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DIVERSIDAD BETA, HETEROGENEIDAD AMBIENTAL Y RELACIONES ESPACIALES EN UNA SELVA BAJA CADUCIFOLIA

TESIS QUE PRESENTA PARA OBTENER EL GRADO DE
DOCTOR EN ECOLOGIA

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MEXICO D.F.

A Marianis, Santi y Miguel

A todas las personas que quiero

En el mundo altamente interdependiente de hoy, los individuos y las naciones ya no pueden resolver por sí solos muchos de sus problemas. Nos necesitamos unos a otros. Por consiguiente, debemos cultivar un sentido de responsabilidad universal... Es nuestra responsabilidad individual y colectiva proteger y cuidar la familia global, apoyar a sus miembros más débiles y conservar y atender el entorno en el que vivimos todos.

Tomado de: Sogyal Rimpoché. 1994. El libro tibetano de la vida y la muerte. Ediciones Urano, S.A., Barcelona.

Indice General

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Resumen

En esta tesis se analizó a la diversidad beta, un componente de la diversidad biológica que ha recibido mucho menos énfasis que otros componentes de la diversidad. Los procesos asociados de forma particular a la diversidad beta son la colonización dependiente de la distancia y la distribución espacial de la heterogeneidad ambiental. Por ello, la descripción y el análisis de la diversidad beta debe basarse en el análisis de su patrón espacial, del patrón espacial de la heterogeneidad ambiental, y de la distancia entre pares de sitios. Mostramos cómo actualmente se cuenta con las herramientas metodológicas y tecnológicas para ello, aunque son relativamente pocos los estudios que abordan el estudio de la diversidad beta desde esa perpectiva.

En la selva baja caducifolia de Chamela, Jalisco, un sistema biológico relativamente poco conocido, analizamos la diversidad beta al interior de un sistema de pequeñas cuencas hidrográficas. En este sistema la diversidad beta es muy elevada. También los es la heterogeneidad ambiental medida con las variables altitud, pendiente, insolación y capacidad de retención de agua del suelo, todas ellas asociadas al contenido de agua en el suelo. Observamos que los patrones de diversidad beta pueden ser explicados por la heterogeneidad ambiental asociada a la disponibilidad de agua, por el patrón espacial de dicha heterogeneidad ambiental y la distancia entre sitios.

Se desarrolló un análisis de sensibilidad que permite separar la contribución relativa de la distancia física y la de la heterogeneidad ambiental a los valores de diversidad beta. Los resultados obtenidos señalan que la distancia física tiene un efecto primordial sobre la diversidad beta; la heterogeneidad ambiental, en cambio, es relevante como determinante de la diversidad beta pero no puede ser aislado del componente espacial. El desarrollo de este análisis de sensibilidad permitió explorar los procesos involucrados en el mantenimiento de la diversidad de especies arbóreas de las selvas bajas caducifolias. Esta herramienta analítica puede ser aplicada a otras circunstancias ambientales y biológicas.

Los resultados derivados del análisis de sensibilidad tienen consecuencias directas sobre la conservación de la diversidad de especies de árboles (y otros organismos asociados) de las selvas bajas caducifolias. Con este análisis proponemos un modelo puede ser útil en el diseño de redes de reservas naturales que tiendan a maximizar la diversidad de especies protegidas.

En esta tesis se analizó a la diversidad biológica desde una perspectiva espacial que rara vez se considera en la literatura. Como corolario de este trabajo puede decirse que el entendimiento de los determinantes ecológicos de la diversidad biológica no puede ser abstraído del contexto espacial. Este enfoque de análisis permite también un acercamiento distinto a la problemática asociada a la conservación de la diversidad biológica.

Capítulo I

Introducción general

Planteamientos generales acerca del mantenimiento de la diversidad de especies a escalas ecológicas

" La pregunta central de la ecología de comunidades se planteó hace décadas. ¿Son las poblaciones presentes en un sitio todas aquellas que llegaron ahí por azar, o sólo son un sub-conjunto especial - aquéllas con características que permiten su coexistencia?" (Roughgarden 1989 [p. 203]).

Esta oración nos propone una perspectiva sencilla acerca de los estudios sobre los determinantes ecológicos de la diversidad biológica. Desde la primera mitad del presente siglo se propusieron dos planteamientos opuestos para explicar el hecho de que en un sitio dado no se encuentra la totalidad de las especies que posiblemente podrían ocuparlo (Roughgarden 1989): ¿Existe alguna regla para la "admisión" de especies un sitio particular, ó se trata simplemente de una muestra aleatoria del conjunto de especies que podrían haber estado presentes en él? Elton (1933) fue el primero en sugerir la idea de que algún tipo de "regla de admisión", o como él lo llamó de "membresía limitada", podría estar regulando la composición de especies en un sitio dado. En cambio, Gleason (1926) propuso que la comunidad presente en un área era meramente el resultado de la inmigración fortuita y oscilante de las poblaciones, dadas ciertas condiciones ambientales y requerimientos de las especies.

A partir de estos dos grandes paradigmas se desarrolló la ecología de comunidades. Desde sus inicios se buscó desarrollar modelos teórico-conceptuales y evidencias empíricas que permitiesen validar alguna de estas posibilidades (Roughgarden 1989). Basados originalmente en los modelos matemáticos de Lotka-Volterra (Lotka 1925, Volterra 1926), se hizo gran énfasis en la competencia como la fuerza motora que define la "membresía limitada" (e.g. Brown 1975, Roughgarden 1989, Huston 1994). Se planteó que la coexistencia de especies en una localidad sólo era posible en ausencia, real o virtual, de competencia (Roughgarden 1989, Huston 1994), y se propusieron varios mecanismos para explicar la ocurrencia de sitios con elevada diversidad de especies. Por ejemplo, se exploró si especies de diferentes tamaños, formas o estrategias de historia de vida podían evitar la competencia al usar los recursos de forma diferencial (e.g. Darwin 1859, Hutchinson 1959, Diamond 1975, Grubb 1977) y si la existencia de heterogeneidad espacial y/o temporal del ambiente (e.g. Roughgarden 1975, Tilman 1982, Tilman y Pacala 1993, Huston 1994) permitía evitar la llamada "exclusión competitiva" de las

especies (Gause 1934) al existir un mosaico de condiciones ambientales con distintos "nichos" que ninguna especie es capaz de monopolizar .

Con el tiempo se ha documentado la existencia de diferentes niveles de variación espacial en las condiciones y la disponibilidad de recursos en el ambiente, así como la existencia de respuestas diferenciales de las especies a tal variación, a escalas que van desde algunos centímetros hasta cientos de kilómetros (e.g. Smith y Urban 1988, Robertson y Gross 1994). También se han observado cambios en las condiciones físicas, en el nivel de disponibilidad de recursos y en la naturaleza e intensidad de factores de disturbio en una localidad a través del tiempo. Por ejemplo, la caída crónica de árboles o el movimiento de mareas crean variaciones temporales importantes del ambiente en bosques tropicales perennifolios y arrecifes coralinos, respectivamente (e.g. Connell 1978). La recurrencia de fuegos (Huston 1994), o la presencia intermitente de depredadores (Paine 1966) son otros ejemplos de factores que generan heterogeneidad temporal en la disponibilidad de los recursos. La incidencia de estos factores de disturbio disminuye la velocidad con la que las especies de mayor jerarquía competitiva tienden a excluir a especies subordinadas, de tal forma que a niveles intermedios de disturbio se ha observado una máxima diversidad (Connell 1978, Huston 1979, 94).

Mucho menor énfasis recibieron los modelos basados en los paradigmas originalmente planteados por Gleason, acerca de un proceso aleatorio de llegada y establecimiento de las especies (Roughgarden 1989, Caswell y Cohen 1993). ¿Qué procesos determinan la probabilidad de llegada de una especie a un sitio dado? El modelo de Biogeografía de Islas desarrollado por MacArthur y Wilson (1963) fue el primero en concebir que las comunidades están abiertas a la invasión indiscriminada de especies, al menos en las fases iniciales de la colonización, durante las cuales la riqueza y composición de especies está determinada por la llegada aleatoria de propágulos (Simberloff y Wilson 1969, 1970). Cuando las especies tienen la misma habilidad competitiva, la "membresía" está dada por un juego de lotería, en donde el único factor limitante a la llegada aleatoria de propágulos es la capacidad de dispersión de las especies (MacArthur y Wilson 1963). Este tipo de ideas dio lugar a la llamada teoría del "no-equilibrio" (Hutchinson 1948, Chesson y Case 1986, Hubbell y Foster 1986). Hubbell y Foster (1986) plantearon que la elevada diversidad observada en los bosques tropicales podía ser explicada a través de este tipo de mecanismo.

A partir de los trabajos seminales de Elton (1933) y Gleason (1926) el estudio de la diversidad biológica se ha desarrollado sustancialmente. Actualmente no es posible

inclinar la balanza hacia la competencia (o las interacciones bióticas en general) o hacia el azar para entender cómo se organiza la comunidad de especies presente en un sitio dado (e.g. Roughgarden 1989, Cornell y Lawton 1992). Los modelos más recientes integran los efectos de interacciones bióticas (intra- e interespecíficas) y de procesos de colonización/extinción estocástica/determinística para explicar la coexistencia de especies (e.g. Tilman y Pacala 1993, Yodzis 1993, Caswell y Cohen 1993).

Un factor importante no incluido en ninguna de las alternativas entre la competencia y los modelos aleatorios es el papel que juega la historia como determinante de la diversidad y composición de especies de un sitio en un momento dado (e.g. Hughes 1989). Los factores ambientales contemporáneos no siempre explican adecuadamente la presencia de ciertos patrones de diversidad; factores tales como eventos climáticos pasados (e.g. Davis 1986), eventos orográficos (e.g. Ferrusquía Villafranca 1998), y procesos de especiación y migración (e.g. Cox 1998, Myers y Giller 1988) tienen una notable influencia sobre la distribución y abundancia actuales de las especies.

Una escala de observación distinta: comparaciones entre sitios

Una pregunta ligeramente distinta a la que se hace Roughgarden es aquella en la que cambiamos de objeto de estudio del conjunto de especies de un sitio a la comparación en la composición de especies entre sitios. La pregunta a enfrentar sería: ¿qué tan diferentes son los distintos sub-conjuntos de especies dentro de una región dada, y porqué son distintos?

El interés por responder esta pregunta es aún más antiguo que los planteamientos de Elton y Gleason. Su origen se remonta a los estudios de la geografía de plantas iniciado por Humboldt a principios del siglo XIX, quien documentó los cambios en la fisionomía de la vegetación a lo largo de gradientes altitudinales y latitudinales y su relación con las condiciones climáticas (Whittaker 1975, Turner 1989). Estas preguntas fueron desarrolladas por numerosos botánicos y zoólogos como deCandolle, Merriam y Warming durante la segunda mitad del siglo XIX (Turner 1989). Para fines del siglo pasado el número de factores ambientales asociados a las diferencias en distribución de las "sociedades de plantas" se vuelve más completa y abarca luz, temperatura, viento, suelo, agua, fuego y topografía, así como interacciones bióticas (animales y plantas; Cowles 1899).

Una visión dinámica de los cambios de composición de especies entre sitios surge a principios del siglo XX con Clements (1936) quien describe las distintas fases

sucesionales de las comunidades, aunque no se preocupa por los patrones espaciales de la distribución de las especies (Turner 1989). Para mediados del siglo XX, Watt (1947) es el primero en integrar la preocupación por la distribución espacial de las especies iniciada por Humboldt, con el concepto de dinámica iniciado por Clements. En un trabajo seminal, Watt describe la variación continua de la vegetación a lo largo de gradientes ambientales así como la sucesión de distintas fases de la vegetación posteriores a un disturbio. Por otro lado, Troll es el primero en proponer una síntesis de lo que consideraba el estudio vertical de las comunidades, es decir el de las relaciones entre sus distintos componentes bióticos y abióticos desde un punto de vista funcional, y lo que llamaba el estudio horizontal de las comunidades, es decir el de la relación entre las unidades espaciales (Forman y Godron 1986, Naveh y Liberman 1993).

Paralelamente a estos estudios se desarrollaron numerosas escuelas que analizaron el cambio espacial en composición de especies. En Europa y Estados Unidos se pueden reconocer varias escuelas del estudio de la vegetación (Whittaker 1975). La escuela nórdica ha enfatizado la importancia de los distintos estratos de la vegetación. La escuela sureña, protagonizada por Braun-Blanquet, incluye en su clasificación de tipos de vegetación a todas las especies. La escuela rusa concibe a las comunidades forestales como unidades del paisaje interrelacionadas con factores climáticos, edáficos y biológicos. La escuela ingresa enfatiza el papel del disturbio y los distintos estadíos sucesionales de la vegetación. La escuela americana, iniciada por Gleason y Clements, se enfoca en el estudio de gradientes ambientales.

Simultáneamente con las distintas escuelas de estudios de la vegetación, se desarrollo la ecología del paisaje, la ciencia que estudia de forma interdisciplinaria la interacción entre los componentes espaciales y temporales en un paisaje (Bunce y Jongman 1993, Koplatek y Gardener 1999), en donde el paisaje es una área de dimensiones variables que es espacialmente heterogénea (Turner 1989). Esta disciplina, que cuenta también con numerosas escuelas (Forman 1995), enfatiza, a diferencia de las escuelas del estudio de la vegetación, el componente dinámico asociado al disturbio humano de los cambios en composición de especies entre sitios (Forman 1995, Klopatek y Gardner 1999). La ecología del paisaje tiene una perspectiva holística, e incorpora a otras disciplinas como son el diseño y planeación del manejo de los recursos naturales (Naveh y Liberman 1993, Zonneveld 1972). La ecología del paisaje trabaja generalmente en áreas que van desde algunas hectáreas hasta algunos kilómetros cuadrados (Hobbs 1999).

Finalmente, también de forma sincrónica, se desarrollaron los estudios biogeográficos, enfocados al estudio de la distribución espacial de las especies dentro de contextos espaciales de gran escala (e.g. continentales) y temporales de largo plazo (e.g. cientos de millones de años; Cox y Moore 1993, Myers y Giller 1988). En estos estudios se analiza el papel que juegan los factores climáticos, las interacciones bióticas, los procesos de dispersión, los cambios orográficos y climáticos del planeta así como los procesos de especies y extinción (Cox 1998, Cox y Moore 1993, Myers y Giller 1998). La biogeografía abarca tanto el estudio de los cambios en composición de especies, como el componente de diversidad de especies a nivel regional.

El concepto de diversidad beta

Los estudios de vegetación que realizó Whittaker en las montañas del este de Estados Unidos (e.g. 1954, 1956, 1960, 1965, 1967), lo llevaron a proponer la existencia de tres tipos distintos de diversidad de especies (Whittaker 1960, 1972). La diversidad *alfa*, o diversidad al interior del hábitat, se refiere al número de especies presentes dentro de una comunidad. La diversidad *beta*, o diversidad entre hábitats, se refiere a la medida del reemplazo de especies a lo largo de los gradientes ambientales. La diversidad *gamma*, o diversidad regional, es el conjunto de especies presentes en una variedad de hábitats y es consecuencia de los valores de diversidad alfa y beta. Si bien el concepto de diversidad beta fue originalmente acuñado por Whittaker para una escala espacial asociada al análisis de gradientes ambientales, este concepto ha sido ampliamente utilizado a distintas escalas espaciales. Los ejemplos de su uso van desde estudios que abarcan unos cuantos centímetros, para comparar la comunidad de parasitoides que ocupan distintos pastos (Dawah et al. 1995), comparaciones de la composición de especies de plantas dentro de extensiones del orden de 4,000 ha (Lapin y Barnes 1995), hasta comparaciones continentales de la composición de especies de aves (Blackburn y Gaston 1996).

La pregunta planteada por Roughgarden (1989) se centra en la diversidad alfa, la cual ha sido el foco de atención de una gran parte de los estudios en ecología de comunidades. La diversidad gamma ha sido ampliamente estudiada por los biogeógrafos, quienes se han planteado numerosas hipótesis sobre la importancia de la latitud, el área, la productividad, la estabilidad climática y la orografía asociada a la tectónica de placas, entre otros para explicar los patrones de diversidad gamma observados (e.g. Myers y Giller 1988, Rohde 1992, Wright et al. 1993, Rosenzweig 1995, Cox 1998).

El componente beta de la diversidad, sin embargo, ha recibido mucho menos atención por parte de los ecólogos teóricos. Harrison (1992 [p. 151]) y colaboradores opinan al respecto:

> "Mientras que los patrones de diversidad alfa, como las relaciones especies-área de las islas y los gradientes latitudinales de diversidad, son temas fundamentales en la literatura ecológica, la diversidad beta ha recibido mucho menos estudio sistemático [...]".

