, 2001):

$$M = \{1 - [(N_0 - m)/N_0]^{1/(\Delta t)}\} \times 100,$$

$$R = \{[(N_0 + r)/N_0]^{1/(\Delta t)} - 1\} \times 100,$$

where N_0 is the initial density, m is the number of dead seedlings, Δt is the time period (months), and r is the number of recruited seedlings. Total observation period was 12 mo.

Because of nonnormality of some variables (even after attempting various transformations), we used GLMs and analyses of deviance to analyze the species effect on the environment in the immediate neighborhood of each canopy focal species, as well as on the understory community's structure and dynamics. The quasi-binomial distribution was used for canopy openness and recruitment and mortality rates, instead of the binomial one, due to overdispersion; in turn, for sapling density and species richness we used a quasi-Poisson for the same reason (Bolker *et al.* 2009). Gaussian distribution was used for the rest of variables. GLMs have been increasingly used when modeling variables with nonnormal distributions due to their higher statistical power compared with nonparametric analysis of variance tests (Crawley 2007, Bolker *et al.* 2009).

In a first analysis we took species as the influencing factor or covariate, and we performed individual statistical tests for each of the following response variables: (a) percent relative soil moisture, (b) soil temperature, (c) litter depth, (d) percent canopy openness, and (e) total solar radiation. For the understory community, response variables were: (a) sapling density, (b) species richness, (c) percent cover, (d) recruitment rate, and (e) mortality rate. For these analyses we used the mean values of all ten response variables (*i.e.*, five environmental and five for the understory community) measured at different times. The factor species took five values: the four focal species and the mixed (nonmonospecific) canopy. These analyses were performed using the GLM function in R (R Development Core Team 2010). For significant models, pairwise comparisons were performed with *post-hoc* Tukey HSD tests.

Finally, by combining all data from the seasonal censuses (instead of their means), we used generalized linear mixed models (GLMMs) to examine the effect of the specific identity (SI, as a fixed factor), and of sampling period (t, as a random factor) on the same ten response variables. The error distribution for these variables is shown in Table 2. The following five models were pairwise and sequentially compared with the likelihood ratio test (Burnham & Anderson 2002, Bolker *et al.* 2009) for each response variable: (1) α, which excludes the two analyzed effects; (2) $\alpha+\beta\mathrm{SI}$, which only included the effect of SI; (3) $\alpha+\gamma t$, which only included the effect of time; (4) $\alpha+\beta\mathrm{SI}+\gamma t$; and (5) $\alpha+\beta\mathrm{SI}+\gamma t+\delta t\mathrm{SI}$. Model selection was based according to the lowest values of the Akaike

TABLE 2. *Models with minor Akaike information criterion (AIC) derived from generalized linear mixed models of the effects of specific identity (SI) and random seasonal variation (t) on five microenvironmental variables and five sapling community variables assessed in a cloud forest understory of southern Mexico. Pairwise comparisons of models for each response variable based on likelihood ratio tests (lrt).*

Response variable	Model	Error distribution	AIC	Factor	lrt
Understory microenvironment					
Soil moisture	$\alpha+\beta\mathrm{SI}+\gamma t$	Gaussian	− 1219.97	SI	**
				t	***
Soil temperature	$\alpha+\gamma t$	Gaussian	1441.02	*t*	***
Litter depth	$\alpha+\beta\mathrm{SI}+\gamma t$	Gaussian	3271.70	SI	***
				t	***
Canopy openness	$\alpha+\beta\mathrm{SI}+\gamma t$	Quasi-binomial	19.54	SI	NS
				t	[a]
Total solar radiation	$\alpha+\beta\mathrm{SI}+\gamma t$	Gaussian	2061.40	SI	***
				t	***
Sapling community					
Sapling density	$\alpha+\beta\mathrm{SI}+\gamma t$	Poisson	1628.27	SI	***
				t	***
Species richness	$\alpha+\beta\mathrm{SI}$	Poisson	2447.24	SI	***
Mortality rate	$\alpha+\gamma t$	Quasi-binomial	134.33	*t*	[a]
Recruitment rate	$\alpha+\gamma t$	Quasi-binomial	35.43	*t*	[a]
Sapling cover	$\alpha+\beta\mathrm{SI}$	Gaussian	− 1041.61	SI	NS

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

[a] Factor significance could not be assessed because of quasi-binomial distributions; for these models in the AIC column are quasi-AIC values.

NS, not significant.

information criterion (AIC) (Akaike 1974). For overdispersed variables with binomial or Poisson distributions, we calculated quasi-AIC (Tjur 1998, Bolker *et al.* 2009); these analyses were performed using the lme4 package (Bates & Maechler 2009) in R.

RESULTS

The analysis of deviance performed to compare slope inclination between the five species identity treatments did not show significant differences ($F_{4,93} = 1.69$, $P = 0.15$). In contrast, GLMs showed that the species identity had significant effects on most microenvironmental forest understory variables: soil moisture ($F_{4,148} = 5.5612$, $P = 0.0003$), litter depth ($F_{4,148} = 6.3325$, $P = 0.0001$), canopy openness ($\chi^2_4 = 0.0308$, $P = 0.0208$), and total solar radiation ($F_{4,148} = 3.4390$, $P = 0.0102$). Soil temperature was the only variable without significant variation between different species ($F_{4,148} = 1.9858$, $P = 0.0996$). Similarly, the analyses of deviance showed significant effects of species on two of the five understory community variables analysed: sapling density ($\chi^2_4 = 26.89$, $P = 0.0200$) and species richness ($\chi^2_4 = 11.394$, $P = 0.0130$).

The *post-hoc* pairwise comparisons of the environmental and understory community variables showed a considerable heterogeneity regarding which species affects which variables (Fig. 1), *i.e.*, no single species had the strongest effects, although *Chiranthodendron* quadrats differed with respect to more response variables than any other canopy type (one microenvironmental variable and two sapling community variables). Mean soil moisture (± 1 SD) was significantly higher under *Cornus* canopies (48.3 ± 7.2%), but values recorded for this variable under this species differed significantly only from those recorded under the canopies of *Quercus* (41.4 ± 6.8%) and the mixed canopies (42.1 ± 6.6%). Mean litter depth was significantly larger under *Chiranthodendron* (6.5 ± 1.6 cm; range: 4.47–5.11 cm), with this species differing from the means of all other treatments. Regarding canopy openness, the areas under *Oreopanax* canopies (6.8 ± 1.4%) showed larger values that differed significantly only from those sites located under *Cornus* (5.6 ± 0.9%). Similarly, the largest mean total solar radiation values were recorded in sites beneath the crowns of *Oreopanax* trees (3.5 ± 0.5 mol m^2/d), which differed significantly from those associated to mixed canopies (3.1 ± 0.5 mol m^2/d). Regarding understory community structure, under the canopy of *Chiranthodendron* we recorded a lower mean sapling density (1.2 ± 1.6 ind./m^2) and mean species richness (0.8 ± 0.8 species), but significant differences were observed only for comparison of these values with those from mixed canopies (2.9 ± 3.2 ind./m^2, and 1.7 ± 1.3 species, respectively).

In short, *Cornus* canopies had a positive effect on soil moisture and a negative one on canopy openness, but did not affect total solar radiation. In contrast, *Quercus* affected soil moisture negatively, but had no significant effect either on canopy openness or on total solar radiation. This pattern contrasts with that observed for *Oreopanax*, as canopy openness and total solar radiation were

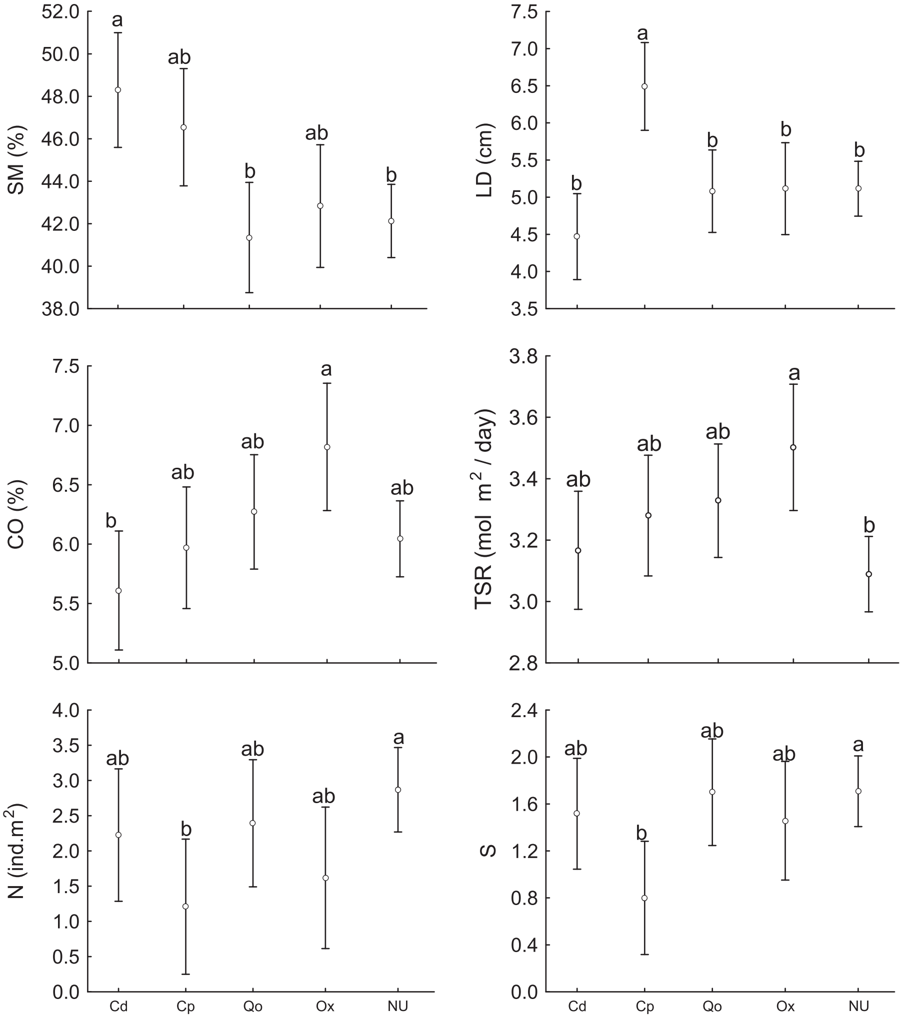

FIGURE 1. Mean values (with 95% CI) of environmental and understory variables under the canopies of four species and under mixed-species canopies (nonunispecific [NU]) in a cloud forest of southern Mexico. Species abbreviations: Cd, *Cornus disciflora*; Cp, *Chiranthodendron pentadactylon*; Qo, *Quercus laurina*; Ox = *Oreopanax xalapensis*. Response variables abbreviations: SM, soil moisture; LD, litter depth; CO, canopy openness; TSR, total solar radiation; N, seedling density; and S, species richness. Different letters indicate significant differences in a generalized linear model and *post-hoc* Tukey HSD tests.

significantly larger under its crowns, while soil moisture remained unaffected. *Chiranthodendron* was the only species with a positive effect of litter depth, although it did not show significant effects on the other microenvironmental variables. *Chiranthodendron* was also the only canopy type with negative effects on two sapling community variables (sapling density and species richness); interestingly, these variables differed significantly between this species and the mixed canopies. No species significantly affected soil temperature and the remaining sapling community variables (cover, mortality, and recruitment rates).

In agreement with the results of the analysis of deviance, the GLMMs showed significant effects of SI on three microenvironmental variables (soil moisture, litter depth, and total solar radiation; Table 2). These models also showed significant effects of time on four microenvironmental variables, including soil temperature. Overall mean litter depth peaked in February (6.7 ± 2.1 cm), near the end of the dry season, and showed a minimum in November, at the end of the rainy season (3.5 ± 1.7 cm) (Fig. 2). Likewise, soil moisture was at its highest in August (65.4 ± 15.1%), in the middle of the rainy season, and dropped to a minimum in February (26.2 ± 8.8%). Conversely, canopy openness had its lowest value in August (4.9 ± 2.0%) and showed two peaks, one in November (6.9 ± 2.6%) and another in February (6.8 ± 1.6%). Total solar radiation peaked in May (4.0 ± 1.1 mol m^2/d), and decreased as winter approached, returning to high levels in the following May (3.8 ± 0.9 mol m^2/d). With respect to sapling community variables, sapling density and species richness were significantly affected by species identity, and sapling density was also affected by time (Table 2). It must be noted that in some cases the selected models according to the AIC included nonsignificant factors; this was particularly clear in the case of the model constructed for sapling community cover.

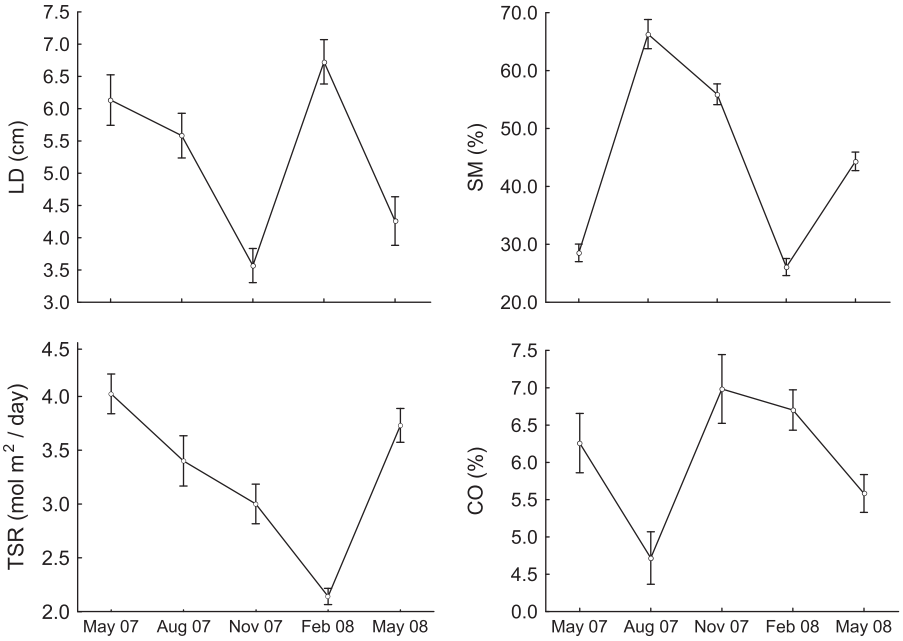

FIGURE 2. Temporal variation throughout the year of environmental variables in the understory of a cloud forest of southern Mexico. Values are means (with 95% CI) of measurements made under the canopies dominated by various species. LD, litter depth; SM, soil moisture; TSR, total solar radiation; and CO, canopy openness.

DISCUSSION

Species effects on understory microsite and sapling community.—In this study, we demonstrated that canopy trees of different species have differential effects on canopy openness, total solar radiation, soil moisture, and litter depth. These results are in agreement with earlier studies that have demonstrated between-species differences in a number of plant traits that can influence litter chemistry, litter biomass, and soil temperature and moisture (Eviner & Chapin 2003, Eviner 2004, Barbier *et al.* 2008). When considering the temporal variation of these environmental variables (*i.e.*, between-season significant differences), the species effects on them were still apparent. This indicates that the temporal variation is independent of canopy-tree species, in agreement with the lack of significant interactions observed in the GLMMs. This result also implies that the species effects can override the seasonal variations of the light and humidity regimes, which in our study forest are not negligible due to the seasonal partial loss of foliage that characterizes it.

The different ways in which the four focal species affect understory microenvironment is not a mere question of magnitude: each analyzed variable changed significantly according to at least one species, while being indifferent to others. For example, *Cornus* and *Quercus* significantly affected soil moisture, but in opposite directions, whereas *Chiranthodendron* was the only species with a significant effect on litter depth. Although these results matched our initial expectations regarding the differential effects of canopy species, only one of the four canopy types (*i.e.*, *Chiranthodendron*) had a significant effect on the sapling community, resulting in lower sapling density and species richness beneath its canopy. Interestingly, the mixed (nonmonospecific) canopies were associated to significantly larger values of these two variables, a result that may be related to a more diverse seed rain than to better germination and establishment conditions. Our results are not conclusive about what factors are responsible for these limitations in the understory community associated to *Chiranthodendron*, but they suggest a crucial role of litter depth, which was significantly larger beneath this species than under any other canopy type (*i.e.*, the remaining three studied species and the mixed-species canopies). Litter depth may potentially have strong effects on understory structure and composition, and the nature of this physical effect—be it positive or negative—on understory vegetation may be nonlinear, reversed beyond certain amount of litter, and species-dependent (Suding & Goldberg 1999). This factor is also known to have both positive and negative effects on understory development by influencing microclimatic soil conditions like moisture (Facelli & Kerrigan 1996, Graae & Heskjaer 1997) and temperature (Becerra *et al.* 2004, Esteso-Martínez & Gil-Pelegrín 2004). Seeds under litter are deprived of light and seeds resting on its surface cannot root easily, limiting both the number of plants that establish in a given microsite, and the number of species represented in them (Vázquez-Yanes *et al.* 1990, Facelli & Pickett 1991, Vázquez-Yanes & Orozco-Segovia 1992, Daws *et al.* 2005). Similarly, *Oreopanax* showed a clear (albeit nonsignificant) trend toward a lower sapling density in their immediate understory, despite being the most abundant species in the understory community. This observation might be related to the better light conditions recorded beneath this canopy type. In Teipan, *Oreopanax* displayed a significant negative association between saplings and adult trees (Mejía-Domínguez 2006), in agreement with a higher survival of this species in darker (more mature) environments reported for similar forests in nearby Chiapas State (Quintana-Ascencio *et al.* 2004).

We can conclude that taxonomic identity of canopy trees is related to particular conditions in the forest understory, but the resulting environmental variation linked to the different canopy species has specific effects on the sapling community (and thus in the forest regeneration process) in some cases only. We claim that in searching for causes of a heterogeneous understory environment where the recruitment of a larger array of species is possible, given their differences in regeneration niche (Grubb 1977, Poorter 2007, Queenborough *et al.* 2007a), a deeper examination of canopy species effects is warranted.

ENVIRONMENTAL HETEROGENEITY IN THE FOREST UNDERSTORY.—Environmental heterogeneity is an implicit component of all ecological studies, but its analysis has preferentially concentrated on its consequences than on its causes (Hutchings *et al.* 2000, Pickett *et al.* 2000, Beckage & Clark 2003). Local heterogeneity has been generally attributed to an uneven distribution of resources and microclimate, often related to fine-scale microtopographic variations (Harper 1977, Bellingham & Tanner 2000, Dalling & Hubbell 2002, Robert & Moravie 2003, Kubota *et al.* 2004). The role of living organisms as sources of heterogeneity has been less emphasized, however, in contravention to the suggestion that many species should be considered ‘ecosystem engineers’, given their significant ability to produce environmental modifications (Jones *et al.* 1994, Pickett *et al.* 2000, Gutiérrez & Jones 2006). In fact, there is ample evidence that the effects of these biotic sources of environmental variability may be either positive or negative, but that they usually result in an increased heterogeneity compared with that uniquely related to abiotic factors (Jones *et al.* 1997, Pickett *et al.* 2000, Eviner 2004, Barbier *et al.* 2008).

The few efforts to examine the role of the specific identity of canopy trees in diverse forests have largely restricted to the analysis of the effects of species composition on litter or soil properties (Ayres *et al.* 2009, Cardelús *et al.* 2009, Kamei *et al.* 2009, McCarthy-Neumann & Kobe 2010), and have been mostly conducted in species-poor forest plantations (Parrotta 1995, Powers *et al.* 1997). The role of canopy trees as drivers of environmental heterogeneity in a forest understory has also been analyzed from the perspective of biological neighborhoods, both in tropical and temperate forests (Canham *et al.* 2004; Uriarte *et al.* 2004, 2005; Comita & Hubbell 2009), or with a nurse or facilitative plants approach (Holmgren *et al.* 1997; Flores & Jurado 2003; Gómez-Aparicio *et al.* 2004, 2005b), both of which acknowledge the ecological relevance of species effects. Some differences, however, exist between these two approaches and the study of the general effects of single canopy species. The analysis of biological neighborhoods, mostly restricted to species-rich communities, involves the examination of the effects of multi-specific sets (*i.e.*, comparisons of heterospecific vs. conspecific neighborhoods, distance to neighbors, and size effects; Hubbell *et al.* 2001; Uriarte *et al.* 2004, 2005; Canham & Uriarte 2006; Queenborough *et al.* 2007b), while the nursing role of plants is often assessed in terms of its potential positive effects on nonconspecifics (Gómez-Aparicio *et al.* 2004, 2005b). By dissecting the effects of four cloud forest canopy species and comparing them with those of mixed canopies, we were able to identify more readily the particular role played by each species (including both positive, negative, and neutral effects *sensu* Wiegand *et al.* 2007), and to relate it to the particular ways in which it modifies the environment in its surroundings.