Si bien la descripción de los patrones de cambios en composición de especies entre sitios y su relación con factores ambientales se ha desarrollado ampliamente a través de la generación de herramientas estadísticas multivariadas (e.g. Gauch 1982, Jongman et al. 1987, Palmer 1983), y la descripción de patrones en la ecología del paisaje ha crecido exponencialmente (e.g. Farina 1998, Forman 1995, Klopatek y Gardner 1999), el estudio de los procesos biológicos involucrados en la generación y mantenimiento de la diversidad beta ha recibido relativamente poca atención (May 1985, Crawley 1997, Wiens 1995).

Los determinantes de la diversidad beta

¿La diversidad beta está determinada por procesos muy distintos de aquellos que determinan la diversidad alfa?. Si bien el estudio de las interacciones bióticas, y en particular de la competencia, es fundamental para el entendimiento de la diversidad local, también lo es para la comprensión y el análisis de la diversidad beta (e.g. McLaughlin y Roughgarden 1993), para la cual otros procesos cobran una importancia especial.

En particular, para entender los determinantes de la diversidad beta, se vuelve relevante el análisis de los procesos involucrados en la llegada diferencial de propágulos a los distintos sitios. La teoría de biogeografía de islas planteó las bases para el estudio de las relaciones entre la fuente de propágulos y las islas, y sugirió que el éxito de colonización de las especies es función de su capacidad de dispersión y de la distancia de la fuente a la isla (MacArthur y Wilson 1963). Desde entonces, el estudio del movimiento de propágulos de especies en ambientes continuos, y no en sistemas de islas, ha permitido identificar al menos dos procesos fundamentales para la diversidad beta. El "efecto de masa" (*mass effect*) se refiere a la llegada de propágulos de especies desde hábitats adyacentes (Shmida y Wilson 1995). La dinámica de metapoblaciones, y los

modelos de fuente y sumidero (*source-sink*) modelan la dinámica poblacional de las especies en parchos de diferente calidad ambiental para la especie, y el movimiento de propágulos entre ellos (e.g. Brown y Kodric-Brown 1977, Shorrocks and Swingland 1990, Gilpin y Hanski 1991, Pulliam 1988).

El establecimiento de las especies en un sitio depende, a su vez, tanto de las condiciones ambientales como de los requerimientos específicos de cada una de las especies. Whittaker (1972) observó que en gradientes ambientales muchas especies de plantas están restringidas a una fracción del gradiente, y que cada especie presenta un patrón de ocurrencia distinto en distintos gradientes. En parte, la amplitud que abarca una especie en un gradiente está determinada por su tolerancia fisiológica a las condiciones presentes en el gradiente. La amplitud del ámbito de tolerancia ambiental de las especies es, por lo tanto, fundamental para determinar la diversidad beta, así como lo es la magnitud de la variación ambiental que existe a lo largo de los distintos gradientes (Whittaker 1972). En síntesis, estos dos factores (la amplitud del ámbito de tolerancia y la heterogeneidad ambiental), junto con la capacidad de dispersión de las especies, son considerados actualmente los procesos fundamentales asociados a la diversidad beta (Schluter y Ricklefs 1993, Soberón y Rodríguez en prep.).

¿Por qué estudiar el componente beta de la diversidad de especies?

Si los ecólogos y los biogeógrafos se han concentrado mucho más en el estudio de la diversidad alfa y la diversidad gamma, ¿tiene algún sentido estudiar la diversidad beta?, ¿aprenderemos algo distinto al estudiar este componente de la diversidad?. Pueden darse varios argumentos para responder afirmativamente a esta pregunta.

Desde sus trabajos iniciales, Whittaker (1960, 1972) planteó la siguiente relación entre los tres componentes de la diversidad:

$$\gamma = \alpha \times \beta.$$

Esto quiere decir que para entender la diversidad gamma tenemos que entender sus dos componentes, la alfa, ampliamente estudiada, y la beta que media la relación entre alfa y gamma (Cornell y Lawton 1992, Schluter y Ricklefs 1993, Soberón y Rodríguez en prep.).

Dentro de este contexto, la diversidad beta es aquella que permite escalar desde la diversidad alfa, o local, hasta a la diversidad gamma, o regional. En la medida que entendamos cuales son los procesos asociados a la distribución diferencial de las especies entre sitios, podremos vincular distintas escalas de estudio. Ricklefs (1987,

Ricklefs y Schluter 1993) propone que existe una estrecha relación entre los procesos locales, asociados a la diversidad local de especies, como la colonización local, la exclusión de especies por competencia y depredación, y la extinción estocástica, y los procesos regionales, asociados a la diversidad regional de especies, como son la especiación, la extinción y el intercambio biótico. Discute que tanto los procesos locales y como los procesos regionales inciden sobre las comunidades a distintas escalas espaciales y temporales, y que su importancia relativa varía entre escalas. Él propone como "puente" fundamental entre las dos escalas a la selección de hábitat. Creo que el entendimiento de los procesos asociados a la diversidad beta nos van a permitir tener una perspectiva más amplia de los procesos "puente" entre las dos escalas.

La diversidad beta y su importancia para la conservación de la diversidad biológica

¿En qué grado el estudio de la diversidad beta es relevante para fines de conservación de la diversidad biológica?. Desde los primeros planteamientos del sistema de reservas del MAB (Man and the Biosphere, i.e. El Hombre y la Biosfera: e.g. Halffter 1991, 1996), la selección de áreas prioritarias para la conservación de la biodiversidad ha considerado criterios basados en expresiones de la diversidad beta. El objetivo de este sistema es seleccionar al menos un sitio de cada tipo de ambiente y, consecuentemente, de cada tipo de comunidad biótica del planeta, que estará representado en el sistema de reservas. Recientemente se han desarrollado índices que permiten sopesar la diversidad alfa y la "complementariedad" en la composición de especies, o sea la diversidad beta, para seleccionar grupos de áreas que permitieran constituir una red de áreas protegidas que maximice el número de especies que encuentran refugio en ellas (Vane-Wright et al. 1991, Pressey et al. 1993).

Muchas propuestas para la identificación de áreas prioritarias para la conservación están basadas en estimaciones de la diversidad alfa (e.g. Myers 1990), gamma (e.g. Ceballos et al. 1998), o en los predictores de alguna de ellas (e.g. Gaston y Blackburn 1995, Burnet et al. 1988, Nichols et al. 1988). Sin embargo, el añadir el componente de la diversidad beta, al igual que en el terreno meramente conceptual, permite entender el puente que existe entre la diversidad alfa y la gamma, y entender cómo éstas se encuentran organizadas en el espacio. En términos de áreas prioritarias para la conservación, la inclusión de la complementariedad en la composición de especies entre sitios (e.g. Pressey et al. 1993) y de sitios con elevada diversidad beta (Noss 1983),

permiten ampliar el entendimiento de los patrones de distribución de especies en el espacio.·

A este respecto, Blackburn y Gaston (1996; [p. 146]) aseguran que:

"Un tema que ha sido mayormente olvidado en los análisis de los patrones de biodiversidad es el de cómo varía el recambio de especies en el espacio [...], aunque visto como complementariedad ha recibido atención significativa en el contexto más restringido de áreas prioritarias para la conservación [...]".

Una tesis sobre diversidad beta

Una vez que intenté convencer al lector de la importancia de hacer estudios sobre diversidad beta, la siguiente pregunta es: ¿qué debo estudiar con respecto a la diversidad beta?

¿Por dónde empezar?

Los estudios sobre diversidad beta que se encuentran en la literatura ecológica son de índole muy distinta. Muchos trataron de definir, medir y representar la diversidad beta desde varios enfoques. Poner en orden esta información y tenerla a la mano puede convertirse en una herramienta de investigación muy útil. Además, es importante considerar qué tipo de preguntas se han planteado en los estudios sobre diversidad beta y cuáles de ellas podrían ser más relevantes, tanto desde un punto de vista conceptual así como por sus posibles aplicaciones a la conservación de la biodiversidad.

En la búsqueda de preguntas centrales en torno a la diversidad beta, la literatura parece estar señalando dos grandes temas, estrechamente ligados, que podrían ser de gran relevancia en el futuro para el estudio de la diversidad beta.
El primer tema es la heterogeneidad ambiental. Planteamiento fundamental de las observaciones de Whittaker (1960, 1972), la heterogeneidad ambiental es uno de los determinantes de la diversidad beta más importantes, y ha sido recientemente utilizada para la identificación de áreas prioritarias para la conservación (Burnet et al. 1998, Nichols et al. 1998). Si bien numerosos trabajos han permitido identificar de forma cada vez más precisa la cantidad de varianza en la composición de especies que es explicada por variables ambientales (e.g. Gauch 1982, Jongman et al. 1987, Palmer 1983), no existe literatura acerca de los procesos involucrados en estas relaciones, o acerca de la

sensibilidad de la diversidad beta a cambios en el nivel de heterogeneidad ambiental. ¿Cuánta heterogeneidad ambiental es necesaria para que se dé la diversidad beta? ¿Qué relación mantiene la magnitud de la heterogeneidad ambiental con la magnitud de la diversidad beta?

El segundo tema, estrechamente ligado al anterior, es el tema del espacio. Al respecto Kareiva (1994 [1]) menciona:

"El espacio [es]: la frontera final para la ecología teórica". [...] la inclusión de la dimensión espacial puede explicar preguntas añejas acerca de la coexistencia de plantas y la riqueza de especies [...]".

Así mismo, Legendre y Fortin (1989 [132]) aseguran que:

"Podemos esperar que un enfoque espacial a los problemas ecológicos traiga consigo un salto cuántico para los ecólogos [...]".

Con referencia a estos escritos es necesario empezar por definir el espacio. El espacio se refiere al componente "horizontal" por el cual se preocupan los geógrafos, a la posibilidad de representar en un plano, como en los mapas, la posición de los distintos elementos que nos interesan; este concepto es similar al de paisaje (landscape) con la diferencia que se han acotado las dimensiones específicas de lo que es un paisaje (e.g. Forman 1995). Dentro de este concepto, es fundamental entender que este espacio o paisaje no es homogéneo, sino que es heterogéneo (Forman y Godron 1986, Farina 1998, Forman 1995). Las relaciones espaciales entre sitios se refieren a la posición relativa de un sitio con respecto al otro, y en particular al conjunto de distancias entre pares de sitios.

Considerando los distintos procesos asociados a la diversidad beta, y la incorporación de la dimensión espacial a su estudio resaltan varios puntos. Por un lado, es importante entender a las relaciones espaciales entre sitios en función del intercambio de propágulos entre ellos, dentro del marco de la teoría de Biogeografía de Islas de MacArthur y Wilson (1963). Por otro lado, el desempeño diferencial de los organismos dentro del espacio está relacionado con su heterogeneidad ambiental, es decir con diferencias en condiciones y recursos disponibles para los organismos entre sitios. Por lo tanto, el entendimiento de cómo está organizada la heterogeneidad ambiental en el espacio (Bell et al. 1993) y sus consecuencias para la diversidad beta (Tilman y Pacala

1993, Legendre y Fortin 1989, Borcard et al. 1992, Leduc et al. 1992, Legendre 1993), es otra forma de incorporar el estudio del espacio al análisis de la diversidad beta.

Con base a estos planteamientos, el objetivo central de la tesis es contribuir a entender la relación que existe entre la diversidad beta, la heterogeneidad ambiental y las relaciones espaciales entre sitios.

¿Dónde realizar el estudio?

La selección de un sistema ideal para realizar esta tesis y contestar la pregunta arriba planteada no fue fácil. Mis propias preferencias indicaban que debía tratarse de un sistema terrestre, preferentemente algún tipo de bosque. Por otro lado, para poder hacer una evaluación rápida y eficiente de la diversidad beta era importante que existiera información previa sobre la identidad taxonómica de las especies. Las fuentes de heterogeneidad ambiental deberían haber sido ya identificadas previamente, para poder escoger un grupo reducido de variables ambientales. Cuanta más información previa disponible sobre el sistema, más fácil sería el análisis e interpretación de los datos.

Para llevar a cabo esta tesis, seleccioné la selva baja caducifolia de Chamela, Jalisco (Lott et al. 1987) y, en particular, un sistema de cuencas ubicado sobre un macizo de granito (Cotler et al. en prensa, Maass et al. 1995, Sarukhán y Maass 1990). Para la región se contaba con un listado florístico (Lott 1993), un herbario con ejemplares de respaldo, así como manuales para la identificación de especies arbóreas (Pérez-Jiménez y Barajas 1990). En general, para la selva baja caducifolia se ha discutido que la diferencia en disponibilidad de agua en el suelo es el principal factor asociado a cambios en composición de especies vegetales entre sitios (Mooney et al. 1995). Existían evidencias previas de una elevada diversidad beta entre la vegetación de los cauces de los arroyos y la de las cimas (Lott et al. 1987). Para el sistema de cuencas experimentales, se tenían ya indicios de que variables como capacidad de retención de agua en el suelo (Galicia 1992), humedad edáfica (Zarco 1994), y disponibilidad de nutrientes (Campo 1995, Slis 1993) presentaban valores contrastantes en la cima y en la base de las cuencas.

Además de esto, las selvas bajas caducifolias son sistemas virtualmente desconocidos en lo que se refiere al origen y mantenimiento de su diversidad de especies de plantas, lo cual contrasta fuertemente con lo que se sabe hoy en día de las selvas altas perennifolias (Murphy y Lugo 1986). La diversidad alfa y gamma de la selva de Chamela había sido señalada como una de las más elevadas en su tipo, además de presentar un

elevado endemismo (Gentry 1995, Lott 1993, Lott et al. 1987). Las selvas bajas caducifolias, además, están entre los sistemas biológicos más amenazados por las elevadas tasas de transformación de la vegetación para usos agrícolas o pecuarios (Maass 1995).

Contenido y aportaciones de la tesis

Procesos espaciales y diversidad beta

En el capítulo II presento una revisión bibliográfica que sirve de marco de referencia para ubicar los procesos y factores involucrados en la determinación de la diversidad beta. En particular, pongo especial énfasis en la naturaleza espacial de la diversidad beta. Una vez establecido ese marco, comparo los distintos tipos de índices de diversidad beta, sus formas de representación espacial, y los estudios que se realizan actualmente al respecto.

Describiendo la relación entre la diversidad beta, la heterogeneidad ambiental y las relaciones espaciales entre sitios

Como fase inicial en el análisis de la relación entre diversidad beta, heterogeneidad ambiental y distancia física, seleccioné un sistema relativamente sencillo y describí con detalle estas relaciones. En el capítulo III de la tesis presento un estudio que cuantifica los niveles de diversidad beta de la comunidad de árboles en las cuencas de estudio. Para esto, seleccioné transectos que representaron condiciones y niveles de heterogeneidad ambiental contrastantes. En este capítulo describo niveles de variación y organización espacial de diversidad beta y su relación con la heterogeneidad ambiental.

Un análisis de sensibilidad

Una vez descritas las características del sistema me propuse contestar las preguntas: ¿qué relación mantiene la magnitud de la diversidad beta con la magnitud de la heterogeneidad ambiental y la de la distancia física?, y ¿es posible separar el efecto de la heterogeneidad ambiental del producido por la separación espacial?.

Con este fin, en el Capítulo IV desarrollo y aplico un análisis de sensibilidad para evaluar la respuesta de la diversidad beta a cambios relativos en la magnitud de la heterogeneidad ambiental y en la magnitud de la separación física entre sitios. Con este estudio analizo el efecto aislado de la heterogeneidad ambiental y la distancia física así como posibles interacciones sinérgicas entre estos determinantes de la diversidad beta.

Aportaciones de la tesis

En la discusión final (Capítulo V) de la tesis señalo las aportaciones específicas de cada uno de los capítulos al entendimiento de la relación que existe entre diversidad beta, heterogeneidad ambiental y relaciones espaciales entre sitios. Discuto además la relevancia de los resultados obtenidos en el contexto más amplio del entendimiento de los procesos asociados a la diversidad beta. Asimismo, analizo el papel que juega la diversidad beta como puente entre la diversidad alfa y la diversidad gamma. Finalmente, basándome en los resultados de esta tesis, planteo la importancia de considerar a la diversidad beta en el estudio de los patrones de biodiversidad y su conservación.