Microclimatic factors may vary every meter in the forest understory (Nicotra *et al.* 1999, Montgomery & Chazdon 2002, Gómez-Aparicio *et al.* 2005a). Our results agree with this finding because we also documented a large environmental heterogeneity in the understory of our study forest. Nonetheless, a parallel analysis conducted by our group revealed the existence of relatively homogeneous patches, with a mean diameter of *ca* 13 m; interestingly, this figure closely matches the mean (± SE) crown diameter of canopy trees in this forest (11.2 ± 4.5 m, for trees > 15 m tall; N. Mejía-Domínguez, unpubl.). This coincidence suggests that the resolution scale of environmental heterogeneity in the forest understory is related to the physical structure of the forest upper canopy, whose variation could be partly attributed to individual species effects.

CANOPY SPECIES EFFECTS ALONG GRADIENTS OF OVERSTORY TREE DOMINANCE.—Plant diversity is larger in tropical forests than in their temperate counterparts (Dirzo 2001). Nonetheless, in the tropics steep gradients in the degree of canopy dominance are well-known, ranging from very diverse forests where no single tree has real dominance, to strongly monodominant forests (Hart 1990, Richards 1996). Thus, one may ask how generalized are the micro-environment-mediated species effects on the sapling community dynamics. At one end, monodominance clearly implies that specific identity loses relevance, so that the environmental heterogeneity within such a forest must be explained in terms of inter-individual variations in canopy architecture or tree size, of the particular gap dynamics of that forest, or other local environmental variations (such as topography) (Runkle 2000). Comparisons of two or more single-dominated communities of different species (in particular of monodominant forest plantations), however, have shown very clear species effects on woody species recruitment patterns (Parrotta 1995, Powers *et al.* 1997), a result of great importance in efforts to restore native tree diversity in degraded areas affected by deforestation (Castro *et al.* 2002, Padilla & Pugnaire 2006).

Increasing the number of species to two is sufficient to generate heterogeneity associated to this taxonomic/ecological factor and, as indicated by our results, the successive inclusion of more species may gradually increase the magnitude of this effect, as long as they prove to affect differentially at least one microenvironmental component. Our study forest comprises many more canopy species than the limited set examined by us (*ca* 40; Mejía-Domínguez *et al.* 2004), and yet we were able to locate points across the forest understory where we could associate the microenvironment to a single canopy species (not necessarily to a single tree). It is conceivable that in much more diverse forests, such as those reported by Gentry (1988) for the Peruvian Amazonia and by Condit *et al.* (1996) for the Malay Peninsula, the individual effects of the different species tend to be confounded due to strong multiple-crown overlap.

Under these circumstances, the biological neighborhood approach may be of greater value in analyzing the causes of understory heterogeneity. Even so, one cannot overlook the fact that the species effects lie at the heart of any biological neighborhood (Wiegand *et al.* 2007), and that the combined effects of various species, probably involving synergisms yet to be studied, plays an important role in the natural regeneration and diversity maintenance of species-rich tropical and subtropical forests.

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CAPÍTULO IV

PATRONES ESPACIALES EN LA LLUVIA DE SEMILLAS, EL BANCO DE SEMILLAS Y EN LAS PLÁNTULAS EN EL SOTOBOSQUE DE UN MESÓFILO DE MONTAÑA: UN ENFOQUE DE VECINDARIO

Mejía-Domínguez, N.R., Meave, J.A., Gómez-Aparicio, L. & García-Solares, Y. Spatial patterns in the seed rain, seed banks and saplings in a cloud forest understorey: a neighborhood approach.

Spatial patterns in the seed rain, seed banks and saplings in a cloud forest understorey: a neighborhood approach

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Abstract

Integrating and combining information on seed dispersal and seedling establishment is needed in order to understand the natural regeneration process in forests, which ultimately influences biodiversity maintenance in a plant community. Neighborhood models analyze both processes as a function of the spatial distribution of canopy individuals, describing specific patterns of seed and seedling shadows on the forest floor. Our goal was to assess spatial patterns of seed rain, seed bank and seedlings, relative to local basal area and mean distance to individuals, for *Cornus disciflora*, *Oreopanax xalapensis*, *Chiranthodendron pentadactylon*, and *Quercus laurina*. This was achieved by means of a neighborhood analysis. Also, we assessed the role of these patterns in the structuring of the tree community in a cloud forest of southern Mexico. Our results reveal clear between-species differences regarding the spatial dispersion patterns of seeds and seedlings, and thus their contribution to community structuring. Individual trees of *Cornus disciflora* were associated to larger seed densities in their vicinity, but this species appears to be facing recruitment limitations, perhaps due to environmental factors, so that this species is predicted to be replaced in the future by *Oreopanax xalapensis*. In turn, *Chiranthodendron pentadactylon* seems to be limited in seed production and in seedling recruitment, so that individuals of this species are not expected to be replaced by conspecifics. Conversely, in spite of the low seedling density of *Quercus laurina*, which could to be caused by dispersal and recruitment limitations, the latter due to an intense predation on seeds, it is conceivable that individuals of this species could be replaced by conspecifics. *Orepanax xalapensis* was the only species for which no demographic limitations (i.e. no limited establishment and no increased mortality) were detected: its regeneration strategy consists in the formation of a seedling bank under the crowns of adult trees of almost every species, so that this species seems to be in advantage in this forest. The examination of the regeneration process of each canopy species in the studied cloud forest through neighborhood models offers a broader overview of the regeneration process, providing evidence for the heterospecific replacement as a forest diversity maintenance mechanism. The examination of variables related to microsite characteristics and variables related to seed predation into the analysis remains as a task for the future.

Key words: diversity maintenance, *Chiranthodendron pentadactylon*, *Cornus disciflora*, natural regeneration, neighborhood analysis, *Oreopanax xalapensis*, *Quercus laurina*, seedling recruitment.

Introduction

Integrating and combining information on seed dispersal and seedling establishment is needed in order to fully understand the natural regeneration process in forests, which ultimately influences biodiversity maintenance in a plant community (Hurtt & Pacala 1995; LePage *et al*. 2000; Hubbell *et al*. 2001; Levine & Murrell 2003). The variations of local dispersion patterns of species and of seedling establishment is a major driver of the structuring of a tree community, as they influence the colonization of new habitats. This has direct implications on the population dynamics of the species present in a community by limiting or promoting their establishment, and by allowing the coexistence of certain species (e.g. Dalling *et al*. 1998; Dalling *et al*. 2002; Muller-Landau *et al*. 2002; Wang & Smith 2002). In any plant community, early relationships of the recruited individuals with their previously established neighbors may determine the intensity of negative interactions, the positive ones and the indirect effects, such as microsite modification in the understory; therefore the spatial distribution of tree species has an influence on the spatial variation of the rest of the community and on some ecosystem properties (Jones *et al*. 1997; Canham & Uriarte 2006).

The spatial variability produced by distribution patterns of seeds of different species may initially define the density and the identity of those individuals that eventually will grow together. This initial seed deposition pattern depends on the abundance and spatial distribution of parent trees, their fecundity and the pre-dispersal predation, the dispersing agent (dispersal syndrome) and the dispersal distance (Schupp 1990; Clark *et al*. 1998; Levine & Murrell 2003; Nathan & de Muller-Landau 2000; Sagnard 2007). Generally, if adults are initially clumped the aggregation of seeds will also be very strong and the dispersal distance is likely to become smaller (Van Ulft 2004; Nathan & Muller-Landau 2000). The relative importance of each process (seed dispersal, seed germination, seedling establishment) may be variable according to the ecological requirements and the biological traits of each species, as well as to the total density and composition of the seedlings community (Jordano & Herrera 1995; Clark *et al*. 1999; Wenny 2000).

Several hypotheses have been put forward regarding the advantages of seed dispersal and its contrast with the recruitment of early stages, and as to how both processes may contribute to community structuring. For example, Janzen-Connell's escape hypothesis argues that dispersal makes it possible for seeds and seedlings to escape from density-dependent mortality due to pathogen attacks, herbivory and the intraspecific competition between seedlings growing together under the crown of a single parent tree (Wilson & Traveset 2000; Nathan *et al*. 2000; Martin & Canham 2010). Similarly, the hypothesis of directed dispersal is defined as a disproportionately large arrival of seeds to favorable microsites for recruitment (Howe & Samllwood 1982; Wenny 2000). Conversely, there is compelling evidence for the role of limited dispersal as a factor affecting post-dispersal recruitment success and the consequent seedling spatial distribution. In this context, dispersal limitations among some species enable little competitive species to be capable of pre-empty available microsites due to limitations in the transportation of propagules of other species (Beckage & Clark 2003; Veldtman 2005).

Spatial patterns of seeds and seedlings on the ground can be assessed through the construction of models that include the principal factors affecting propagule dispersal: seed production (fecundity), density of parental trees and distance from them (Clark & Ji 1995; Ribens *et al*. 1994; Nathan & Muller-Landau 2000). Some individual-based models incorporate the spatial distribution of the species, as they attribute to this distribution the regulation of the spatial variation of the individuals present in the community, thus condensing neighborhood dynamics theory (Pacala *et al*. 1996; Law & Dieckmann 2000). Forest dynamics models incorporate this kind of information with the aid of increasingly more refined statistical procedures that describe the specific patterns of seed and seedling shadows in the forest; also, these models allow one to evaluate the role of these patterns in the regeneration dynamics (Ribbens *et al*. 1994; Canham & Uriarte 2006). Numerous methods are available to determine the best-fit curves or individual dispersion models (Greene & Calogeropoulos 2002), among which the method requiring fewer variables is the modeling approach promoted by Ribbens *et al*. (1994). Under this approach, methods of maximum likelihood are used to estimate the terms of the different dispersion functions, considering the spatial dispersion and the sizes of potential parental trees surround each sample, given a certain neighborhood radius (Greene *et al*. 2004).

The goals of this study were: (1) to evaluate spatial patterns of the seed rain, soil seeds banks and seedlings relative to the basal area, and the mean distance to parental trees, by using a neighborhood analysis with different neighborhood radiuses and three different dispersion functions, and (2) to assess the role of these patterns in the natural regeneration, and consequently in the structuring of the tree community in a cloud forest.

Methods

Study area

The study was conducted in the cloud forest of Teipan, Oaxaca, in the Southern Sierra Madre, México

(16°15´ N; 95°58´ W), at an elevation ranging between 2200 and 2500 m a.s.l. Mean annual precipitation ranges between 1400 and 1500 mm and is highly seasonal, as 96.8% of the rainfall concentrates from May and October. Mean annual temperature is *ca*. 12.3 ºC, with the coldest month being January (lowest monthly mean of 8ºC) and the warmest being May (highest monthly mean 26ºC) (IG-UNAM 1970; García 2004).

In Teipan the cloud forest consists of two readily distinguishable vertical strata: an upper canopy that spreads from 11 to 32 m, and a lower canopy or sub-canopy (4-10 m). The upper canopy is species rich but *Cornus disciflora* is the clear dominant, followed closely by *Quercus laurina*, whose individuals reach the largest heights and diameters. Conversely, the sub-canopy is almost completely dominated by two species, namely *Psychotria galeottiana* and *Miconia* sp., both of which are homogeneously spread across the study plot. Other species contributing substantially to forest structure are *Cleyera theaeoides*, *Ternstroemia tepezapote*, *Oreopanax xalapensis*, *Chiranthodendron pentadactylon* and *Clethra mexicana* (Mejía-Domínguez *et al*. 2004).

Field work

In 2002 a permanent 1-ha plot was established 1 km north of Teipan. All individuals with DBH 2.5 cm were censused and measured yearly between that year and 2007. In 2004 began the monitoring of the sapling community in 100 systematically distributed 1-m^2 quadrats; their number was increased to 153, by adding new quadrats chosen to represent the neighborhoods of the four study species listed further below. In these quadrats all saplings of tree and shrub species with heights ≤ 50 cm but already having shed cotiledonary leaves were recorded in May 2007. Saplings were individually identified to species and tagged, and the height and grid-location recorded, both in the quadrat. In subsequent censuses (August, November, February 2007, and May 2008) the presence and sizes of these saplings was recorded again, together with the data for newly recruited saplings.

In May 2007 50 traps were placed across the 1-ha plot to capture seed rain of tree species. Each trap was 1 m height and 50 cm in diameter, and included a nylon permeable fabric cone 80 cm deep. Seeds fallen in the traps were manually retrieved and separated in the dates of subsequent sapling censuses. All data so gathered for all seasons were combined to represent the yearly rainfall by species.

To describe seed bank attributes and their spatial variability, 100 soil samples obtained with a soil sampler 5.5 cm deep and 7 cm in diameter, taken in a randomly selected subset of all quadrats. Soil samples were air-dried for the manual extraction and separation of the seeds, and their subsequent taxonomic determination, which was achieved by morphological comparison with a seed collection of the locality. Soil was sampled in the dry and the rainy season of 2007 and 2008 to account for seasonal variability, but samples fro each quadrat were combined to represent yearly local seed bank traits.

Spatial patterns of seed rain, seed bank and saplings were analysed for the following four species: (1) *Cornus disciflora* DC. (Cornaceae), the species with the largest Relative Importance Value (RIV) based on previous censuses (the sum of relative density, basal area and frequency); (2) *Quercus laurina* Bonplan (Fagaceae), which ranked second in RIV due to large tree sizes despite a relatively low density; (3) *Oreopanax xalapensis* (Kunth) Decne. & Planch. (Araliaceae), which ranked sixth in the canopy but dominating in the sapling community; and (4) *Chiranthodendron pentadactylon* Larreat. (Sterculiaceae), which ranked eight in RIV but selected based on distinct leaf characteristics, including size, toughness and decomposability, which could affect light conditions and litter properties on the soil, and eventually seedling establishment. For the first two species, a zoochorous syndrome inferred from their diaspore morphology suggests that small mammals disperse their seeds; the ornithochorous syndrome of *Oreopanax xalapensis* indicates birds as the most likely dispersal vector (Camacho-Cruz *et al*. 2000), whereas for *Chiranthodendron pentadactylon*, its dehiscent capsules reflect an anemochorous syndrome and point out to wind as its dispersal vector. Henceforth these species will be referred to by the generic epithets only.

Data analysis

Measuring from the spatial location of each 1-m^2 quadrat in the 1-ha plot where the sapling community, the seed rain and the seed bank were assessed, six neighbourhood radiuses were defined (5, 10, 13, 15, 25 and 50 m). The 5-m neighbourhood was selected under the expectation that no model would be good for this distance given that tree crowns are larger on average. The 25- and 50-m radius neighbourhoods have been frequently used in forest communities, and the selection of the 10-, 13- and 15-m radius neighbourhoods was based on the results of a previous study indicating these as relevant distances in the spatial structuring of the sapling community and the physical micro-environment in this forest (Mejía-Domínguez *et al*., in press). As the precise location of each adult tree of the four focal species was known, we were able to calculate basal area, mean distance to trees and basal area over this distance for each sampling point, for each species, and for each neighbourhood radius, by means of the TreeNeighborhoods (Canham 2006) and MLAGUI (Gómez-Aparicio 2010) softwares.

We used likelihood methods and model selection (Johnson and Omland 2004, Canham and Uriarte 2006) for analysis of our data. Following the principles of likelihood estimation, we estimated model parameters that maximized the likelihood of observing the seed rain, seed bank and sapling data measured in the field given a suite of alternate models. Models were fitted independently for each combination of the four tree species and three dependent variables studied. Alternate models differed in (1) the independent variable considered (basal area, distance, or basal area/distance to neighbouring trees), (2) the size of the neighbourhood (5, 10, 13, 15, 25 or 50 m), and (3) the form of the function (Gaussian, Weibull, lognormal). This gives a total of 64 potential models for each combination of species and dependent variable.

In the case of sapling density, we also adjusted the same type of models to the values of the three independent variables measured for the adults each of the three remaining species; this could be done for *Oreopanax* and *Quercus*, the only two species with saplings recorded in the study.

We fitted the following functions:

Gaussian $$y(x) = a * \exp - \frac{1}{2}\left(\frac{x-b}{c}\right)^2$$

Weibull $$y(x) = a * \exp - bx^c$$

Log-normal $$y(x) = a * \exp - \frac{1}{2}\left(\log \frac{x-b}{c}\right)^2$$

where: a, b and c are the parameter to be estimated, and *x* is the independent variable.

Although these three kinds of models have been frequently used in the analysis of neighbourhoods and dispersal patterns, there is no strong evidence indicating that one of them is more able to model these processes better than the others.

We estimated function parameters through the maximum likelihood approach with the nlme (Ribbens 1994), and the likelihood and neighlikelihood (Canham & Uriarte 2006) libraries in the R package (R Development Core Team, 2010). Models for *Oreopanax* seed rain and seed bank were fitted by using a "zero-inflated" Poisson distribution (Rathbun and Fei 2006). The most parsimonious models were selected through the Akaike Information Criterion (AIC), for each combination of response and independent variables by species.

Results

Spatial patterns of the seed rain

There were few coincidences among the study species regarding the neighbourhood radiuses for which the best-fit models were obtained, as well as the type of functions involved in these models. In terms of neighbourhood radius, only in the case of *Quercus* the best-fit model was made for the 50 m radius; the best-fit models for the remaining three species involved much smaller radiuses (*Chiranthodendron*, 25 m; *Cornus*, 15 m; *Oreopanax*, 10 m, Table 1). Similarly, there were obvious discrepancies in terms of the best-fit functions. In the case of *Chiranthodendron* this response variable was best modelled as a function of basal area over mean distance with the Weibull function, with seed rain density being inversely related to basal area and distance (Fig. 1b). The best-fit models for *Cornus* and *Quercus* involved the log-normal function, and basal area of adult conspecifics as predictor variable (Figs. 1c and 1a). For *Quercus* seed rain density peaked (> 50 seeds/m^2) at a basal area over mean distance ratio of 0.2 (Fig. 1a). Finally, in the case of *Oreopanax* the best-fit model of its seed rain density involved a Gaussian function, with seed rain density growing exponentially (> 140 seeds/m^2) as basal area increased (Fig. 1d). For this variable, the best-fit model for this species had the highest R^2 value (0.60).

Spatial patterns of the seed bank

As was the case with the previous response variable, the neighbourhood radiuses for which the best-fit models were obtained differed. Both for *Quercus* and *Chiranthodendron* the neighbourhood radius for which the best-fit models were constructed was 25 m, but for *Oreopanax* and *Cornus* it was 50 m (Table 2). In turn, the most common function included in the best-fit models was log-normal but for *Oreopanax*, whose best-fit model was shaped after a Gaussian function (Table 2). Seed bank density of *Cornus* was best modelled as a function of the mean distances to its conspecifics, describing a Gaussian curve with a maximum seed bank density at ca. 30 m (Fig. 2c). In the case of *Chiranthodendron*, seed bank density was a function of mean distance; this function included many zero or near zero values, and had a maximum of 0.5 seeds/m^2 at a distance of around 13 m (Fig. 2b). The graphic representation of the *Quercus* seed bank best-fit model shows that seed bank density peaked (2 seeds/m^2) at a basal area/mean distance ratio of 0.5 (Fig. 2a). Similarly, the seed bank density of *Oreopanax* described a Gaussian curve with a peak of 3.2 seeds/m^2 at a basal area/mean distance ratio of 0.2 (Fig. 2d).

Spatial patterns of saplings

Sapling density was modelled not only for those structural variables defined by conspecific trees, but also for the remaining of the study species. This resulted in one best-fit model for each specific neighbourhood (i.e. those defined by its conspecifics and by all heterospecifics) and for each species, but this procedure could be applied in the case of two species only (*Oreopanax* and *Quercus*; a total of eight models). Half of them included a log-normal function, and these were followed by those models based on Gaussian functions (three models), whereas only model was fit after the Weibull function (Table 3). Similarly, the best-fit models were obtained for a range of neighbourhood radiuses, from 50-m (three models) to 13-m radius (one model), with the remaining four models being constructed for radiuses intermediate between them (Table 3). *Quercus* sapling density was best-modelled as a function of basal area of conspecific trees (Fig. 3a). In the case of *Oreopanax*, sapling density was best modelled as a function of mean distance to *Quercus* trees (Fig. 4a).

The responses of sapling density of *Quercus* regarding each neighbourhood showed that the largest numbers of saplings corresponded to the largest basal area values of its conspecifics and for low (near zero) basal area values of *Chiranthodendron* and *Oreopanax* (Fig. 3a, b, d). Mean distance to *Cornus* affects sapling density of *Quercus*, while describing a Gaussian curve that peaks at around 35 m (Fig. 3c). Nonetheless, in all cases *Quercus* sapling density is lower than 1 ind./m^2, in strong contrast with the much higher densities of up to 150 ind./m^2 of *Oreopanax* predicted by some models. Yet these large modelled densities were by no means the rule, as the predicted *Oreopanax* sapling density was even more variable than that of the other species. High densities for this species were only predicted when mean distance to *Quercus* individuals was used a predictor variable, a relationship that took a negative exponential shape, with the largest *Oreopanax* densities occurring at around 5-10 m from oaks (Fig. 4a). Interestingly, *Oreopanax* densities showed very negative responses to other *Oreopanax* variables, so that densities as low as 2 ind./m^2 were predicted to occur at low adult conspecific basal area, a density value very similar to that predicted to occur (2.6 ind./m^2) at around 5 m^2/ha of basal area of *Chiranthodendron* (Fig. 4b and d). A very similar behaviour was observed when density was modelled as a function of mean distance to adult *Cornus* trees (Fig. 4c).