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Capítulo II

The analysis of beta diversity within a spatial context

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Introduction

Ecologists are growingly concerned about the spatial nature and structure of ecological processes. Advances in the understanding of phenomena affecting species abundance and distribution (e.g. Schluter and Ricklefs 1993, Brown 1984, Wiens et al. 1993), the development of landscape ecology (e.g. Turner 1989, Klopatek and Gardner 1999), the increasing use of geographic information systems (e.g. Clark et al. 1995, Johnston 1998), and the larger computing capacity for data management have strongly influenced the way ecologists address spatial patterns. Ecologists are now concerned with spatial patterns of species distributions (e.g. Brown et al. 1995, Thompson et al. 1996), and their metapopulations dynamics in space (e.g. Murdoch 1994, Hanski 1998); they are now aware of the spatial structure of ecological phenomena (e.g., Legendre 1993, Koenig 1999), and count on tools that allow the description of such structure (e.g. Burrough 1987, Legendre and Fortin 1989, Rossi et al. 1992, Koenig and Knops 1998). Furthermore, in the development of ecological theory, space has been considered the final frontier for ecological theory (Kareiva 1994), and theoretical models are being developed within the context of a spatial ecology (e.g. Tilman and Kareiva 1997).

The understanding of species diversity and its determinants, a central question in community ecology (Roughgarden 1989), has also been analysed within a spatial context. Spatial patterns of species diversity have been described at a global (e.g. Scheiner and Rey-Benayas 1994), continental (e.g. Currie and Paquin 1987), regional (e.g. Fraser 1998), or local scales (e.g. He et al. 1994). The analysis of spatial patterns of changes in species composition, despite the great importance they may have upon ecological theory and applied issues (Blackburn and Gaston 1996, Harrison et al. 1992, Ricklefs and Schluter 1993, Williams 1996) has received far less attention. Moreover, beta diversity is the component of species diversity that accounts for differences in species composition among sites, and is thus strongly determined by spatial patterns and processes. In fact, the spatial organisation of environmental heterogeneity, and spatial relationships among sites, are claimed to be among the critical factors affecting beta diversity (e.g., Leduc et al. 1992, Cody 1993, Farnsworth and Ellison 1996, Harrison 1997).

In this paper we present a review of the concepts involved in the definition of beta diversity, and the analysis of its determinants. Within this context, we examine the usefulness of different methods designed to quantify and represent beta diversity, and to assess the relative contribution of the various factors affecting such species diversity

component. After defining beta diversity, we outline the theoretical background needed to understand the spatial nature of beta diversity. Secondly, we review the available methods developed to measure and represent beta diversity in order to detect those that are useful for spatial analysis. We also assess how the study of beta diversity determinants is gradually incorporating spatial patterns and processes. Finally, we propose some future research issues for basic and applied studies.

Definitions

Beta diversity, in its widest sense, is a measure of the dissimilarity in species composition and abundance over space. This term was originally proposed by Whittaker (1972) as one of three components of species diversity, together with alpha, and gamma diversity. Gamma diversity refers to the total diversity within a region, and alpha to the diversity at a locality within that region. Beta diversity is a link between these two components, i.e., the change in species composition between localities within the region. We propose that these definitions should apply to any region and any set of localities within it, independently of their dimensions. We do not agree with the differential use of beta or delta diversity (changes in species composition among regions) and that of gamma or epsilon diversity (total species number) proposed by Whittaker (1972) depending of the dimensions of the studied area. We think that much confusion arises from the need of clarifying the magnitude of the studied area before choosing the right terminology. Examples of the proposed universal use of alpha, beta and gamma diversities can be found for areas ranging from a few centimetres, in the case of grass parasitoid communities (Dawah et al. 1995), up to continental ones, in the case of bird species composition (Blackburn and Gaston 1996).

Within this broadest context for the concept of beta diversity, terms such as differentiation, between habitat diversity, and species complementarity are all synonyms to beta diversity (Magurran 1988, Colwell and Coddington 1994). Other terms have been used to define some variations of this basic concept. Cody (1986) restricted the concept of beta diversity to the differences in species composition along an environmental gradient, and differentiated it from delta diversity, the differences in species composition among patches of the same habitat separated by a given distance. The differentiation among similar habitats or contrasting environmental conditions can be very ambiguous.

Compositional pattern diversity, or mosaic diversity, represents a different kind of diversity that is a combination of both alpha and beta diversity patterns in space (Scheiner

1992). The concept of nestedness is related to beta diversity (Wright and Reeves 1992), but is only applicable to sets of discrete patches such as islands or fragments. In that case, a nested structure represents the conditions where assemblages with progressively less number of species are non-random subsets of the species that occur in more species-rich assemblages (Patterson 1987).

Independently of the name given to beta diversity, it accounts for a community perspective on the differential distribution of single species. This component of species diversity is as important as alpha diversity in determining total species richness in a region (Harrison et al. 1992, Ricklefs and Schluter 1993), as stated in the expression (Whittaker 1972):

Gamma diversity = Alpha diversity X Beta diversity.

Beta diversity could be the link that allows the understanding of the relationships between local and regional diversity (Cornell and Lawton 1992).

Processes and determinants

Exploration of the processes involved in single species distribution can help to understand the determinants of beta diversity. "Island biogeography" models explain distribution of a species as a function of species-specific distance-dependent colonisation and area-dependent extinction rates (e.g. MacArthur and Wilson 1967, Kadmon and Pulliam 1993, Brown et al. 1996). Such rates are related to species life histories, generally expressed as the r-K continuo (e.g. McArthur and Wilson 1967). In particular, colonisation rates are related to species traits associated with dispersal abilities, which is in turn affected by dispersal vehicles (e.g. Howe and Smallwood 1982).

A further conceptual step of the above models is to consider that species colonisation and extinction rates are dependent also on the differential suitability and frequency of islands (or patches). This idea was incorporated into the so-called "meta-population" or "source-sink" models (e.g. Dias 1996, Levin 1970, Hanski 1981, Hanski and Gyllenberg 1997, Pulliam 1996). In contrast, "spatially explicit" models assume that all patches are similar in their suitability, but differential local density-dependent (within and among species) factors determine species colonisation and extinction rates (Tilman and Kareiva 1997).

Based on ideas provided by the above models, Figure 1 synthesises major processes and determinants of beta diversity. Frequency of environmentally different patches conforms the scenario where beta diversity takes place. Each species has a

certain probability of arrival to any of those patches, depending on the distance between propagule source and the target patch, and species dispersal ability (determined in many cases by mutualistic interactions). Effective species colonisation and persistence depend on the matching between species tolerance range and patch abiotic environmental characteristics (i.e., "patch suitability"), and on the species performance in relation to the biotic environment. Then, beta diversity may change due to the spatial organisation of source and sink sites, contrasting species dispersal abilities, contrasting species tolerance ranges or different levels of environmental variation among patches.

The role played by biotic interactions cannot be denied under any circumstances. The spectacular roles played by predation in rocky shore communities (Paine 1966), inter-specific competition in barnacle communities (Connell 1961), and herbivory on cacti populations (Caughley and Lawton 1981) are examples of the importance that biotic interactions may have as local community organising forces. The virtual lack of studies on biotic interactions at the landscape or biogeographic scales (but see Travis 1996), however, imposes a serious limitation to analyse how biotic interactions influence beta diversity at regional scales. This is a critical issue that must be addressed in future work. Here, we will restrict our discussion to how distance among sites, frequency and suitability of patches and species dispersal abilities affect beta diversity.

The spatial context

Underlying the above conceptual framework is a spatial thinking (Fig. 1). Island-continent models and multiple patch models are abstractions of the way environmental heterogeneity is organised in space. Space can be considered, for abstraction purposes, as a surface resulting from a bidimensional projection of the spherical surface of the earth, where X and Y co-ordinates of an Euclidean plane integrate the two dimensions (Burrough 1986). Along such surface or space, environmental conditions take different values, that is, there is environmental heterogeneity (Farina 1998, Wiens 1995). Recent developments in landscape ecology have allowed for a better understanding of the way environmental heterogeneity varies in space (e.g. Klopatek and Gardner 1999). We now know that values taken by environmental variables vary continuously along space, in a complex and multivariate fashion (e.g. Forman and Godron 1981). Also, environmental variables do not take values at random in space; in general, closer sites have values that are more similar than those of more distant sites have. This implies that environmental heterogeneity has a spatially auto-correlated nature (Bell et. al. 1993, Legendre 1993), that is likely to be

organised hierarchically (Allen and Star 1982), in a series of successively nested structures (Legendre 1993).

It is within this context that determinants of beta diversity should be understood. Species colonisation and extinction rates are very likely to be affected by distance relationships among sites, but also by the spatial structure of environmental heterogeneity (e.g. Wiens et al. 1993). Therefore, the understanding of patterns and processes associated to beta diversity need to be analysed within a spatial context. The relative contribution of the different processes must consider the tight relationships between distance-dependent colonisation rates, spatial structure of environmental heterogeneity, and spatial structure of biotic interactions. An overview of recent literature allows the exploration of how beta diversity has been or can be addressed from a spatial perspective.

Measurements

Beta diversity was originally measured along environmental gradients. Many beta diversity indices such as Cody's β_C, Routledge's β_R, β_I and β_E, and Wilson and Shmida's β_T indices (Pielou 1975, Magurran 1988) compute the number of new species found, and those of species not found any more, from one locality to an adjacent one. These indices consider a built-in linear spatial pattern through the analysis of sites along transects. In this case, the role played by distance among sites cannot be analysed within transects, but rather through comparisons among transects of varying length. These turnover indices do not allow multiple comparison of sites.

Most common indices of beta diversity are independent of the spatial location of sites, but they can be successfully applied to spatially referenced data. Pair-wise compositional similitude indices such as Jaccard, Sorensen and Morisita-Horn compare presence-absence or abundance data among sites (Magurran 1988). With the use of such indices, spatial pattern of beta diversity, and more particularly auto-correlation of species composition, was first addressed by Whittaker (1977). He proposed to regress compositional similitude between all possible pairs of points along a transect to the corresponding between-point distances. The calculation of the rate of change in species composition assumes an implicit spatial auto-correlation structure, and the magnitude of beta diversity is defined by such auto-correlation. The analysis can be applied to single-dimensional transects, or to a bidimensional plane.

Spatial auto-correlation of beta diversity can be assessed using multidimensional
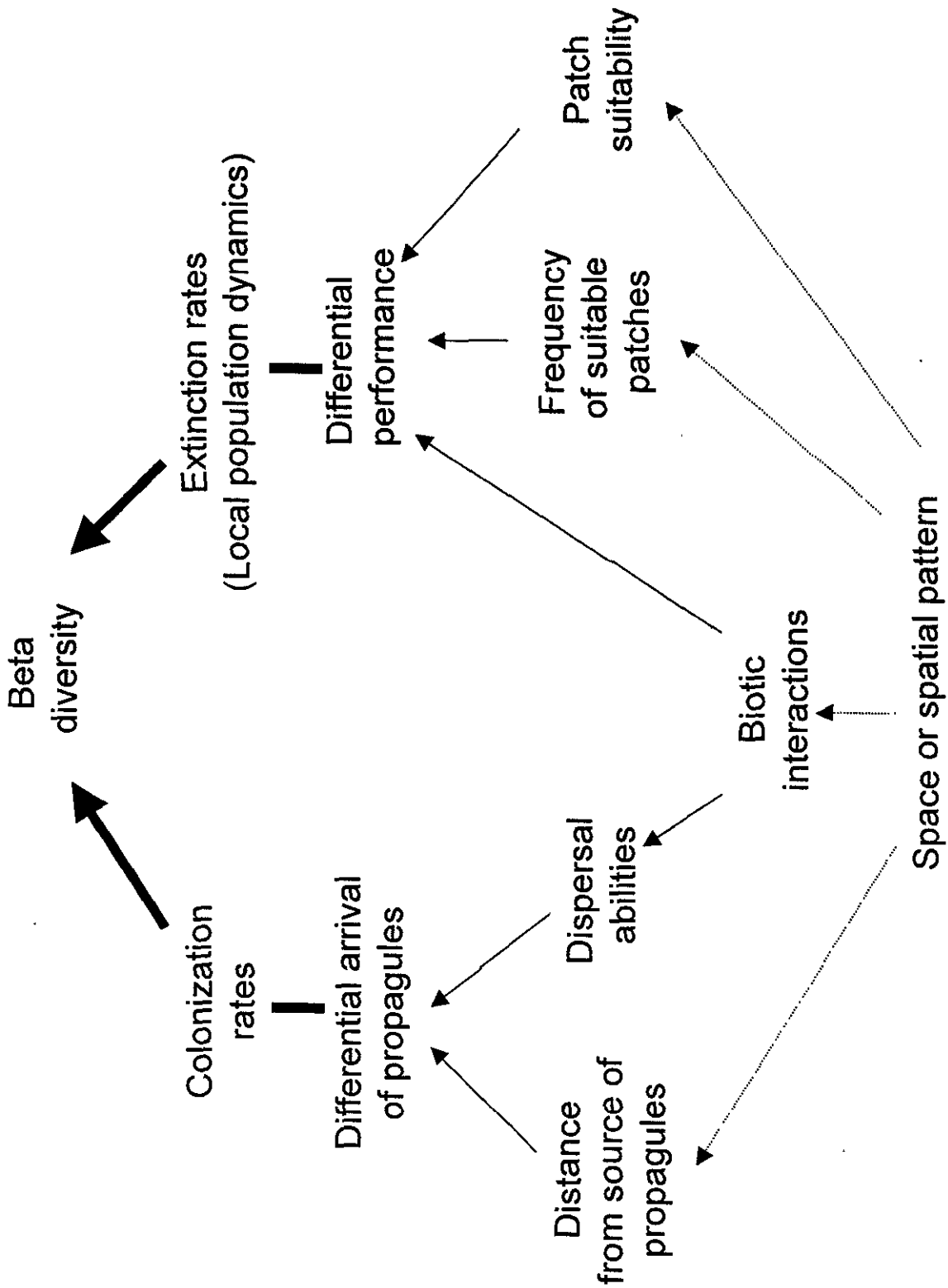
Fig. 1. Determinants of beta diversity. Wide arrows indicate the two main components of beta diversity. Single continuous arrows indicate factors affecting these components. Single discontinuous arrows indicate the relationship between these factors to a spatial context.

data with the help of Mantel's test (Legendre and Fortin 1989, Fortin 1999). Associations among species in the presence of spatial auto-correlation can be analysed using a null model that includes the spatial pattern of each species (Roxburgh and Chesson 1998).

Description of the spatial pattern of beta diversity, without the analysis of its spatial auto-correlation, is possible with the mosaic diversity index (Scheiner 1992), that evaluates the arrangement of subsets in a mathematical space of site/species' data matrix. Description of spatial pattern of beta diversity is hindered when using indices such as the nestedness index (Wright and Reeves, 1992), the regional/local species richness ratio (Whittaker 1977, Ricklefs and Schluter 1993), and the complementarity index of Colwell and Coddington (1994). In these cases, an overall picture of the arrangement of species among sites can be obtained, but no spatial reference to such patterns is possible.

Graphical representations

Spatial representation of beta diversity is possible through a variety of indices adjusted to a bidimensional context. For this purpose, space is necessarily divided into a tessellated or cell-structure, where sites with given alpha diversities have equal dimensions. Beta diversity is then calculated among such equally sized cells and represented graphically.

Maps with equiprobabilistic isolines can be obtained from species composition pair-wise comparisons using a similitude index, between all cells and a starting point (e.g. Mourelle and Ezcurra 1996). Zones of rapid beta diversity are those where the change in the similitude index is high, compared to zones of low beta diversity where the index changes smoothly (e.g. Rapoport 1982, Mourelle and Ezcurra 1996). Neighbouring-cell analysis enables the comparison of each cell to adjacent neighbouring cells (Mourelle and Ezcurra 1997), by using modifications of the transect-wise beta diversity indices (Williams 1996, Mourelle and Ezcurra 1997).

The major drawback of these spatial representations of beta diversity is that an overall comparison among all cells is not possible. In the first case, reference is made to a starting cell, and spatial pattern will be dependent on the location and characteristics of this cell (compare Fig. 2 b and c). In the second case, only adjacent neighbours are considered for the computation of neighbouring beta diversity; errors due to number of neighbouring cells on the edge of the studied area are expected (Fig. 2 e, g). In both

cases, the spatial pattern is highly dependent on the index used (compare Fig. 2 b and d, and see Williams 1996).

A true comparison among all cells is possible through a multivariate ordination of species composition data (Owen 1990). Spatial pattern of beta diversity will be revealed when site scores of the multivariate ordination axis are represented on a bidimensional map; spatial pattern of beta diversity will vary among axis (compare Fig. 2 e and f).

The above information reviews the availability of methods that enable graphical analyses of spatial patterns of beta diversity. Such tools, however, are not free from methodological limitations, and none of the above methods provides a single perspective on the spatial patterns of beta diversity. Thus, careful spatial analysis of beta diversity may require the use of different procedures to attain a broader perspective on this issue.