Models and functions

After describing the information related to the various models for each species and for each phase of the life cycle, it is worth pointing out patterns related to the predictor variables involved in the best-fit models. Overall, the independent variable that had the highest ability to predict both seed rain and seed bank densities was the basal area/mean distance ratio, and only in one case was the basal area *per se* the best predictor of these two response variables (Table 1 and 2). Conversely, basal area turned out to have the highest ability to predict sapling density, whereas the combination of this variable with distance (i.e., basal area/mean distance ratio) was in no case the best predictor (Table 3). Among all best-fit models, the function most commonly used was the log-normal, although the Gaussian function followed close (Table 1-3). Finally, although the best-fit models were very heterogeneous regarding neighborhood radius, no model constructed for the 5 m radius was among the best-fit ones (Table 1-3).

Linking seed rain, seed bank and sapling spatial patterns

So far we have presented separately the results of the analyses of the spatial distribution of the different processes that ultimately determine the spatial pattern of sapling establishment in this forest. It is clear, however, that the final spatial pattern of the sapling subpopulation, and eventually of the adult subpopulation, results from the way in which these processes are linked with each other, as each of them may be driven by a particular relationship with the adult conspecifics. A certain abiotic or biotic factor may be innocuous during one phase of the life cycle but have a strong influence on another one; this prevents the existence of consistent relationships of the spatial patterns of these phases with the adult conspecifics. Therefore, several possibilities emerge, ranging from those cases in which all analyzed phases show the same distributional pattern, to those in which each phase is characterized by a different pattern (with all intermediate combinations).

Each of the four studied species showed a different pattern regarding this issue, with the ultimate responses being the presence or the absence of saplings in the plot. For *Oreopanax*, a species with numerous individuals in the sapling stage, models predicted a large sapling density in the vicinity of *Quercus* and *Cornus*, but a lower sapling density in the presence of its conspecifics; the latter relationship is consistent with the inverse relationships described for the previous phases of seed rain and seed bank. Similarly, for the seed rain and seed bank of *Quercus* inverse relationships with conspecific basal area were also observed; nonetheless, sapling density was directly related to the presence of conspecific trees. Moreover, the models predicted that the number of *Quercus* saplings is inversely related with the basal area of adult individuals of *Oreopanax* and *Chiranthodendron*, and directly related to the distance to *Cornus* individuals.

For the other two species no saplings were recorded in the study plot, making it impossible to evaluate any relationship between this and the previous phases (seed rain and seed bank), and its conspecifics. However, the relation between the distribution pattern of the seed rain and the seed bank revealed important between-species differences. *Chiranthodendron* seed densities, both in the rain and in the bank, were inversely related to conspecific basal area and distance, although seed density in the bank was lower than predicted by the model for seed rain. In contrast with this consistency, the distribution pattern of seeds in the bank of *Cornus* was opposite to that of its seed in the seed rain, i.e., in places with higher *Cornus* densities we found a larger number of seeds from the seed rain relative to the number of seeds in the bank.

Discussion and conclusions

Natural regeneration and replacement of canopy species

The analysis of the specific seed distribution and sapling recruitment patterns is crucial to understand the complexity of the natural regeneration process in any forest, and to be able to formulate hypotheses regarding community structuring and the replacement of species by each other (Dalling *et al*. 2002; Muller-Landau *et al*. 2002; Wang & Smith 2002). A neighborhood analysis allows to include the spatial distribution of canopy trees as a relevant component of the variation observed in the distribution patterns of new individuals, and to define potential early relationships between species. In the cloud forest of Teipan, the observed seed and sapling distribution patterns strongly suggest that in most cases there will be a heterospecific replacement, that is, that species will not be replaced by individuals of the same species, with one exception. It is important to acknowledge that local interactions between parental trees and individuals in early stages of development may by obscured by the action of birds dispersing seeds of the studied species (M. González-Espinosa, pers. com), as this would contribute to the "spatial dilution" of the observed patterns, in agreement with the relatively low percentage of the variance that was explained by some models.

Quercus is the only species that seems to guarantee its conspecific succession, as its saplings establish almost exclusively in the presence of its parent trees. Conversely, it is likely that Cornus will not be replaced in the future by individuals of the same species, but that it will be replaced by any species having the attribute of being shade tolerant. A similar situation was observed for Oreopanax, since its saplings display a clear "evasive behavior " from conspecific trees. Finally, Chiranthodendron, whose presence seems to be a limitation for the establishment of new individuals, limits even those of its own species, suggesting that no conspecific replacement will take place but without providing any clue as to the identity of potential successors.

Quercus is a clear example of the fact that seed predation may limit the establishment of new individuals of the same species as a consequence of density-dependent (basal area) seed-predation (basal area of parent trees) (Bustamente & Simonetti 2000; Harms 2000). *Quercus* seeds are extremely attractive to granivores (Herrea 1995; Hulme 1998), and apparently when these seeds reach the soil become even more vulnerable to predation, so that the interaction with conspecific adults becomes more intense in this phase. The hypothesis that predation is responsible for the low seed densities near parent trees is supported by the fact that the "protected" seeds that were artificially introduced germinate and become established (M. Mejía-Domínguez unpublished data). Thus, seeds leave the seed bank not via germination. This fact further suggests that for *Quercus* the environmental conditions in the understory neither seem to restrict the germination of its seeds nor affect the establishment of its saplings in the presence of conspecifics. Moreover and according to our predictions, *Quercus* saplings are located far away of other canopy species such as *Oreopanax*, *Cornus* and *Chiranthodendron*, which suggests the possibility that *Quercus* may only be able to replace individuals of the same species, thus guaranteeing its replacement.

Apparently without limitations, and at least as far as seedling emergence, *Oreopanax* forms a sapling bank under the adult individuals of almost any species. Nonetheless, for *Oreopanax* we found strong evidence for the Janzen-Connell phenomenon between saplings and adults, as well as between seeds and adults, as both stages tend to “stay away” from their conspecific adults, more precisely from those sites with larger basal area (Wright 2001; Hansen *et al*. 2008). Thus it may be inferred that *Oreopanax* saplings will not succeed those canopy individuals belonging to the same species, although its sapling bank forming strategy is likely to allow this this species to succeed other dominant species such as *Cornus*, and even *Quercus* under certain circumstances.

For *Cornus*, the lower seed bank density compared to seed rain density in presence of its conspecific trees, suggests that seed predation took place on the soil more intensely under the canopies of parent trees (Janzen 1970; Hansen *et al*. 2008). The absence of *Cornus* saplings is apparently explained by understory environmental conditions, which apparently are negative for its establishment. The closed canopy of the forest in Teipan, which created low irradiation in the understory (Mejía-Domínguez *et al*. 2011), contrasts with the better-lit conditions reported for the establishment of *Cornus* (Saldaña-Acosta 2009). Moreover, in an experiment in which *Cornus* seeds were introduced and protected against predators that were conducted in the same research plot, no seed germinated (M. Mejía-Domínguez unpublished data). Thus, for *Cornus* the factor limiting sapling establishment related to understory environmental conditions suggest that this species will no be replaced by conspecifics, but by other shade-tolerant species such as *Rapanea juerguensenii* or *Zinowewia* sp., both of which have been recorded under *Cornus* canopies (Mejía-Domínguez), or even by *Oreopanax*, whose saplings preferentially establish in area dominated by *Cornus* crowns. Interestingly, in other study *Cornus* was observed to be able to establish in the cloud forest understorey, although a negative relation was found between sapling density and adult tree size (Baraud-Macías *et al*. submitted).

Chiranthodendron, a species having low seed rain and seed bank densities, is likely to have a limited seed production owing to competition for resources between parent trees, which in turn is due to high densities and the consequent agglomeration of adult trees (Clark & Ji 1995; Herrera 1998; Sagnard 2007), or perhaps due to an increased fruit and seed predation, for the same reason (Gómez *et al*. 2003). However, it seems more likely that the scarcity of *Chiranthodendron* seeds is related to the dispersal vector (wind) that disperses seeds to large distances (Breedlove 1986). Moreover, *Chiranthodendron* seeds seem to require other environmental conditions, e.g. a larger amount of solar radiation, for its germination and subsequent establishment. The absence of saplings in the vicinity of *Chiranthodendron* is probably related to the deep litter layer that accumulates under its canopy, which seems to prevent their establishment (Mejía-Domínguez *et al*. 2011), and even prior to that, to the absence of seeds. For *Chiranthodendron* it is difficult to make predictions about what species could replace it, as virtually no sapling of this or other species were found in the close vicinity of its adult individuals.

Generally, in the context of interactions between saplings and adult trees the effects of neighbours were more frequently dependent on basal area, and for some species the effects of conspecifics were negative and differential between seeds and saplings. For instance, *Oreopanax* is a clear example of the Janzen-Connell effect operating at all examined phases of the life cycle, but for *Quercus* this effect seems to apply for the seeds-conspecific adult's relationship only. Mean distance appears to be the best predictor of the relationships between conspecific adults and the number of seeds, as this variable seems to be mainly related to dispersal vectors in the first place (Breedlove 1986). However, the models constructed in this study do not include characteristics of the establishment microsite that could differentially affect the establishment of seedlings of different species, and these characteristics may or may not be related with parental trees or with any canopy-tree species (Pickett *et al*. 2000; Jones *et al*. 2000; Mejía-Domínguez *et al*. 2011). If canopy tree species do affect understory micro-environmental conditions, these variables could be built into the model in order a gain a better insight as to what the most real scenario is of the relationships between saplings and their conspecifics, and ultimately to increase the proportion of variation explained by the model (Uriarte *et al*. 2004; Martin & Canham 2010). In this case of Teipan, it would be convenient to incorporate into the neighbourhood analysis microsite variables, e.g. litter depth, as well as to incorporate seed predation, a process that seems to play a crucial role in this forest.

Predictions pointing to a heterospecific replacement for the dominant species in this forest suggest that the regeneration process leads towards diversity maintenance as its final consequence in the structuring of the forest, which is well beyond the simple prediction of differing structures and compositions in the future. This conclusion adds to the existing evidence about the complexity of the natural regeneration process in tropical forests and its relevance in searching for factors involved in the maintenance of their diversity.

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Table 1. Seed rain density neighbourhood models for species as function of mean distance (dist), basal area (BA) and basal area/mean distance ratio (BA/dist). CHPE = *Chiranthodendron pentadactylon*, CODI = *Cornus disciflora*, ORXA = *Oreopanax xalapensis*, QULA = *Quercus laurina*. *Zero inflated Poisson distribution. Best-fit model in bold.

Response variable	**Target species**	**Specific neighbourhood**	**Independent variable**	**Model**	**Neighbourhood radius(m)**	**AIC**	**R^2**
Seed rain density (seeds/m^2)	QULA	QULA	BA	Log-normal*	50	843.61	0.06
			BA/dist	**Log-normal***	**50**	**628.07**	**0.38**
			dist	Log-normal*	15	821.22	0.10
Seed rain density (seeds/m^2)	CHPE	CHPE	BA	Weibull*	25	97.17	0.16
			BA/dist	**Weibull***	**25**	**97.14**	**0.17**
			dist	Gaussian*	5	99.85	0.09
Seed rain density (seeds/m^2)	CODI	CODI	**BA**	**Log-normal***	**15**	**292.14**	**0.10**
			BA/dist	Log-normal*	25	299.28	0.04
			dist	Log-normal*	50	302.69	0.02
Seed rain density (seeds/m^2)	ORXA	ORXA	BA	Gaussian*	10	357.19	0.60
			BA/dist	Gaussian*	13	547.53	0.15
			dist	**Gaussian***	**50**	**353.52**	**0.43**

Table 2. Seed bank density neighbourhood models for species as function of mean distance (dist), basal area (BA) and basal area/mean distance ratio (BA/dist). CHPE = *Chiranthodendron pentadactylon*, CODI = *Cornus disciflora*, ORXA = *Oreopanax xalapensis*, QULA = *Quercus laurina*. *Zero inflated Poisson distribution. Best-fit model in bold.

Response variable	**Target species**	**Specific neighbourhood**	**Independent variable**	**Model**	**Neighbourhood radius(m)**	**AIC**	**R^2**
Seed bank density (seeds/m^2)	QULA	QULA	BA	Log-normal	25	218.66	0.08
			BA/dist	**Gaussian**	**25**	**210.62**	**0.11**
			dist	Gaussian	10	228.48	0.05
Seed bank density (seeds/m^2)	CHPE	CHPE	BA	Gaussian	5	120.01	0.16
			BA/dist	Gaussian	5	121.03	0.14
			dist	**Log-normal**	**25**	**117.12**	**0.12**
Seed bank density (seeds/m^2)	CODI	CODI	BA	Gaussian	10	819.83	0.10
			BA/dist	Gaussian	10	822.29	0.09
			dist	**Gaussian**	**50**	**790.50**	**0.10**
Seed bank density (seeds/m^2)	ORXA	ORXA	BA	Gaussian*	25	77.89	0.35
			BA/dist	**Log-normal***	**25**	**73.98**	**0.11**
			dist	Log-normal*	50	78.42	0.69

Table 3. Sapling density neighbourhood models for species as function of mean distance (dist), basal area (BA) and basal area/mean distance ratio (BA/dist) for conspecific and three species remain. CHPE = *Chiranthodendron pentadactylon*, CODI = *Cornus disciflora*, ORXA = *Oreopanax xalapensis*, QULA = *Quercus laurina*. Best-fit models for specific neighbourhood in bold. ***Best-fit model for target species.

Response variable	Target species	Specific neighbourhood	Independent variable	Model	Neighbourhood radius(m)	AIC	R^2
Sapling density (ind./m^2)	ORXA	ORXA	**BA**	**Gaussian**	**13**	**472.19**	**0.03**
			BA/dist	Gaussian	13	475.99	0.01
			dist	Gaussian	5	479.27	0.01
		QULA	BA	Gaussian	10	475.60	0.09
			BA/dist	Gaussian	5	479.68	0.02
			dist ***	**Log-normal**	**25**	**454.49**	**0.26**
		CHPE	**BA**	**Gaussian**	**25**	**468.52**	**0.08**
			BA/dist	Gaussian	25	484.65	0.03
			dist	Log-normal	50	472.51	0.07
		CODI	BA	Gaussian	25	473.34	0.03
			BA/dist	Gaussian	50	467.56	0.10
			dist	**Log-normal**	**50**	**459.62**	**0.10**
Sapling density (ind./m^2)	QULA	**QULA**	**BA *****	**Gaussian**	**15**	**154.80**	**0.12**
			BA/dist	Gaussian	15	159.59	0.06
			dist	Log-normal	25	164.74	0.03
		CHPE	**BA**	**Weibull**	**15**	**156.40**	**0.08**
			BA/dist	Weibull	25	158.63	0.06
			dist	Gaussian	25	160.26	0.07
		CODI	BA	Weibull	10	168.09	0.01
			AB/dist	Weibull	10	168.09	0.01
			dist	**Log-normal**	**50**	**163.21**	**0.03**
		ORXA	**BA**	**Log-normal**	**50**	**157.76**	**0.06**
			BA/dist	Log-normal	50	161.41	0.03
			dist	Gaussian	5	162.20	0.05

Figures

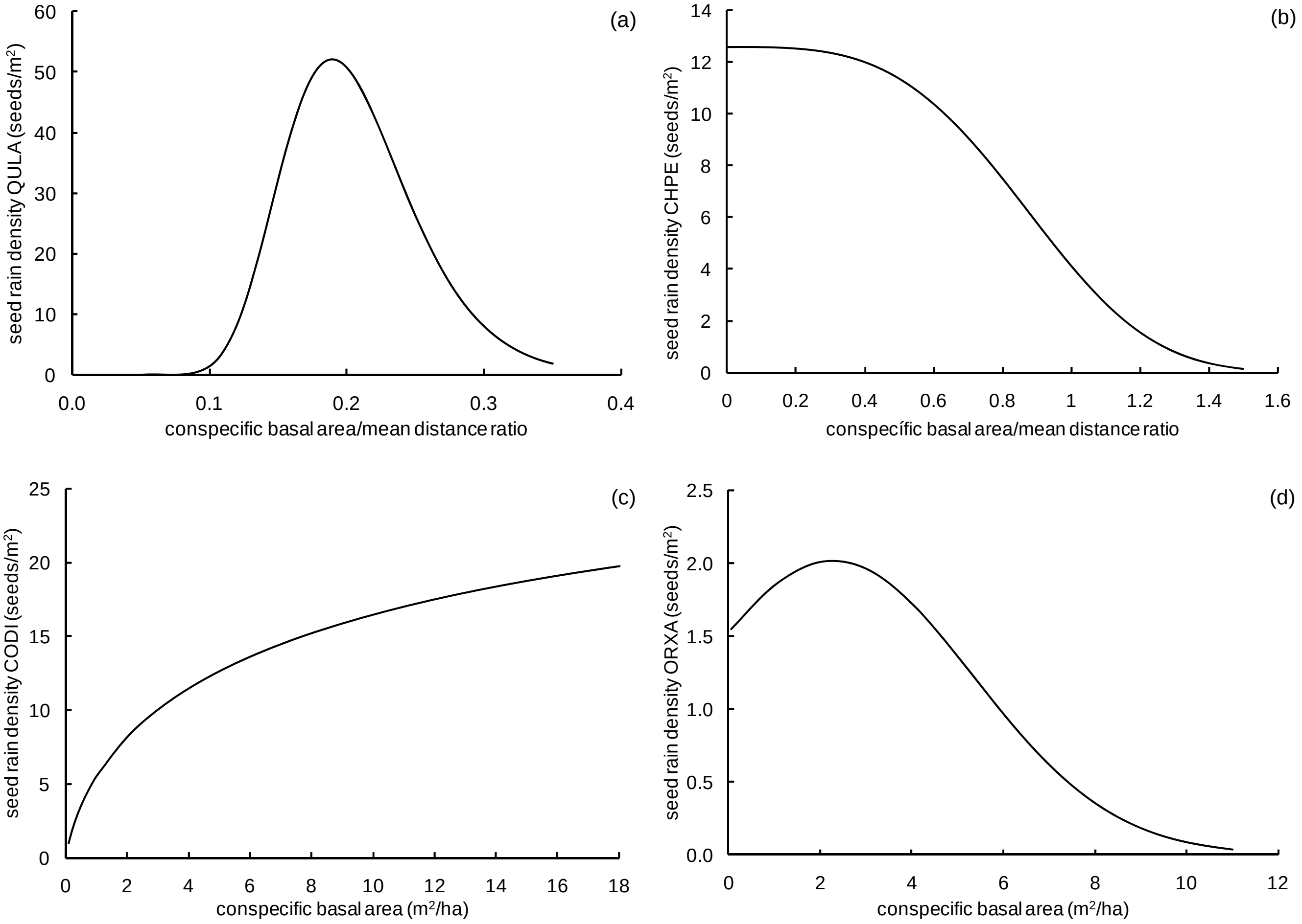

Fig. 1. Models predictions of seed rain density of: (a) *Quercus laurina* (QULA), (b) *Chiranthodendron pentadactylon* (CHPE), (c) *Cornus disciflora* (CODI), and (d) *Oreopanax xalapensis* (ORXA).