Untangling multiple factors involved

Among earlier studies we found a strong focus on environmental factors as explanatory variables of changes in species composition, but with reference to the spatial distribution of such sites (e.g., Whittaker 1977, Myklestad and Birks 1993). Such is the case of gradient analysis (e.g., Whittaker 1977, Wolf 1993), and of some biogeographically oriented studies (e.g., Willig and Sandlin 1991,Willig and Gannon 1997). In this sense, new ordination methods (e.g., Jongman et al. 1987, Palmer 1993) are very powerful for determining of the relative weights attributed to different environmental variables. However, in most cases it is not possible to assess the contribution of distance among sites to the observed beta diversity (e.g. Kitayama and Mueller-Dombois 1995, and Frisvoll and Presto 1997).

However, Whittaker's (1977) classical studies on beta diversity were the first to establish the complex relationships among distance, and spatial pattern of environmental heterogeneity. He noted that distance among sites was as important as environmental heterogeneity in determining beta diversity and its spatial structure. Later, Cody (1986, 1993) disentangled the environmental heterogeneity component from the one associated only to distance, developing a method that assigns the relative contribution of each component to beta diversity values (Cody 1993).

A more realistic approximation to the study of environmental heterogeneity as a determinant of beta diversity is the consideration of spatial auto-correlation as a fully-fledged controlled variable, where spatial structure of environmental factors and species composition are explicitly analysed. Using different plant and animal communities,

Fig. 2. Comparison of the resulting beta diversity spatial pattern using different techniques. A theoretical database built for this purpose contains 25 sites with 10 species, with one dominant species per vegetation type and, and a gradient in vegetation types ranging from the lower right corner to the upper left one, where beta diversity is largest in the lower right corner of the studied area. The arrows indicate the direction in which beta diversity is calculated from a centre of comparison. (a) Map of different vegetation types, showing a higher density of different patches at the lower right corner. (b) Isocomposition maps (Rapoport 1982) using Jaccard (presence/absence) index (Magurran 1988), with centre of comparison (base cell) at the lowest right corner; beta diversity is highest at the lower right corner. (c) Isocomposition contour map using Jaccard index, with base cell located at the centre of the study area; beta diversity pattern diverges from the expected one. (d) Isocomposition map using Morisita-Horn index (Magurran 1988), with base cell located at the lower right corner. (e) Scores obtained from a principal component analysis (Owen 1990) for the first axis that explains 55% of the variance in species composition among sites, where beta diversity pattern diverges from the expected one. (f) Scores from the principal component analysis for the second axis that explains 19% of the variance, where beta diversity is largest close to the lower right corner. (g) Neighbouring beta diversity using Wilson and Shmida index for presence/absence data, calculated for any given cell as average turnover with respect to its 8 neighbours (Mourelle and Ezcurra in press), and where the pattern of beta diversity pattern diverges from the expected one.
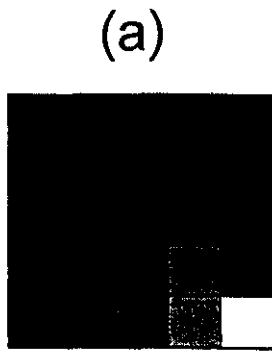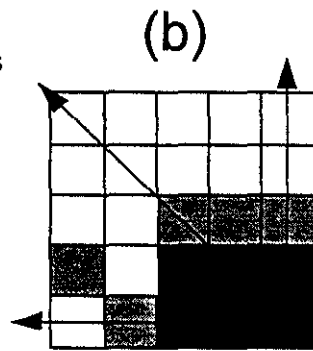
(a) Vegetation types
A
B
C
D
E
F
G
H

(b) Jaccard similitude index (base cell at lower right corner)
0 - 0.19
0.2 - 0.39
0.4 - 0.59
0.6 - 0.79
0.8 - 1
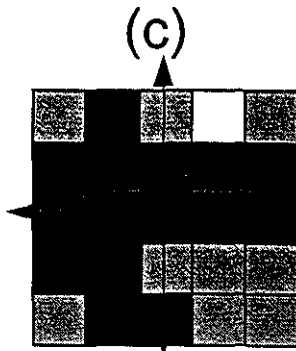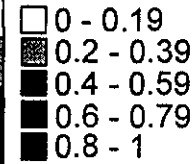
(c) Jaccard similitude index (base cell at center)
0 - 0.19
0.2 - 0.39
0.4 - 0.59
0.6 - 0.79
0.8 - 1
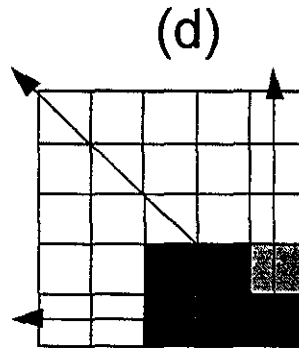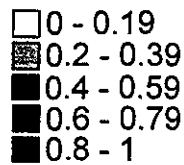
(d) Morisita-Horn similitude index (base cell at lower right corner)
0 - 0.19
0.2 - 0.39
0.4 - 0.59
0.6 - 0.79
0.8 - 1

(e) 1st. ordination axis values
0 - 0.9
1 - 1.9
2 - 2.9
3 - 3.9
4 - 4.9
5 - 5.9
6 - 6.9
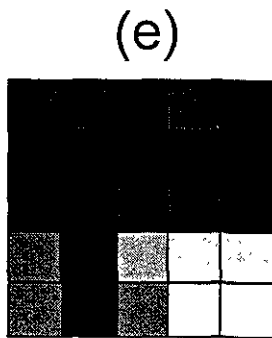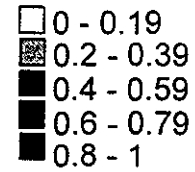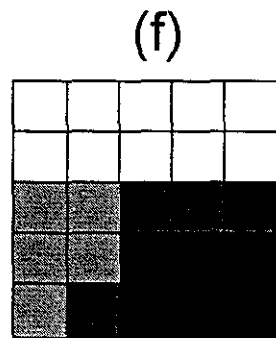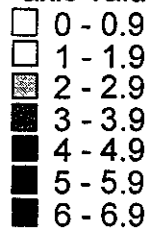
(f) 2nd. ordination axis values
-3 - -1.1
-1 - 0.9
1 - 2.9
3 - 4.9
5 - 7
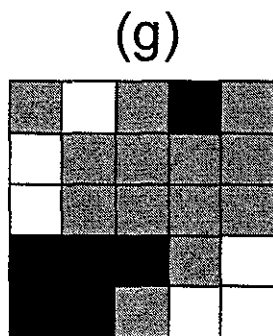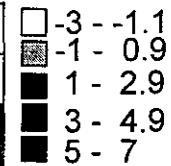
(g) Wilson and Shmida´s neighboring beta diversity
0.10 - 0.19
0.20 - 0.29
0.30 - 0.39
0.40 - 0.49

29
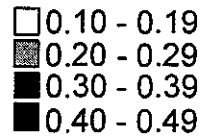
communities, Legendre and co-workers (Borcard et al. 1992, Leduc et al. 1992, Legendre 1993) successfully used geostatistical and multivariate tools to asses the proportion of spatial variance in species composition due to the individual and combined effects of space and environmental heterogeneity.

The analysis of distance dependent colonisation rates as a determinant of beta diversity has considered spatial relationships but ignored, in most cases, environmental heterogeneity. This topic, first addressed in the Island Biogeography theory by MacArthur and Wilson (1967), has been drawn back to attention with the increasing widespread fragmentation of native vegetation to study beta diversity in virtual island systems. For example, recent analyses of nested-subsets rest on that theoretical background (Patterson 1987). In fragmented scenarios, species distribution tend to have a nested-subset structure when species composition is identical among fragments. Exceptions to this trend may happen when gradual, highly predictable species losses occur, as fragments tend to become smaller.

Distance dependent colonisation rates are highly determined by species dispersal abilities. In a literature review, Cook and Quinn (1995) noted that the amount of nestedness observed was consistently related to species with high dispersal capacity, even though they accounted for a small subset of the whole community. Certainly, the trade-off between the species dispersal ability and its ecological tolerance range (Stearns 1977) is involved in the nested patterns. Species with a high dispersal ability tend to depend on disturbed environments while species with a low dispersal ability tend to grow in a wider range of conditions (MacArthur and Wilson 1967, Stearns 1977). Thus, life history attributes related to ecological tolerance range and their relation with the spatial pattern of environmental heterogeneity should be considered in the study of beta diversity.

The most challenging issue in the study of beta diversity is to consider simultaneously species dispersal abilities, distance dependent colonisation processes and spatial pattern of environmental heterogeneity. In a review, Patterson (1990) and Wright and Reeves (1992) found that highly nested-subset structures (i.e. scenarios with low beta diversity) were consistently associated either to the colonisation of species with high dispersal ability, or to the extinction of species sensitive to fragmentation, or to a low environmental heterogeneity. In Great Britain, Harrison and co-workers (1992), on the other hand, did not find differences in beta diversity among groups of plant and animal species with different dispersal abilities; beta diversity was more related to the environmental heterogeneity resulting from the extension of the sampling areas. Mourelle

and Ezcurra (1996, 1997) analysed cacti beta diversity along biogeographic transects in Argentina using spatial auto-correlation, and neighbouring turnover analysis. They found that beta diversity was associated to environmental climatic variables, and to species dispersal abilities. For plant species with high dispersal ability, Quintana-Ascencio and Menges (1996) found in Florida that among patch environmental variation (e.g., patch size and patch isolation) was a better predictor of beta diversity than environmental conditions within patches (e.g. fire frequency). Harrison (1997) in serpentine grasslands detected that environmental patchiness enhances beta diversity, through its effects on local species colonisation and extinction rates.

Understanding of the relative role played by the different determinants of species turnover is hindered by the fact that their importance changes among ecological systems and with the use of different spatial scales. This was evident in the study of mangrove epibiont communities by Farnsworth and Ellison (1996). At local scales (few meters) or regional ones (hundreds of square kilometres), beta diversity was mainly determined by distance from propagule source. At intermediate scales, however, environmental heterogeneity was the major determinant. The same was true for woody plant communities in Oregon; relative importance of abiotic environmental factors, disturbance, and spatial position changed among local and regional scales (Ohman and Spies 1998). Therefore, generalisations regarding the importance of the different factors and processes as determinants of beta diversity within a spatial context is not yet possible, as information for different biological systems at different spatial scales is still emerging.

Conclusions

According with our review, beta diversity is a synthesis of the differential distribution of single species in space. These are in turn associated to differences in environmental heterogeneity and the spatial pattern of such heterogeneity, spatial relationships among sites, distance dependent colonisation rates, species dispersal abilities, and spatial scale. The analysis of space and spatial patterns is thus inherent to the analysis of beta diversity.

Presently, methodological tools are already available to deal with a spatial perspective on beta diversity. Nevertheless, the multifactorial nature of the problem has hindered the understanding of the processes determining beta diversity. The analysis of spatial patterns of beta diversity is needed to understand local and geographical determinants of species distributions. Beta diversity is the link between the most widely

discussed components of species diversity, namely alpha and gamma diversity (Harrison et al. 1992, Ricklefs and Schluter 1993, Cornell and Lawton 1992). Understanding how alpha diversity scales into regional gamma diversity may enhance our comprehension of how species diversity is maintained and organised across different spatial scales. At present, however, our capacity to establish generalisations is weak, since we are in the beginning of the spatial analysis of beta diversity and its multiple determinants for many biological systems.

The spatial analysis of beta diversity is also important in an applied background. Description and understanding of the spatial structure of beta diversity is, for example, fundamental for the identification of priority areas for conservation of biodiversity (Blackburn and Gaston 1996, Williams 1996, Mourelle and Ezcurra 1996, 1997). The description of areas with complementary species composition is fundamental in the process of planning reserve networks; areas with high beta diversity are critical as they contain a great number of species within a restricted area. In the near future, the capacity to identify areas for conservation will be enhanced by obtaining a deeper knowledge of the spatial patterns of beta diversity.

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Capítulo III

Environmental and spatial determinants of beta diversity in a tropical dry forest

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Introduction

Beta diversity is the component of species diversity that evaluates the differential species composition among sites (Whittaker 1972, Magurran 1988). This component interacts with the so-called local (or "alpha") species diversity in determining the total (or "gamma") species diversity found in a region (Harrison et al. 1992). The beta component of species diversity is of critical importance in the identification of priority areas for conservation (Blackburn and Gaston 1996, Williams 1996, Mourelle and Ezcurra 1997); regions with high beta diversity will be amongst the most species-rich ones (Noss 1983). Beta diversity is also important for conservation biology as a measure of inter-site differences in species composition; maximising species complementarity is one of the major goals to be met by reserve networks (Margules et al. 1991).

As far back as the classical studies of Whittaker (1954, 1960, 1977), environmental heterogeneity has been identified as one of the major determinants of beta diversity. Many statistical tools and studies have been developed to identify the weight that each environmental variable has in explaining the spatial change in species composition (e.g. Jongman et al. 1987, Palmer 1993). As a result, predictive studies on regional and/or local diversity, based on environmental heterogeneity, are now arising (Nichols et al. 1998, Burnett et al. 1998).

A different approach to study the relationship between environmental heterogeneity and beta diversity is now possible through the understanding of the way this environmental heterogeneity is spatially organised (Kareiva 1994, Legendre 1993, Koening 1999). Environmental heterogeneity is not distributed randomly in space. Instead, closer sites tend to have more similar environmental values than distant ones (Bell et al. 1993, Legendre 1993). Also, distance among sites tends to be inversely related to species colonisation rates (MacArthur and Wilson 1967; Hanski and Gyllenberg 1997), and thus similarity in species composition among sites tends to decline as distance among sites increases (Whittaker 1977, Kadmon and Pulliam 1993). This means that just as environmental heterogeneity and colonisation rates, beta diversity may have a spatially auto-correlated structure. Even though Whittaker (1977) described this pattern long ago, the spatial structure of beta diversity and its relation to environmental heterogeneity has seldom been analysed.

In this paper we describe the relationship between the spatial structure of beta diversity of a tree community and that of the environmental heterogeneity. We have chosen, for this purpose, a tropical dry forest (TDF), a plant community for which

information on species diversity and the associated factors and processes is relatively scarce (Bullock et al. 1995). Tropical dry forests cover more than 40% of all the tropical areas of the world (Murphy and Lugo 1995) and they are nearly as diverse as the humid tropical forests (Gentry 1995). Tropical dry forests are undergoing rapid reductions due to severe deforestation and other human disturbance actions. Presently, *ca.* 0.1% of their original cover remains in Central America (Maass 1995). In Mexico, these forests are being transformed faster than any other ecosystem, at estimated annual deforestation rates that vary between 1.4% and 2.0% (Masera et al. 1992, Trejo 1998). Sound ecological research is urgently needed to understand tropical dry forest, design reserves, and develop adequate forest management procedures.

Water has been hypothesised to be the most important limiting factor to plant establishment and growth in tropical dry forests (Mooney et al. 1995, Murphy y Lugo 1995). Seasonal water availability has been associated to the timing of plant phenology (Bullock and Solís-Magallanes 1990, Borchert 1994), to above- and below-ground productivity (Martínez-Yrizar et al. 1996, Kummerow et al. 1990) and to nutrient cycling (Jaramillo and Sanford 1995, Campo et al. 1998)

Changes in community structure have also been associated to differences in soil water availability in tropical dry forests (Sampaio 1995, Bullock et al. 1995, Borchert 1994). In general terms, soil water availability depends on the balance of three major processes: i) water runoff and infiltration into the soil, closely associated to topography and soil characteristics (Ruhe 1975; Darlymple et al. 1968), ii) water retention in the soil associated to soil holding capacity and topography (Hewlett 1982), and iii) water evaporative demand associated to solar radiation interception (Dubayah 1994, Ezcurra et al. 1991, 92), which is in turn affected by slope angle and aspect.

In this work we focused on the tropical dry forest found in the pacific coast of Mexico, for which previous information on floristic and species diversity are already available (Lott et al. 1986, Lott 1993). The local species diversity and levels of endemism of plant and vertebrate species found here are considered among the highest when compared with similar areas in the Neotropics (Gentry 1995, Ceballos y García 1995). We restricted our analysis to several topographic gradients in small watersheds on the same geological formation to reduce the sources of environmental variation. After describing the general attributes of the TDF tree community in the watershed, we focused on the following questions: What is the magnitude of beta diversity and environmental heterogeneity among and within topographic gradients, and how are they related?, what is

the spatial pattern of beta diversity among and within gradients, and how are they related to the magnitude and spatial pattern of environmental heterogeneity?, and how consistent is the relationship between beta diversity and environmental heterogeneity among the two spatial scales?