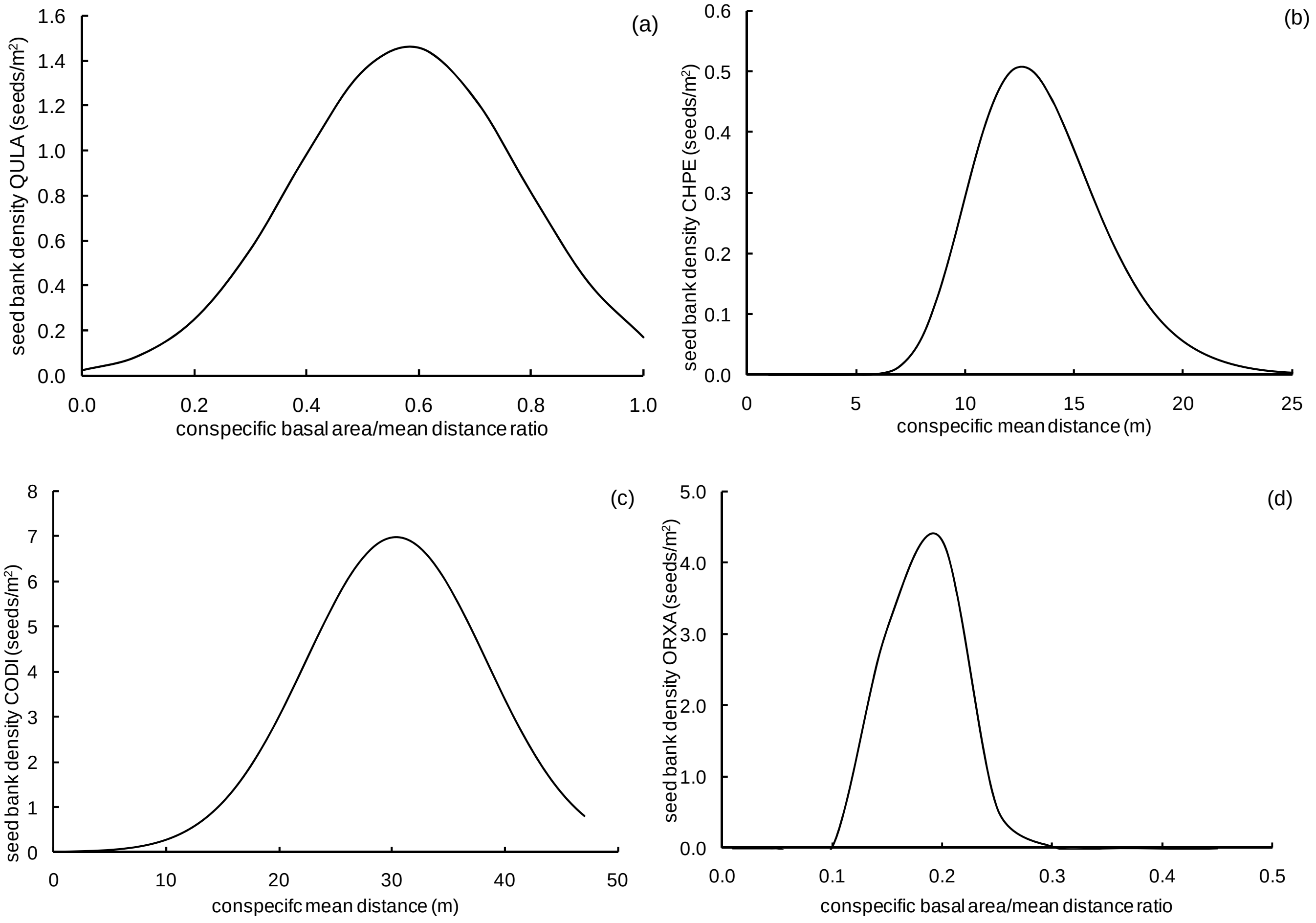

Fig. 2. Predictions of seed bank density of: (a) *Quercus laurina* (QULA), (b) *Chiranthodendron pentadactylon* (CHPE), (c) *Cornus disciflora* (CODI), and (d) *Oreopanax xalapensis* (ORXA).

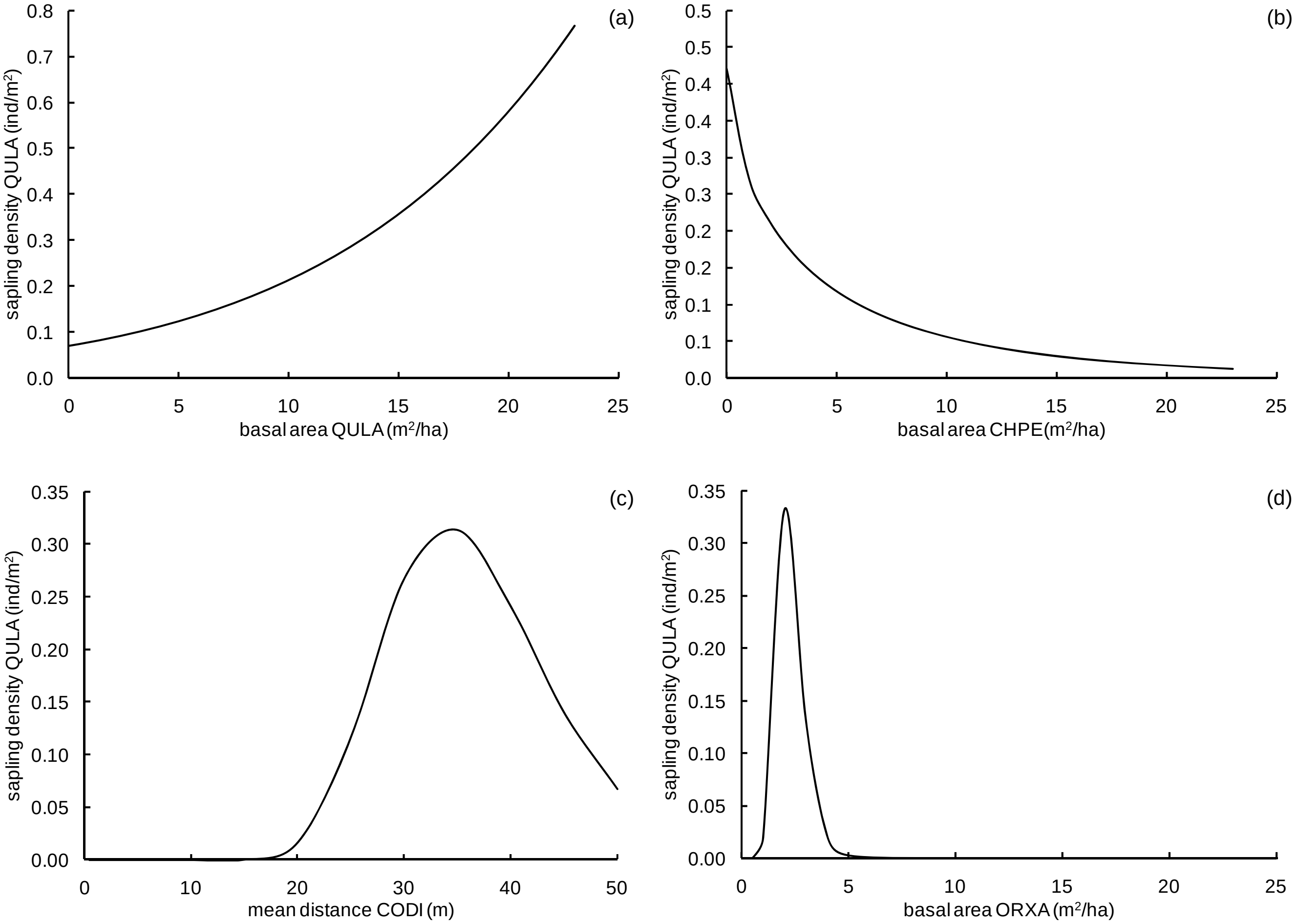

Fig. 3. Predictions of sapling density of *Quercus laurina* (QULA) with respect to (a) their conspecifics, (b) *Chiranthodendron pentadactylon* (CHPE), (c) *Cornus disciflora* (CODI), and (d) *Oreopanax xalapensis* (ORXA).

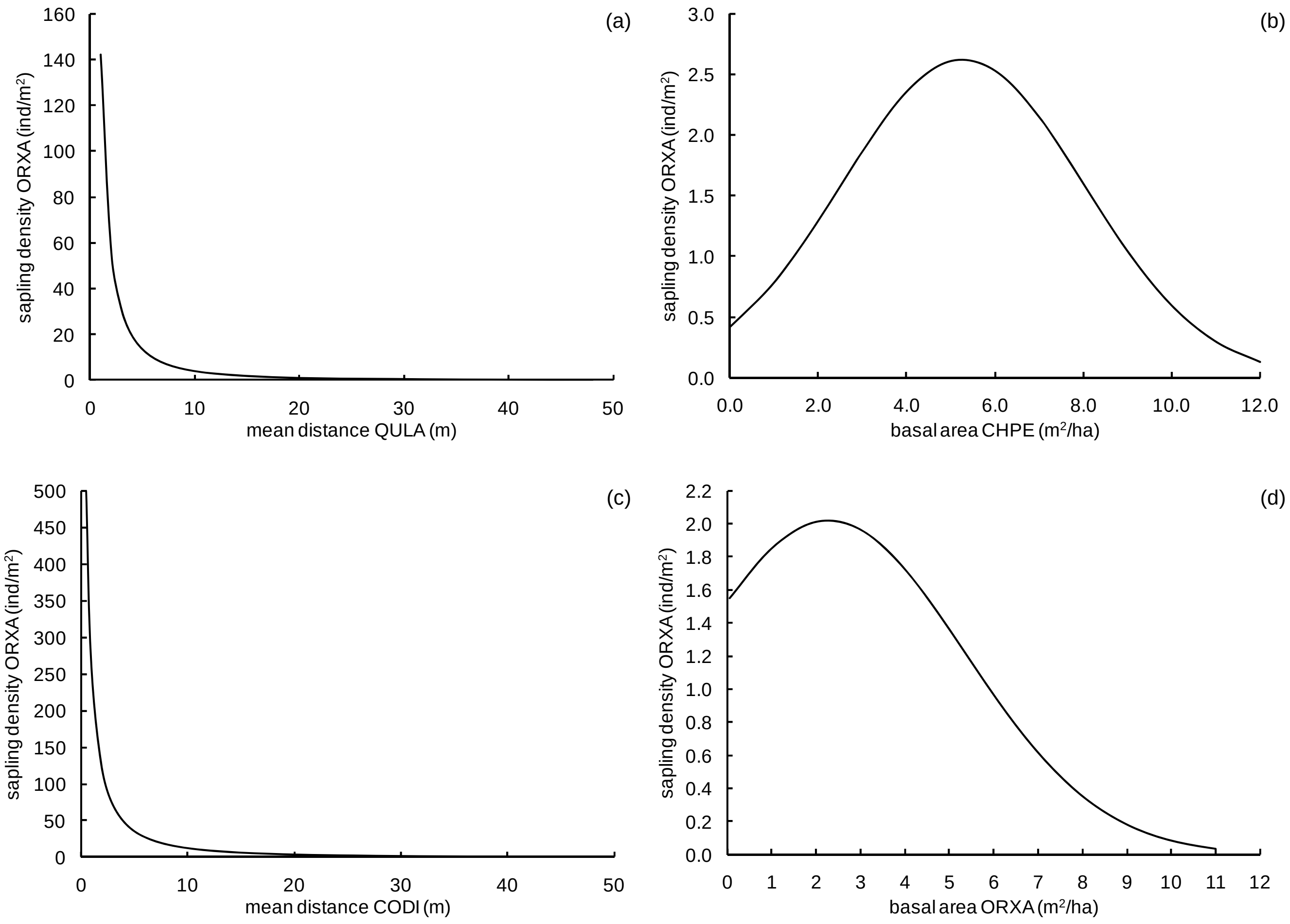

Fig. 4. Predictions of sapling density of *Oreopanax xalapensis* (ORXA) with respect to (a) *Quercus laurina* (QULA), (b) *Chiranthodendron pentadactylon* (CHPE), (c) *Cornus disciflora* (CODI) and conspecifics.