Materials and Methods

Study site

The study was conducted at the Chamela Biological Station of the National Autonomous University of Mexico. This 1600-ha area is part of the 13000-ha Chamela-Cuixmala Biosphere Reserve, located in the state of Jalisco, South of Puerto Vallarta and only 2-km from the Pacific coast (19° 30'N, 105° 3' W, SEMARNAP 1995). More than 1200 plant (Lott 1993) and 420 vertebrate species have been recorded at Chamela-Cuixmala (Ceballos y Garcia 1995, Gentry 1995).

The climate of Chamela is warm with a mean annual temperature of 24.9 °C, and a mean annual precipitation of 748-mm. Rainfall is strongly seasonal with 80% falling between July and October (Bullock 1986, García-Oliva et al. 1991).

The reserve is mainly dominated by tropical dry forest, with small areas of tropical semideciduous forests along riparian zones of main streams (*sensu* Rzedowski 1978). Average canopy height in tropical dry forest is around 10 m, and most mature individual trees measure between 5 and 10 cm of DBH (diameter at breast height, 1.30 m above ground). In the semideciduous or Arroyo forest, average canopy height is around 18 m and trees with DBH larger than 30 cm are common. Some of the most abundant tree species found within the TDF at Chamela are *Plumeria rubra* (Apocynaceae), *Cochlospermum vitifolium* (Cochlospermaceae) *Gliricidia sepium* (Leguminosae), *Comocladia engleriana* (Anacardiaceae), *Celaenodendron mexicanum* (Euphorbiaceae), *Caesalpinia eriostachys* (Leguminosae), *Cordia elaeagnoides* (Boraginaceae), *Guapira macrocarpa* (Nyctaginaceae), and *Bursera instabilis* (Burseraceae, Durán et al. in press.).

Experimental design

We selected a system composed of five small watersheds (16 to 28 ha each) where ecosystem processes are currently under study (Maass et al. 1995, Sarukhán and Maass 1990); we only selected three parallel watersheds. The soil of this area is an association of entisol, inceptisol and alfisol developed from a granite bedrock (Cotler et al.
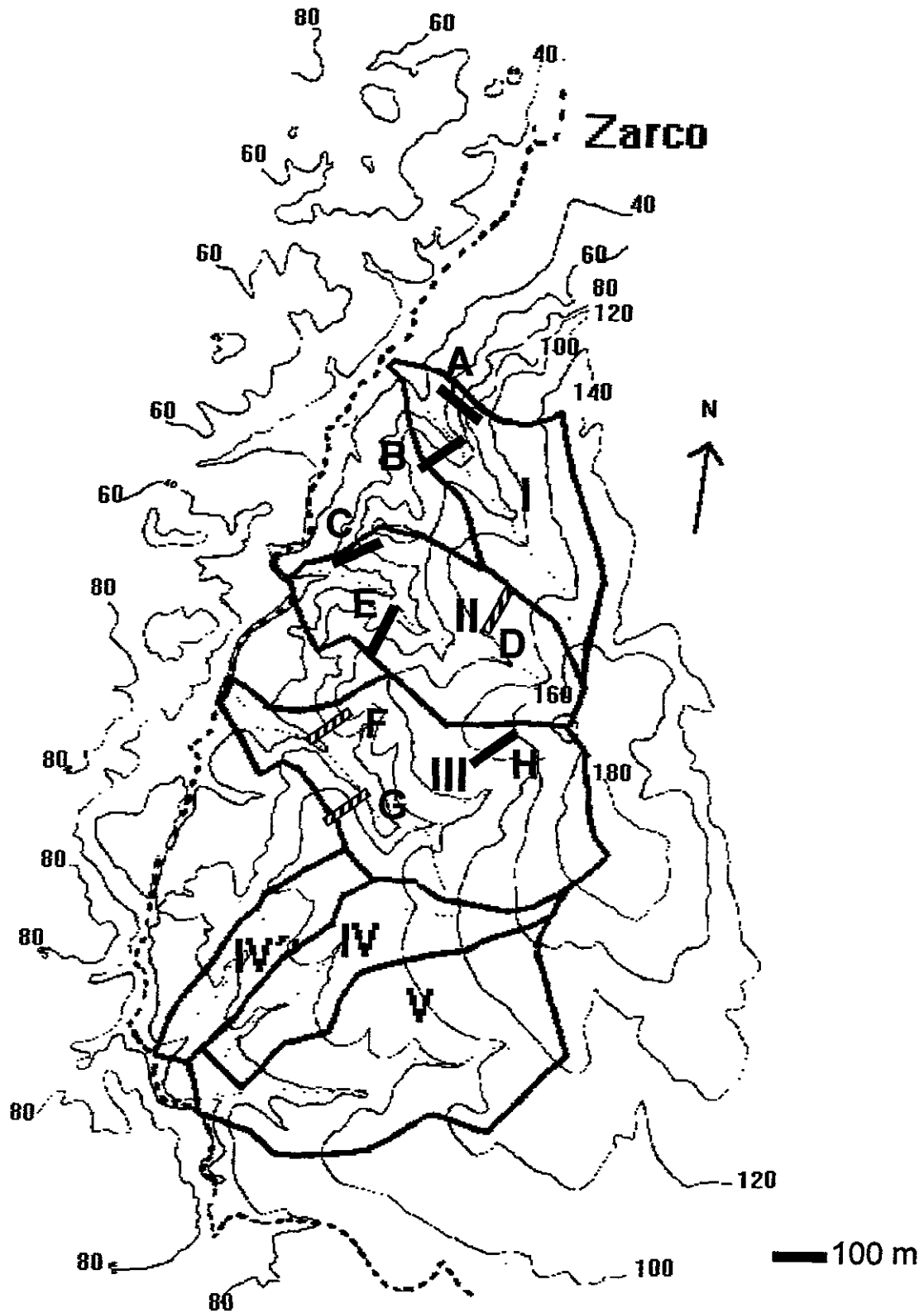
Fig. 1. Study site and experimental design. Bold lines indicate the limits of each watershed; single lines are altitudinal countour lines (altitude in meters over sea level); dashed line shows a temporary stream. Rectangles represent approximate position and dimensions of transects; dashed transects are those selected for within transect analysis.

in press, Solís 1993). The elevation gradient within the watersheds ranges from 40 to 190 m, where changes in soil depth and texture (Galicia 1992), soil water availability (Zarco 1994), and nutrient availability (Solis 1993, Campo 1995) have been described.

Eight 30 X 100 m transects were laid parallel to the major altitudinal change of the study watersheds from the main stream channel to the local crest (Fig. 1). Each transect was divided into thirty 10 X 10 m quadrats. Position of transects was located within a 1:20 000 topographic map (SEDUE 1980).

Vegetation sampling

Within each 10 X 10 m quadrat (N = 240), all trees with a DBH larger than 5 cm were numbered, tagged and identified. Species were identified in the field and from reference specimens. Voucher herbarium specimens are available at the Station herbarium, and the reference collection is available from the authors. Species names follow nomenclature given by Lott (1993).

Environmental data sampling

Four environmental variables, associated to soil water content were measured within each 10 X 10-m quadrat. i) Elevation over sea level, as an indicator of relative position within watershed, was measured at the four corners of each quadrat and then averaged. ii) Slope, associated to water runoff and infiltration, was measured in the same way as elevation. iii) Total annual solar radiation interception (total annual insolation) on top of the canopy, associated to water evaporative demand, was modelled from slope, aspect and angle to the horizon measured at the four corners of each sampled quadrat using Joule 2.0 program (Ezcurra 1996, Ezcurra et al. 1991, 1992). iv) Soil available water holding capacity (AWHC), associated to water retention in soil, was estimated using the well known relationships between soil type, porosity and soil holding capacity (e.g., Brady 1990); field determination of depth, stoniness and texture (finger probe) of each horizon was done from a soil core (< 1 m deep) taken at the centre of each sampled quadrat; SAWHC was calculated using well known databases (Siebe et al. 1996); a correction factor considering the percentage of the total quadrat surface covered by exposed rock was used.

Among transect data analysis

Species data from each one of the 10 X 10 m quadrats were organised into

abundance and presence/absence data matrices for the eight transects.

The changes in the tree community among transects was assessed through the description of species richness (total number of species), species diversity (Shannon-Wiener Index base 2, calculated as indicated in Magurran 1988), and density (total number of trees). Beta diversity was quantified by calculating the dissimilitude among all pairs of transects using the formula

$$\beta = 1 - C_j$$

where C_j is the Jaccard similitude index

$$Cj = \frac{j}{a+b-j}$$

being j the number of species shared by both sites, a the number of species in a site a, and b the number of species in a site b (Magurran 1988). Accordingly, a value of $\beta = 0$ means total compositional similarity among pairs of sites, and a value $\beta = 1$ means total dissimilarity. Beta diversity was described qualitatively through the analysis of the species composition of three contrasting transects (see "within transect analysis" for characteristics of such transects); sharper differences in species abundance among these transects was noted.

Environmental heterogeneity was described by comparing average values taken by the four environmental variables at each transect. Differences in average environmental conditions among transects were tested by using one way-ANOVA and Kruskal-Wallis non-parametric ANOVA and a *posteriori* multiple comparisons among means with the Tukey test (SAS Institute Inc. 1989-1996).

The relationship between beta diversity and environmental heterogeneity among the eight transects was established with a Canonical Correspondence Analysis (CCA; McCune and Mefford 1995, Palmer 1993). Average values of the 4 environmental variables and presence/absence data were centered and normalized; ordination site scores, derived from a linear combination of variables, and biplot scores for environmental variables were graphed. Biplot scores and intra-set correlation were used to assess the relationship between environmental variables and canonical axes.

Spatial pattern of beta diversity was assessed using a modification of a method originally proposed by Whittaker (1977). First, distance among pairs of transects was obtained from the position of transects on the topographic map (SEDUE 1980). Secondly, beta diversity values, obtained from all possible pairs of transects, were averaged for five

categories of distance. Finally, average values were regressed against inter-transect distance using linear models (SAS Institute Inc. 1989-1996).

Within transect data analysis

In order to analyse beta diversity within transects, 3 example transects were selected based on available geomorphological information on the study watersheds (Galicia 1992, Galicia et al. 1995, López Blanco et al. 1998), previous field work (G. Segura et al. unpubl. data), and environmental data obtained from the "among transect". Transects D, G and F were chosen because of their contrasting environmental conditions, specifically with respect to position within the watersheds, aspect, slope and soil type, to represent the variation in topographical and edaphical conditions found within the watersheds (Fig. 2). To summarise these contrasts transects were called Crest transect (D), South slope transect (G) and North slope transect (F). Data from soil cores was used to describe soil types for characterisation purposes.

The changes in the tree community within each transects were assessed by calculating species richness, species diversity (see above) and total number of trees per quadrat for the three contrasting transects. Within transect beta diversity was quantified by comparing all pairs of 10 X 10 m quadrats using Jaccard similarity index for the three contrasting transects (see above). Beta diversity within the three contrasting transects was also quantified through the analysis of species accumulation curves (Connor and McCoy 1979). Within each transect, an average species-area curve was obtained from 100 random shuffling of presence/absence data for individual quadrats (Connor and McCoy 1979); the resulting curve was fit to the Clench model (Soberón and Llorente 1993):

$$Species = \frac{a*Area}{1+(b*Area)}$$

where *a* and *b* were estimated parameters of the model; the *a/b* ratio was used as a measure of beta diversity.

Within transect beta diversity was assessed qualitatively by comparing single species distribution along the three contrasting transects. We compared the species observed distribution against a homogeneous one using a chi-squared test, for the twelve most abundant species, those for which enough data was available to perform such a test. The species were: *Bursera instabilis, Celaenodendron mexicanum, Cochlospermum*
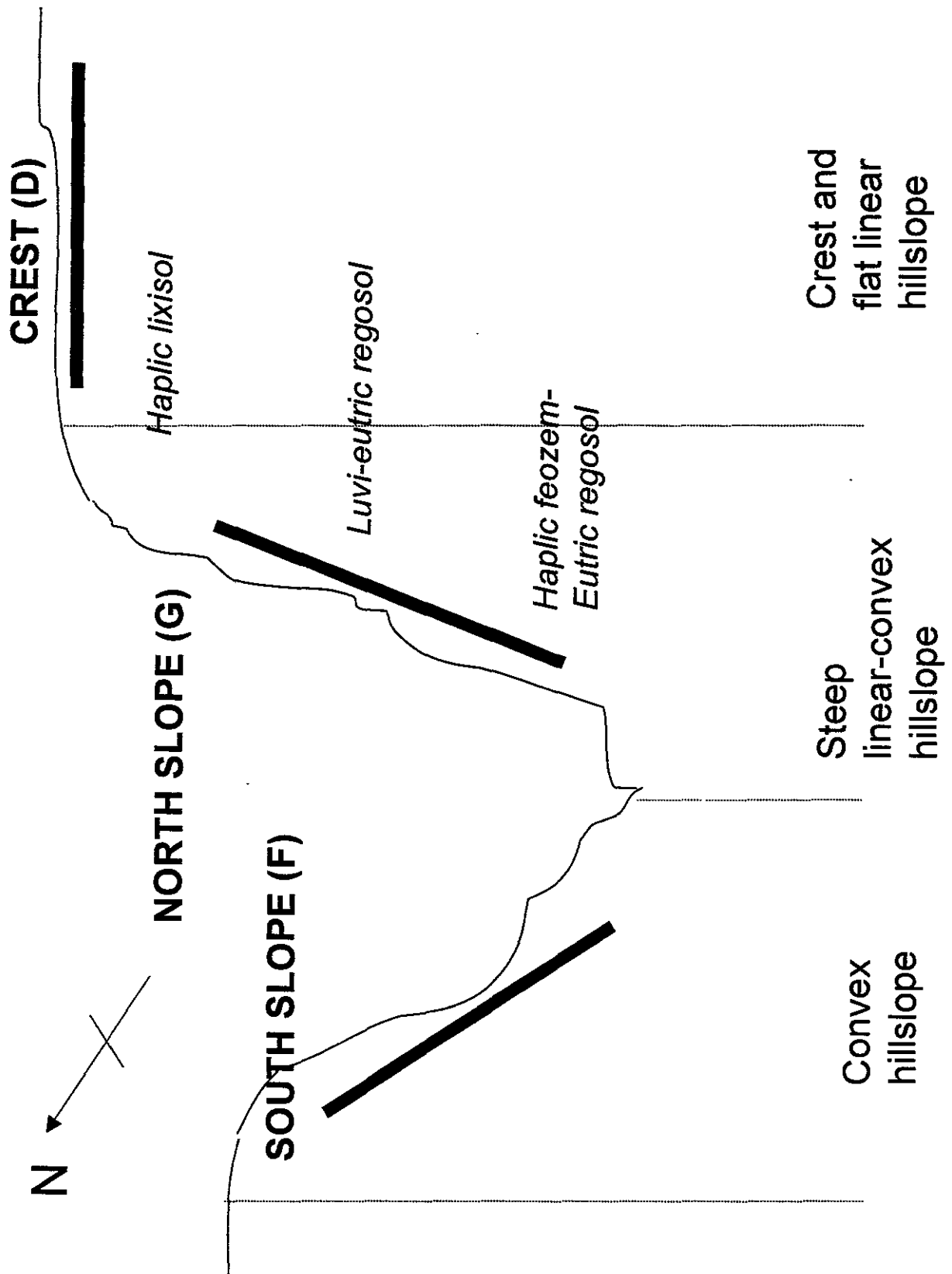
Fig. 1. Diagramatic representation of the study watershed and three contrasting transects. Topographic features and aspect of three contrasting types of hillslope units are represented based on previous available data (Galicia 1992, Galicia et al. 1995, Lopez-Blanco et al. 1998). Soil types at different sections of the topographic gradient are given in italics based on data gathered in this work. Solid bars represent aproximate location of the three contrasting transects.

vitifolium, Comocladia engleriana, Esenbeckia nesiotica, Guapira macrocarpa, Gliricidia sepium, Helietta lottiae, Lonchocarpus eriocarinalis, Lonchocarpus sp., Plumeria rubra, and *Thouinidium decandrum.*

Environmental heterogeneity within transects was described using the average (and standard error) values taken by the 4 environmental variables at 10 m intervals along the transect; a distance of 0 m corresponded to quadrats closer to the mainstream channel.

The relationships between environmental heterogeneity and beta diversity within transect, and the spatial pattern of beta diversity were assessed as described in above section. For each one of the transects, the observed spatial pattern of beta diversity within transects was compared to a null model in which species were randomly distributed along the transects. The null model was constructed by shuffling at random the observed spatial location of species along the transect (presence/absence data); this procedure was repeated 100 times and average (and its standard error values) null model values of species similarity among pairs of quadrats was compared with data obtained in the field, for different distance categories among pairs of quadrats.

The spatial pattern of environmental heterogeneity was described using the same procedure used for the spatial pattern of beta diversity, where average values of the absolute difference among pairs of quadrats for each environmental variable were regressed against inter-quadrat distance using linear models (see Legendre and Fortin 1989 for similar procedures known as semivariograms). The spatial pattern of environmental heterogeneity was related to that of beta diversity by calculating the correlation between species composition similarity and differences in environmental conditions at different distances among pairs of quadrats.

Comparisons among scales

To asses the relative role of environmental heterogeneity as a determinant of beta diversity at the two spatial scales (among and within), a relative environmental heterogeneity index was built. Environmental heterogeneity (EH) was calculated as a multidimensional euclidian distance

$$EH = \sqrt{((E\imath - Ej)2 + (S\imath - Sj)2 + (I\imath - Ij)2 + (W\imath - Wj)2}$$

where *E* is elevation, *S* is slope, *I* is total annual insolation and *W* is AWHC for any pair of sites i and *j*. Absolute values of EH were then standardised so that maximum EH at any of

the two scales was *1*. In the case of among transect analysis, all pairs of the eight transects were compared; in the case of within transect analysis, all 30 quadrats were compared within each transect. In both cases beta diversity values were regressed against relative environmental heterogeneity (SAS Institute Inc. 1996) and the parameters of the resulting linear models were compared.

Results

A total of 3128 trees were tagged and identified in the total sampled area (2.4 ha). A total of 118 species were identified among these trees.

Among transects analysis.

Comparison of the community characteristics of the 8 transects showed a great variance in community structure and species diversity among them (Table 1). Number of species within a single transect varied from 27 to 63 of the 118 species found. Density ranged from 239 and 532 trees. Shannon-Wiener species diversity index took values between 2.85 and 3.52, although most values were above 3.

Beta diversity values among transects varied from 0.21 up to 0.7; in average, pairs of transects shared less than 50% of species (average $\beta = 0.42$). Transects D, F and G shared between 50 and 60% of common species (Table 2).

Qualitative analysis of beta diversity among transects showed that more than 50% of the species recorded were present in 3 transects or less; only 8 out of the 118 species were present in all the transects. These species were *Caesalpinia eriostachys*, *Comocladia engleriana*, *Guapira macrocarpa*, *Lonchocarpus sp.*, *Lysiloma microphylla*, *Tabebuia chrysantha* and *Tabebuia impetiginosa*. When analysing species abundance data from 3 selected transects (D, F and G), the largest differences in composition among transects resulted from a high dominance of *Celaenodendron mexicanum* in transects F and G and its complete absence in transect D (Table 3). *Guapira macrocarpa* was very abundant in just one transect (F). Instead, *Cochlospermum vitifolium* and *Euphorbia tanquehuete*, were most abundant in the transect D. *Plumeria rubra* was the only species, out of 88 analysed, with high abundance in the three transects (Table 3). Almost 40% of the species were recorded in only one transect and they less than 3 individuals; this was the case of *Lippia macvaughii*, *Pterocarpus orbiculatus* or *Sciadodendron excelsum* (Table 3).

Environmental conditions differed among transects (Table 4). Elevation ranged

Table 1. Species richness, diversity (Shanon diversity index base 2) and density of trees in eight 30 X 100m transects. Values in bold indicate the three selected transects for further analysis.

	A	B	C	D	E	F	G	H
Richness	59	60	63	**43**	63	**52**	**64**	27
Density	357	371	532	**415**	369	**532**	**369**	239
Diversity	3.42	3.37	3.36	**3.05**	3.39	**3.16**	**3.52**	2.85

Table 2. Beta diversity values among all pairs of transects. Beta diversity was calculated using Jaccard similarity index, where maximum beta is 1 when pairs of transects do not share any species. Values in bold outline those corresponding to the three selected transects for further analysis.

	A	B	C	D	E	F	G	H
A	0.00	0.47	0.52	**0.51**	0.44	**0.46**	**0.36**	0.23
B		0.00	0.42	**0.47**	0.47	**0.70**	**0.42**	0.49
C			0.00	**0.34**	0.51	**0.53**	**0.34**	0.29
D				**0.00**	0.39	**0.49**	**0.41**	0.56
E					0.00	**0.34**	**0.41**	0.32
F						**0.00**	**0.41**	0.32
G							**0.00**	0.21
H								0.00

Table 3. Changes in species abundance among three selected transects. Values in bold indicate strongest contrasts in species abundance among transects.

Species	D	F	G	Species	D	F	G
Adelia oaxacana	0	4	12	*Helietta lottiae*	14	17	0
Alstonia longifolia	4	3	0	*Ipomoea wolcotiana*	2	3	0
Allenanthus hondurensis	0	1	0	*Jacaratia mexicana*	0	0	2
Amphipteringyum adstringens	11	7	3	*Jacquinia pungens*	0	0	1
Apoplanesia paniculata	0	0	2	*Jatropha chamelensis*	0	0	2
Bourreria purpusii	16	4	9	*Jatropha standleyi*	0	1	4
Brogniartia sp.	0	1	0	*Lippia macvaughii*	0	0	1
Bunchosia palmeri	0	0	1	*Lonchocarpus constrictus*	3	0	1
Bursera sp.	0	0	6	*L. eriocarinalis*	24	23	11
Bursera arborea	1	1	2	*L. magallanensis*	2	0	0
Bursera excelsa	6	1	1	*Lonchocarpus sp.*	21	23	40
Bursera fagaroides	2	1	0	*Lueha candida*	0	1	0
Bursera heterestes	1	17	7	*Lysiloma microphylla*	0	2	8
Bursera instabilis	**1**	**23**	**6**	***Macahonia acuminata***	**19**	**1**	**0**
Caesalpinia caladenia	0	0	1	*Malpigia ovata*	1	1	0
Caesalpinia eriostachys	0	7	10	*Morisonia americana*	0	0	1
Caesalpinia platycarpa	0	0	1	*Pitiricarpa constricta*	11	31	3
Caesalpinia sclerocarpa	1	4	2	*Pithecelobium mangense*	1	3	0
Capparis indica	0	1	8	*Pithecelobium platycarpa*	0	0	1
Capparis verrucosa	0	0	2	*Plumeria rubra*	55	55	33
Casearia corymbosa	1	1	11	*Poepigia procera*	0	0	2
Casearia tremula	0	0	2	*Psidium sartorianum*	11	15	0
Ceiba grandifolia	1	0	2	*Psychotria microphylla*	0	0	1
Celaenodendron mexicanum	**0**	**67**	**34**	*Psychotria sp.*	0	0	1
Cnidosculus spinosus	0	3	2	*Pterocarpus orbiculatus*	0	0	1
Cochlospermum vitifolium	**78**	**3**	**2**	*Randia sp.*	2	5	3
Colubrina heteroneura	2	1	0	*Randia thurberi*	1	0	0
Comocladia engleriana	**11**	**27**	**4**	*Coccoloba sp.*	0	1	0
Cordia alliodora	2	0	0	*Ruprechtia fusca*	0	0	8
Dalea congestiflora	9	2	0	*Samida mexicana*	14	4	0
Diospyrus aequoris	0	2	0	*Savia sessiliflora*	0	0	1
Discognite mexicana	**0**	**0**	**20**	*Sciadodendron excelsum*	0	0	1
Erythrina lanata	1	1	4	*Sideroxylum stenospermum*	5	2	1
Erythroxylum rotundum	0	2	1	*Sp. 1*	0	1	0
Esenbeckia nesiotica	8	17	6	*Spondias purpusii*	0	0	1
Euphorbia tanquehuete	**25**	**4**	**0**	*Strychnos brachistantha*	0	0	1
Exostema caribaeum	4	9	1	*Styphnolobium protanterum*	0	0	2
Ficus cotinifolia	0	0	1	*Tabebuia chrysantha*	7	19	8
Forchameria pallida	0	0	2	*Tabebuia impetiginosa*	1	16	13
Gliricidia sepium	18	9	0	*Thouinidium decandrum*	0	0	9
Guapira macrocarpa	**9**	**74**	**25**	*Thouinia paucidendata*	0	0	3
Guetarda elliptica	2	3	2	*Trichilia trifolia*	0	0	6
Haematoxylum brasileto	6	6	0	*Urera caracasana*	0	0	2
Heliocarpus pallidus	0	0	5	*Zanthoxylum caribaeum*	1	2	0

Table 4. Average, standard error (s.e.), coefficient of variation (C.V) and range of environmental conditions present at eight 30 X 100 m transects based on data form all 10 X 10 m quadrats. AWHC = available water holding capacity. Values in bold indicate three selected transects for further analysis. Small letters indicate significative differences among transects resulting from Tukey test multiple comparisons among means.

	Elevation (m)					Total annual insolation (MJ/ha.y)					AWHC (l/m^2)				
Transect	Average	s.e.	C.V.	Maximum	Minimum	Average	s.e.	C.V.	Maximum	Minimum	Average	s.e.	C.V.	Maximum	Minimum
A	62.66^a	2.13	18.58	84.00	48.75	13.01^{ab}	0.28	11.86	16.14	9.70	47.79^{ab}	4.63	53.09	92.24	11.81
B	87.31^{bc}	2.87	18.02	108.25	63.00	7.15^c	0.77	58.93	16.64	3.16	31.79^b	3.38	58.20	72.28	2.61
C	77.03^{bc}	3.37	23.97	105.50	49.50	14.51^{abd}	0.25	9.52	16.84	12.40	47.65^{ab}	2.69	30.90	94.55	28.93
D	**136.70^d**	**0.52**	**2.07**	**142.00**	**131.25**	**15.52^{bd}**	**0.07**	**2.64**	**16.38**	**14.88**	**44.47^{ab}**	**5.36**	**66.07**	**102.68**	**5.38**
E	96.48^e	2.62	14.88	117.50	74.00	8.27^c	0.60	39.70	13.44	2.39	46.97^{ab}	5.89	68.70	147.53	1.14
F	**97.25^{ce}**	**2.18**	**12.26**	**111.00**	**77.67**	**15.94^{bd}**	**0.16**	**5.49**	**17.77**	**14.02**	**54.50^a**	**3.37**	**33.86**	**79.31**	**21.11**
G	**100.67^e**	**4.12**	**22.39**	**135.50**	**69.25**	**6.58^c**	**0.55**	**45.52**	**13.16**	**3.51**	**40.07^{ab}**	**3.06**	**41.83**	**80.27**	**14.34**
H	136.88^d	1.34	5.36	150.50	123.50	14.82^{abd}	0.15	5.68	16.03	13.35	35.04^b	3.85	60.23	81.46	0.00

from 49 to 150 meters over sea level, representing most of the altitudinal variation found within the three studied watersheds. Average elevation values were significantly different among transects (Kruskal-Wallis test χ^2 = 167.46, d.f. = 7; p< 0.0001). Elevation showed to be nearly constant in some transects (coefficient of variation = 2.07) and very variable in others (C.V. = 23.97). Slope values differed significantly among two groups of transects (χ^2 = 116.3; d.f. = 7; p < 0.0001): the relatively flat ones (A D, F and H), and the steep ones (B C, E and G). Variation of slope values within transects was generally large (25.1 to 49.9). Highest total annual insolation values (17.8 MJ/ha.y) were three times larger than lower ones (2.4 MJ/ha.y) and average values were significantly different among transects (χ^2 = 171.9; d.f. = 7; p < 0.0001). Lowest total annual insolation values corresponded to steep slopes with a North-facing aspect, whereas highest values corresponded to steep slopes with a South-facing aspect. Variance in insolation ranged from very homogeneous transects (C.V. = 2.64) to very heterogeneous ones (C.V. = 59.0). Significant differences among average AWHC values within transects were found (F = 3.2; d.f. = 2, 232; p < 0.01), nevertheless a large variance in AWHC occurred within all transects. Extreme values obtained for quadrats within transects ranged from virtually no holding capacity (1.1 l/m^2) to a quite large one (147.5 l/m^2).

We found a clear relationship between environmental heterogeneity and beta diversity at this among transect scale. Results from the CCA analysis showed that the three first canonical axes explained 22.0, 17.8 and 14.3% of the total variance in species composition. These axes were highly correlated with elevation (-0.69, 0.42 and -0.51, respective correlation coefficient values for these three axes), slope (0.47, 0.60 and 0.65) and insolation (-0.68, -0.65 and –0.09) but not with AWHC (-0.19, -0.23 and -0.05). Transects A and H were the most different with respect to an insolation gradient, whereas C and H were the extremes on a slope-elevation gradient (Fig. 3).

Spatial pattern of beta diversity showed a tendency of closer transects to be more similar in composition than distant ones (Fig. 4). The resulting model had a low slope (-0.0001) that was nevertheless significantly different from 0 (t = -3.80; p = 0.0191), and the model had a high determination coefficient (R^2 = 0.83).