CAPÍTULO V

DISCUSIÓN Y CONCLUSIONES GENERALES

CAPÍTULO V. DISCUSIÓN Y CONCLUSIONES GENERALES

En este estudio se examinaron los procesos espaciales involucrados en la regeneración natural de un bosque mesófilo de montaña con el fin de identificar los factores específicos que participan en los procesos de estructuración de las comunidades arbóreas. La pregunta central de esta investigación se relaciona con los efectos de las distintas especies del dosel de un bosque sobre las condiciones ambientales que prevalecen en el sotobosque y la dinámica de la comunidad de plántulas, responsable de la regeneración del bosque. Para contestar esta pregunta fue necesario integrar distintas maneras de analizar los efectos de la distribución espacial de los árboles del dosel sobre el sotobosque y sobre la estructura espacial de los nuevos individuos establecidos, tratando de descubrir las posibles causas de esta estructuración. Inicialmente se hipotetizó que la identidad taxonómica de los individuos del dosel es la principal causa tanto de la heterogeneidad y la estructura espacial de las condiciones ambientales, como de la distribución de los nuevos individuos en el sotobosque. Esta hipótesis se fundamenta principalmente en dos razones. La primera es que los árboles del dosel tienen el potencial de modificar las condiciones microambientales bajo sus copas; la segunda es la posibilidad de que estos árboles sean una especie de “diseñadores” de la plantilla inicial de propágulos, al ser los productores de semillas. Sin embargo, vale la pena aclarar que durante el desarrollo de la investigación fue necesario reinterpretar la línea lógica con la que originalmente fue concebida la relación entre los objetivos particulares de cada capítulo y la pregunta central del estudio.

En estudios previos realizados en el sitio se observó que en apariencia las plántulas presentes en el sotobosque se distribuían a manera de parches discontinuos en el espacio. En este contexto espacial surgieron varias preguntas: ¿con qué factores podría estar relacionada esta distribución?, ¿sería posible que la aparente distribución desigual de las condiciones ambientales coincidiera con estos grupos de plántulas? Estas preguntas obtuvieron respuesta cuando los resultados del primer análisis, presentado en el Capítulo II, revelaron que la comunidad de plántulas (estructura y dinámica) y de los factores ambientales en el sotobosque tenían una estructura espacial, y que era posible predecir la densidad de plántulas a partir de su relación espacial con la distribución de variables ambientales. Los resultados de esta primera etapa hacia la compresión de la estructuración de esta comunidad proporcionaron indicios de que probablemente la estructura espacial de las condiciones microambientales en el sotobosque influía en gran medida en la distribución espacial de los nuevos individuos. Este primer conjunto de resultados permitó avanzar hacia la búsqueda de respuestas para la siguiente pregunta, que era ¿cuál es el factor o factores que modifican las condiciones microambientales en el sotobosque y que a la vez afectan la comunidad de plántulas? Las conclusiones de numerosas investigaciones en bosques tropicales apuntan a que el dosel del bosque es el principal factor modificador de las condiciones en el sotobosque (Hubbell *et al*. 1999, Pickett 2000, Ayres *et al*. 2009). En el Capítulo II se reporta la coincidencia de la distancia de autocorrelación espacial con el radio promedio de las copas de los árboles del dosel en el bosque de estudio, y este resultado reforzó la idea de que la distribución agregada de las plántulas podría estar relacionada con la identidad especifica de los individuos del dosel.

Los resultados del Capítulo III muestran claramente que la identidad específica de los árboles del dosel es capaz de explicar parte de la variación microambiental observada en el sotobosque de esta comunidad pero, a diferencia la expectativa inicial, no lo hace con suficiente contraste. En efecto, los resultados brindan evidencias de que cada especie tuvo un efecto diferente, pero lo más importante es que algunas especies no mostraron una verdadera diferenciación de todo el conjunto de condiciones debajo de sus copas. Además de que este resultado difirió de la esperada relación directa entre el microambiente y la identidad del árbol, también mostró que la estructuración del microambiente es un proceso más complejo y que no puede atribuirse en su totalidad a un solo factor (Pickett *et al*. 2000, Comita *et al*. 2009). Aunque la identidad específica de los árboles del dosel es un factor que causa una diferenciación “difusa” en el sotobosque, este estudio permitó proponer que este factor sí es responsable de gran parte de la heterogeneidad ambiental en el sotobosque. En última instancia, no hay duda de que se trata de un factor con una contribución significativa a la complejidad del proceso de regeneración en bosques mesófilos de montaña similares, y seguramente en bosques más diversos, pero no en bosques monodominados. A pesar de la certeza de esta conclusión, es importante enfatizar que la identidad específica de los árboles del dosel en un bosque mixto no es un factor “contundente”, y que sólo explica parcialmente las diferencias microambientales a las que están expuestas las plántulas.

La falta de relación entre los cambios estacionales de las variables ambientales y la estructura y la dinámica de la comunidad de plántulas, a pesar de los evidentes cambios en la distribución de las primeras, sugiere que las variables ambientales no afectan de manera concluyente el establecimiento de los nuevos individuos. No obstante, los resultados de las predicciones de la estructura de la comunidad de plántulas (Capítulo II) sugieren que el establecimiento está determinado por la profundidad del mantillo, debido a las limitaciones que parece representar para la germinación de las semillas y el establecimiento de las plántulas. Además, esta condición en el sotobosque tiene como causa una identidad taxonómica específica, *Chiranthodendron pentadactylon*. El mantillo es evidentemente una barrera al establecimiento de las plántulas, pero a partir de los resultados de esta investigación en este momento sólo parece indicar donde *no* se pueden establecer las plántulas de algunas especies, sin aportar más información acerca de dónde sí y sus porqués. En contraste con el papel del mantillo, el resto de las variables ambientales analizadas parecen jugar papeles poco relevantes en la configuración y dinámica de la comunidad de plántulas, devolviéndonos a la hipótesis de la falta de relación con el establecimiento de los nuevos individuos en el bosque. En este contexto, nuevamente surgen otras preguntas: ¿qué pasaría si no estuviera presente *Chiranthodendron pentadactylon* en el bosque? ¿Tendríamos menos evidencia sobre la relevancia de las variables abióticas y de la identidad específica en el proceso de regeneración?

Para complementar los análisis realizados en los Capítulos II y III, el Capítulo IV reporta los resultados de un estudio que integró un enfoque de vecindario, el cual hizo posible examinar simultáneamente los efectos de la identidad específica y de la distribución espacial de los árboles del dosel sobre la comunidad de plántulas, analizando a la vez las fases previas del ciclo de vida (semillas de la lluvia y del banco) como indicadores de la plantilla inicial de propágulos. La pretensión de este análisis era evaluar las consecuencias finales de la concatenación de los patrones iniciales de deposición de semillas con los micrositios preferidos de establecimiento de las especies analizadas. Estas relaciones se podrían observar en la manera en la que la distribución de las plántulas responde a la presencia de sus conespecíficos y de otras especies del dosel, bajo la premisa de que cada especie requiere condiciones específicas para su establecimiento en el bosque (Grubb 1977, Webb y Peart 2000, Van Ulft 2004). En general, el contraste de dos tipos fundamentalmente diferentes de vecindarios, es decir, del conespecífico *versus* el heteroespecífico, permitió comprender la manera en que éstos afectan diferencialmente los patrones de distribución de semillas y del establecimiento de plántulas. Sobre este punto, la tendencia general observada fue que las especies del dosel serán reemplazadas por individuos de distinta especie. Este reemplazo heteroespecífico parece estar controlado principalmente por factores bióticos, en particular por la depredación, la cual está relacionada directamente con la biomasa de los árboles adultos, en coincidencia con los postulados del efecto Janzen-Connell (Uriarte *et al*. 2005a, b, Jansen *et al*. 2008). Sobre este punto cabe señalar que en el análisis de las interacciones locales entre árboles parentales y los individuos en etapas tempranos, hay un riesgo de que éstas sean aparentemente menos importantes de lo que son realmente, debido a la acción de la aves, organismos capaces de mover muy eficientemente a las semillas, lo que en última instancia puede difuminar los patrones que resultarían exclusivamente de la interacción (M. González-Espinosa, pers. com), al introducir y retirar semillas a tasas no relacionadas con las condiciones locales. Aun así, los resultados del Capítulo IV apuntan a la conclusión de que las interacciones biológicas con los adultos conespecíficos parecen ser el factor más importante en la estructuración de la comunidad arbórea. No obstante, retomando los resultados de la identidad específica y a la luz de los patrones espaciales reconocidos en el Capítulo III, surge la posibilidad de reivindicar a las condiciones abióticas en el sotobosque como factores importantes en el proceso de regeneración natural. En este momento podemos predecir que *Oreopanax xalapensis* se establecerá preferentemente lejos de individuos conespecíficos, muy probablemente debido a la condición de alta radiación solar debajo de las copas de esta especie (variable que difirió significativamente del resto de las especies analizadas). Asimismo, la densidad de plántulas de *Oreopanax xalapensis* está relacionada con la cercanía a *Cornus disciflora*, cuyas copas proporcionan mayor humedad en el suelo y menor radiación solar. *Quercus laurina*, cuyas plántulas se establecen preferentemente debajo de sus copas, encuentran condiciones de menor humedad, lo que a la vez está posiblemente relacionado con tasas de infección por patógenos bajas (Benitez-Malvido y Kossmann-Ferraz 1999). Asimismo, la profundidad del mantillo, variable relacionada con *Chiranthodendron pentadactylon*, afectó negativamente el establecimiento de las plántulas al funcionar como una barrera a la germinación más que por modificar las relaciones bióticas.

La combinación de los factores o la relevancia de cada proceso en el establecimiento parece ser específica para cada especie y dependiente de la fase del ciclo de vida. Si pensamos en todas las posibles combinaciones espaciales de especies en el bosque, es más probable que estas combinaciones coincidan espacialmente con la combinación de condiciones bióticas y abióticas necesaria para el establecimiento de una especie de identidad distinta. En otras palabras, es más probable que los propágulos encuentren esas condiciones lejos de su árbol parental. Sin embargo, es necesario enfatizar que esto no significa que el proceso de estructuración del bosque sea azaroso, sino que más bien apunta a que los factores son diversos y difieren entre especies, lo que hace difícil establecer reglas de carácter más general. De todos modos, sí es posible describir patrones generales y más claramente sus consecuencias. En este caso, la complejidad del proceso de regeneración en los bosques mesófilos de montaña, como el aquí estudiado, permite el mantenimiento de la diversidad de especies siguiendo con la tendencia general observada para otros bosques tropicales (Webb y Peart 1999, Stoll y Newbery 2005, Queenborough *et al*. 2007).

Esta integración final deja ver evidencias a favor del papel fundamental de los factores bióticos en la estructuración de una comunidad, pero también a favor de los factores abióticos, a la vez que revela la importancia de la dispersión en el proceso de regeneración natural y en última instancia en la estructuración de la comunidad. En suma, todas estas evidencias son indicios de que este proceso complejo tiene detrás mecanismos que resultan de la interacción entre los factores bióticos y abióticos que definen el escenario de establecimiento, con la disponibilidad de semillas todos como factores y procesos espacialmente explícitos. Si el estudio de la regeneración natural no se enmarcara en un contexto espacial, sería difícil comprender completamente la estructuración de la comunidad, ya que ello sería equivalente a dibujar a todas las especies y a los factores que la afectan sobre un "único" punto del espacio (Margaleff 1986).

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