Within transects analysis

Tree community structure, measured as richness, Shannon diversity and density, varied largely among quadrats within transects. Tree density ranged from 3 to 22, 4 to 16 species could be found per quadrat, and Shannon species diversity ranged from 1.10 to
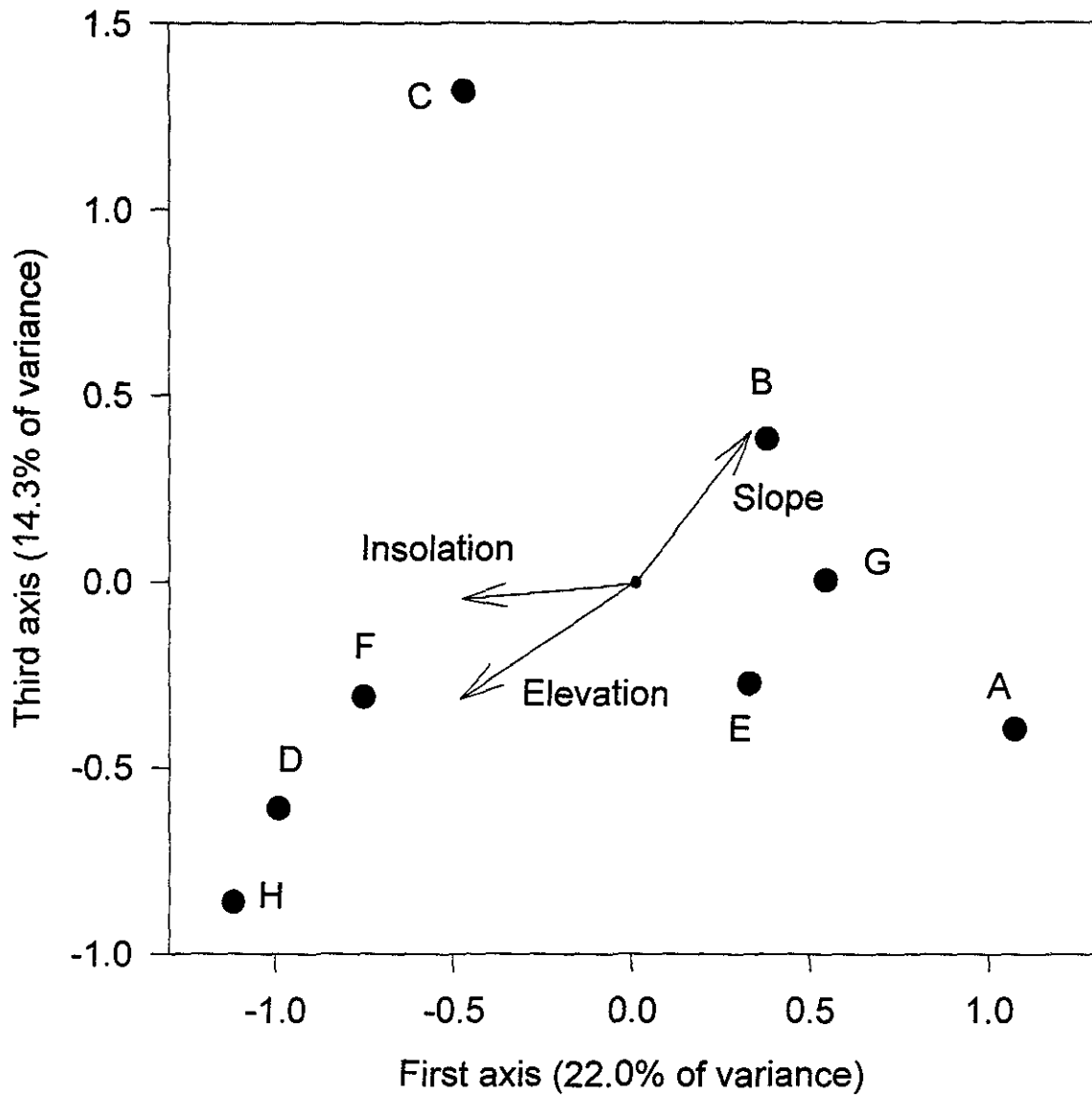
Fig. 3. Canonical Correspondence Analysis ordination diagram of the eight 30 X 100 m transects
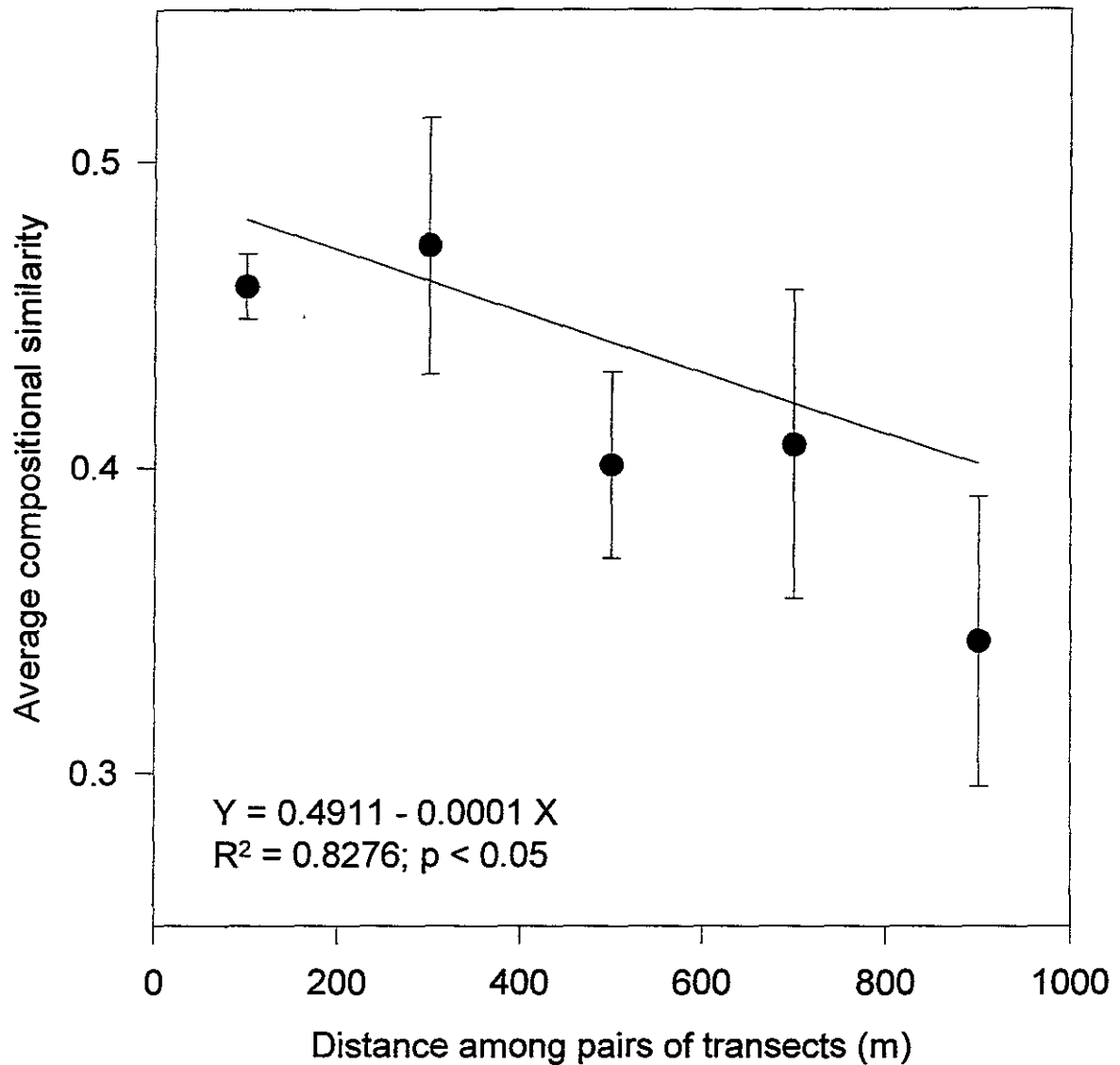
Fig. 4. Spatially autocorrelated structure of beta diversity. Points represent average (and standard error) values of species composition similarity among pairs of transects for 5 distance categories. All possible comparisons among the 8 30 X 100 m transects were performed.
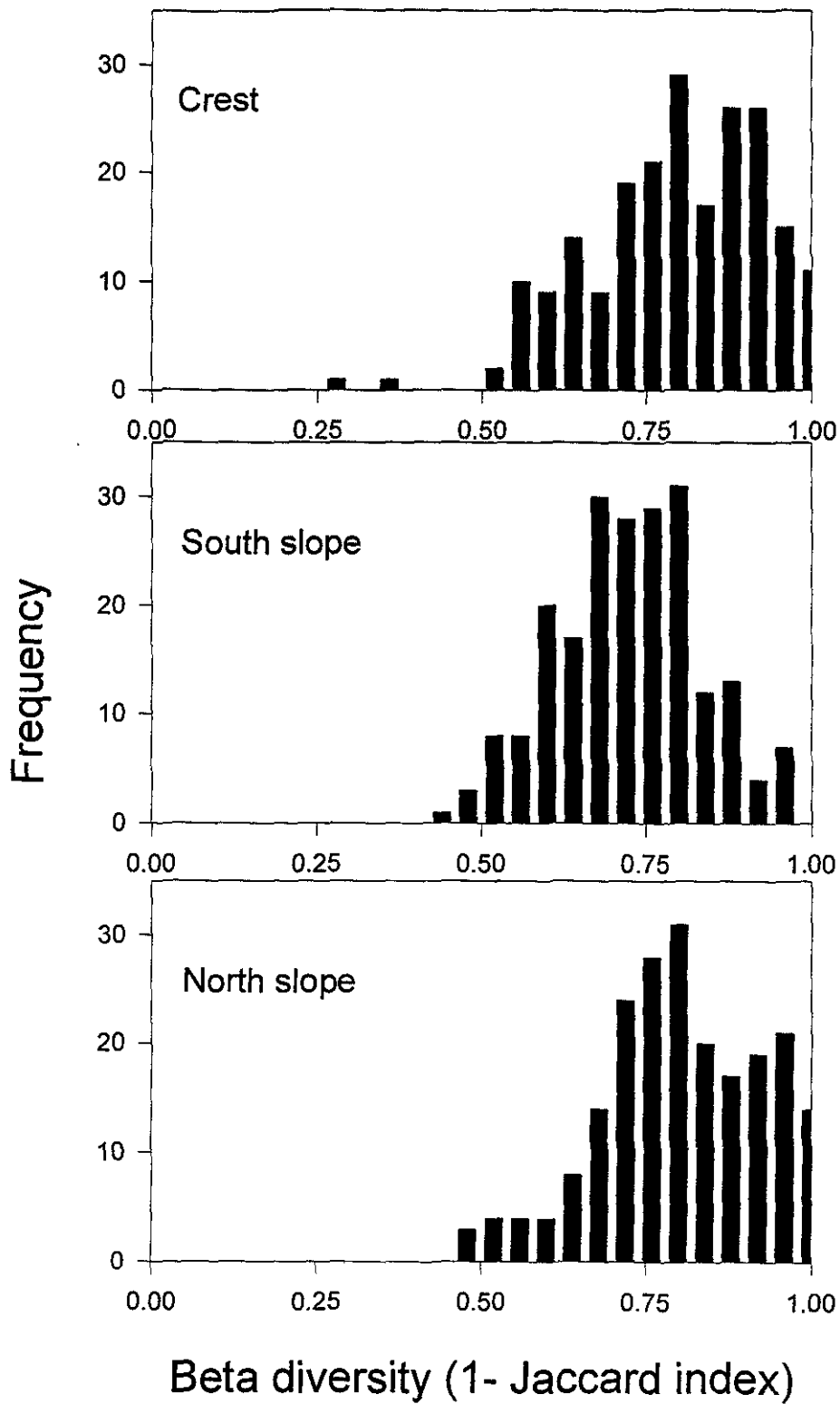
Fig. 5. Beta diversity values of the pair-wise comparison of all pairs of 10 X 10 m quadrats within Crest, South slope and North slope transects.

2.67.

Beta diversity values within quadrats was high in all 3 transects (Fig.5). Most beta diversity values ranged from 0.5 to 1, meaning that similarity was less than 50% in most cases ($\beta = 0.5$), and even reached total dissimilarity ($\beta = 1$). A significant variation was found among average values for the 3 transects (F = 110.8; d.f. = 2,632; p < 0.0001), but differences among them were not comparable to the elevated variance in beta diversity values found within each transect (0.78, 0.71 and 0.79 average values for Crest, South slope and North slope respectively). Beta diversity, measured as species accumulation rate (a/b = 50.9, 63.0 and 84.9 respectively), was also lowest in the crest transect, and highest in the north slope one (Fig. 6).

Qualitative assessment of beta diversity within transects showed that North slope transect had a higher proportion of species with clumped distributions (3 out of 8 species), than the Crest (1 out of 10 species) and South slope transects (2 out of 10 species; Fig. 7). *Cochlospermum vitifolium* ($\chi2 = 7.6$; d.f.= 9; p < 0.00001) was clumped towards the upper section of the Crest transect. *Celaenodendron mexicanum* ($X^2 = 53.5$; d.f. = 9; p < 0.0001) was most abundant in the lower section of the South slope transect, whereas *Guapira macrocarpa* ($\chi2 = 23.8$; d.f. = 9; p < 0.01) was rare in the central section of that transect. *Esenbeckia nesiotica* ($\chi2 = 37.3$; d.f. = 9; p < 0.001) and *Plumeria rubra* ($\chi2 = 34.6$; d.f. = 9; p < 0.001) were present only in the upper part of the North slope transect, whereas *Thohuinidium decandrum* ($\chi2 = 25.4$; d.f. = 9; p < 0.01) was only found in its lower part (Fig. 7). *Bursera instabilis, Comocladia engleriana, Gliricidia sepium, Helietta lottiae, Lonchocarpus eriocarinalis,* and *Lonchocarpus sp.* showed a random distribution along the transects in which they occurred.

Environmental heterogeneity within transects presented a clear environmental gradient for elevation and insolation values (Fig. 8). In the case of soil AWHC a great variance within transects was observed. Elevation was highest at the Crest transect, and showed only a reduced variation; the South and North slope transects showed a clear increase in elevation. Altitudinal range was largest in the North slope transect. Total annual insolation did not vary along the crest and the south slope transects. Instead, at the North transect, insolation was up to three times lower in its lower part than at its highest section, due to the contrasting slope values taken along this transect, and to the shade of the facing slope to the lower part of this transect.

A relationship between environmental heterogeneity and beta diversity within transects was found but the amount of variance in species composition explained by

The plot contains the following text/equations:

Crest - Y = (744.3 X) / (1 + (14.62 X))
South slope - Y = (828.7 X) / (1 + (13.1 X))
Medium slope - Y = (782.8 X) / (1 + (9.219 X))

Legend:
- Crest - Predicted
- South slope - Predicted
- North slope - Predicted
- Flat - Observed
- Medium - Observed
- Abrupt - Observed

Axis labels: Cumulative number of species (y-axis), Area (ha) (x-axis)
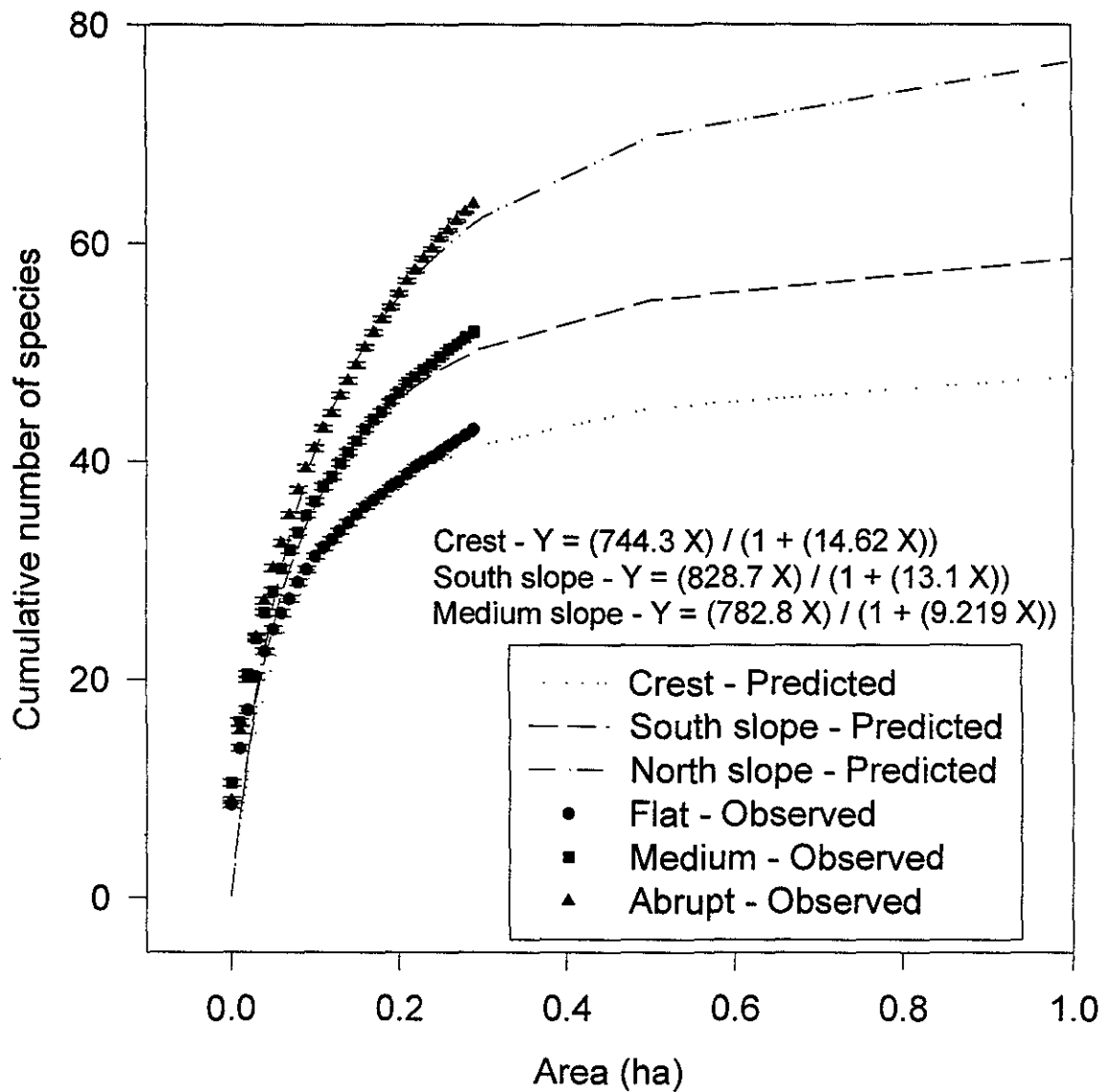
Fig. 6. Observed and modelled species-area curves for the three contrasting transects.
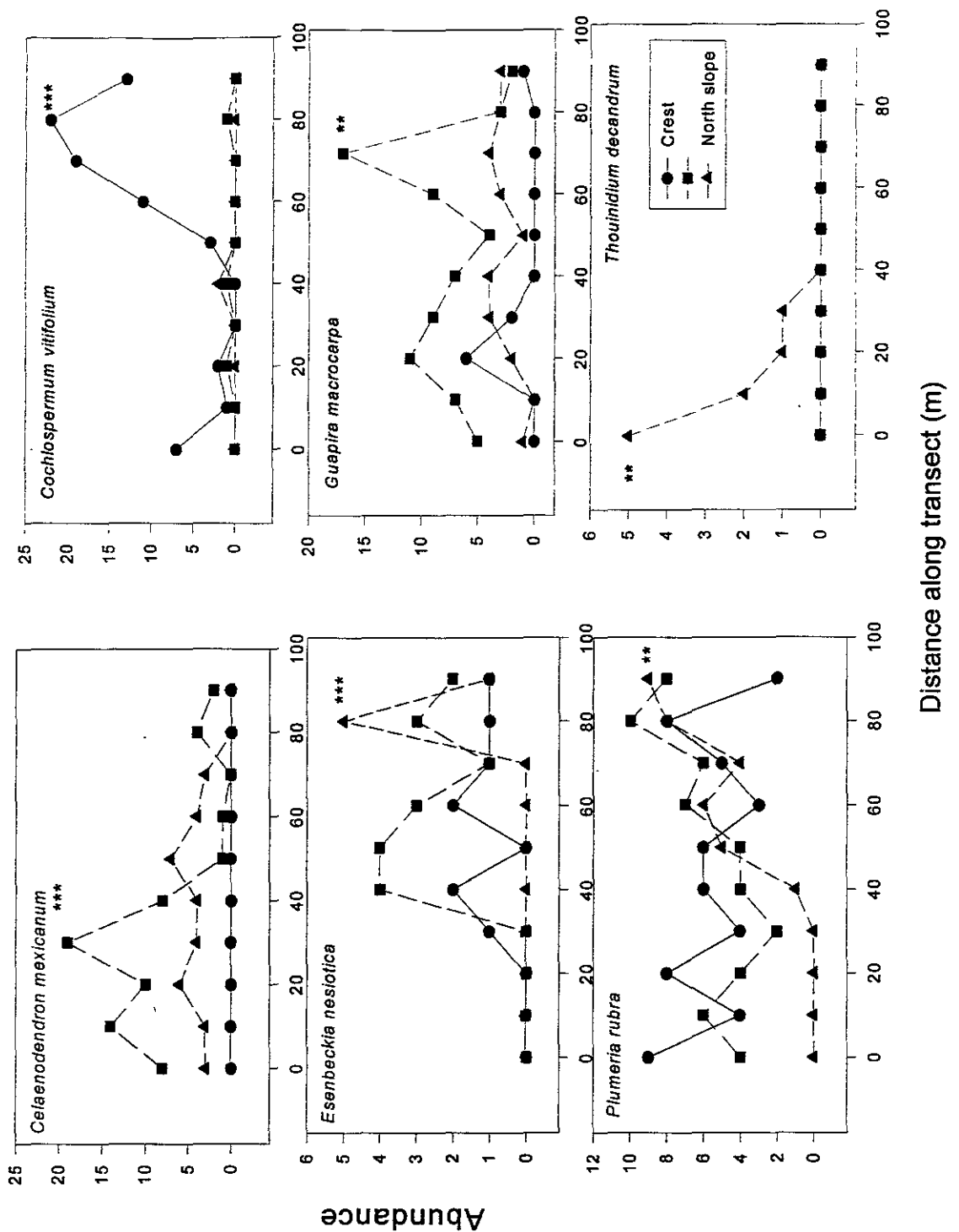
Fig. 7. Qualitative assessment of beta diversity within three contrasting transects through the analysis of the spatial pattern of single species distribution along the transects. Each point indicates the number of trees within the three 10 X 10 m quadrats located in the same row of the 30 X 100 m quadrats. Observed distributions were compared to a null model that considered homogeneous distribution; degree of significance is indicated as: * p < 0.05, ** p < 0.01, *** p < 0.001.
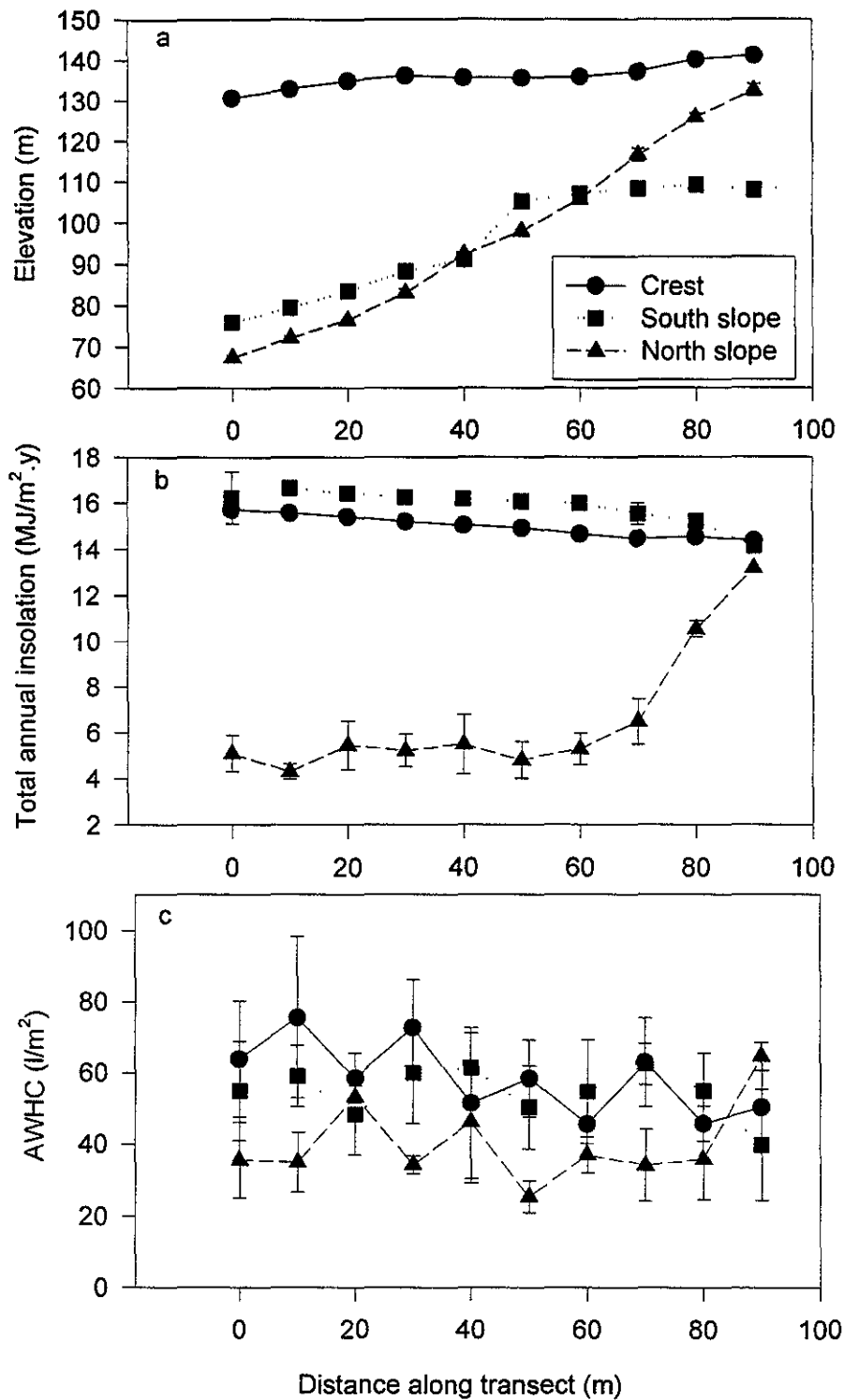
Fig. 8. Abiotic environmental conditions along the three contrasting transects. Each point represents an average (and standard error) value corresponding to the three 10 X 10 m quadrats found in the same row of the 30 X 100 m transects.
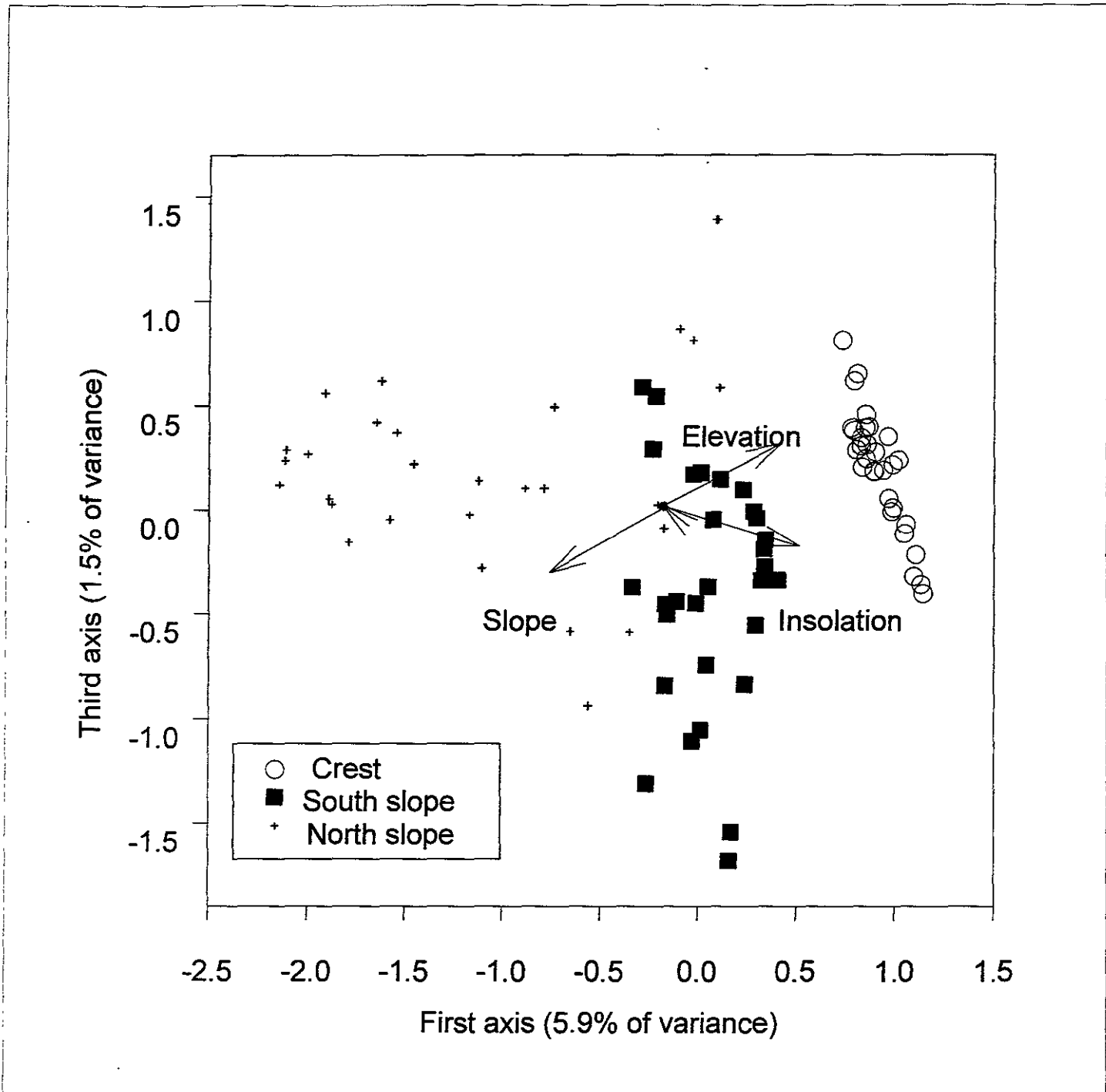
Fig. 9. CCA ordination diagram of the 90 10 X 10 m quadrats within the three contrasting transects.

environmental variables was low (Fig. 9). The first 3 canonical axes derived from a CCA only explained 5.9%, 1.6% and 1.5%, respectively, of the total variance in species composition. However, correlations of canonical axes with insolation (0.831, -0.502 and -0.234 respectively), elevation (0.745, 0.333 and 0.576) and slope (-0.720, 0.533 and -0.444) were high. Quadrats from the Crest transect presented clearly different scores than those from the other two transects (Fig. 9). Quadrats from the South and North slope transects overlapped in some extent, where insolation and elevation tended to be more similar. At the lower insolation extreme (middle lower part of Fig. 9), quadrats from the North transect showed a distinct species composition; South transect quadrats at the lower elevation extreme (middle left part of Fig. 9) were also quite different from the rest of the quadrats. Axes 1 and 3 were chosen to represent most contrasting values taken by single quadrats from the three transects (Fig. 9).

The analysis of the spatial pattern of beta diversity showed that in the case of the North slope transect closer quadrats were floristically more similar than distant ones (Fig. 10 c). This pattern was weak in the South slope transect (Fig. 10 b) and was absent in the Crest transect (Fig. 10 a). Observed spatial pattern of beta diversity of the North slope transect was different from that derived from the null model (Fig. 10c); this was not true for the South slope (Fig. 10b) and Crest transects (Fig. 10 a).

Analysis of the spatial pattern of environmental variables within the three transects showed that both elevation and insolation values were organised into a simple gradient (Fig. 11). Amplitude of environmental heterogeneity within these gradients was lowest in the Crest transect and largest in the North slope transect, as had been shown before (Fig. 8).

The analysis of the correlation between the spatial pattern of environmental heterogeneity and that of beta diversity, showed that in the North slope transect spatial structure of beta diversity was largely correlated with the spatial structure of elevation and insolation ($r = 0.97$, $p < 0.0001$ and $r = 0.85$, $p < 0.01$ respectively; compare Figs. 10 and 11). These correlations were smaller for the South slope transect ($r = 0.67$, $p = 0.048$ for both variables) and very small for the Crest transect ($r < 0.01$ in both cases).

Comparisons between the two scales

The sensitivity of the amount of beta diversity to magnitude of environmental heterogeneity seems to be equivalent at both spatial scales, *i.e.* among and within transects (Fig. 12). Beta diversity values tended to be higher as environmental
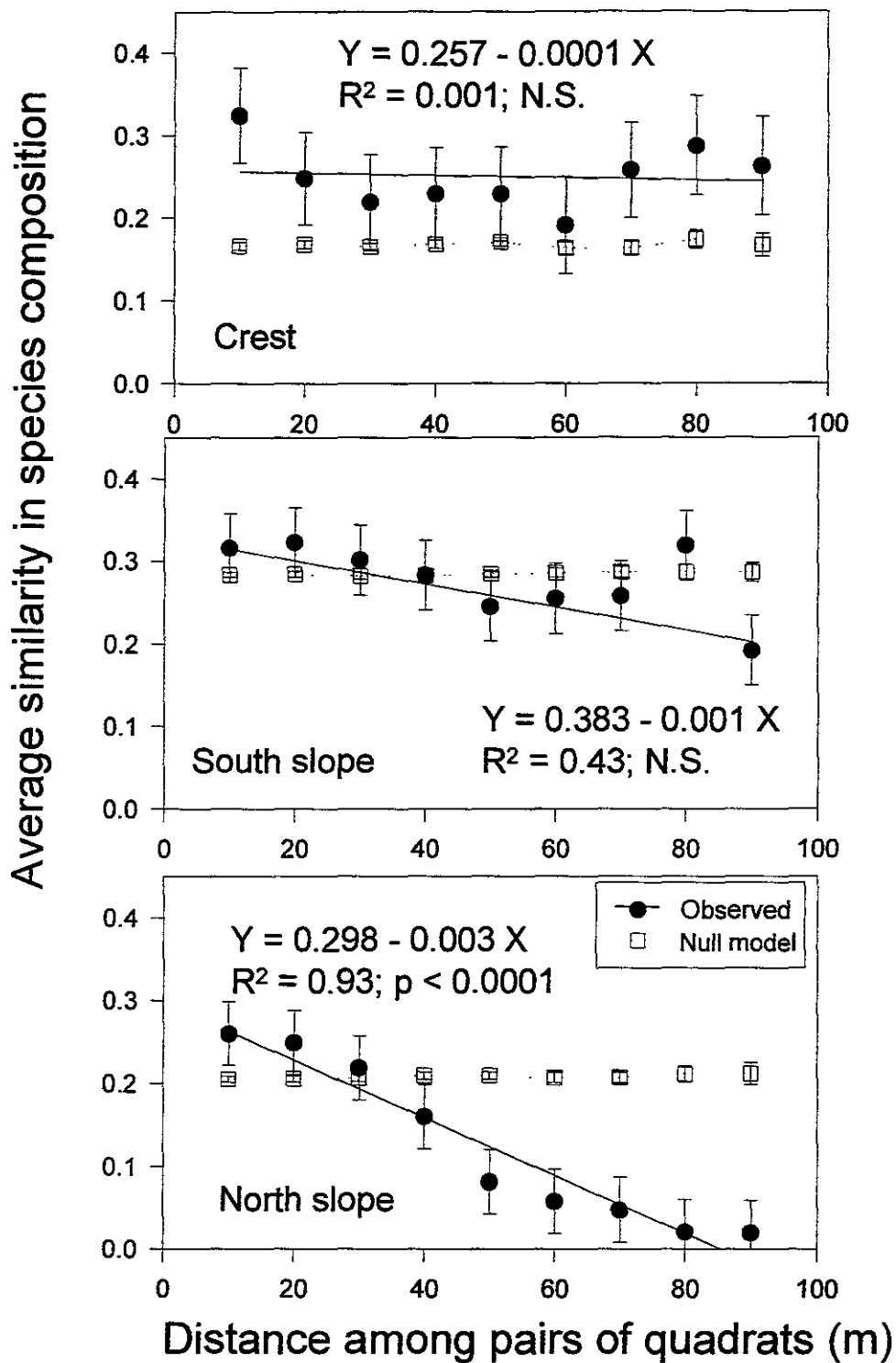
Fig. 10. Spatial pattern of beta diversity along the three contrasting transects. Observed and randomly predicted values are contrasted. Average values (and standard error) values are given at 10 m intervals.
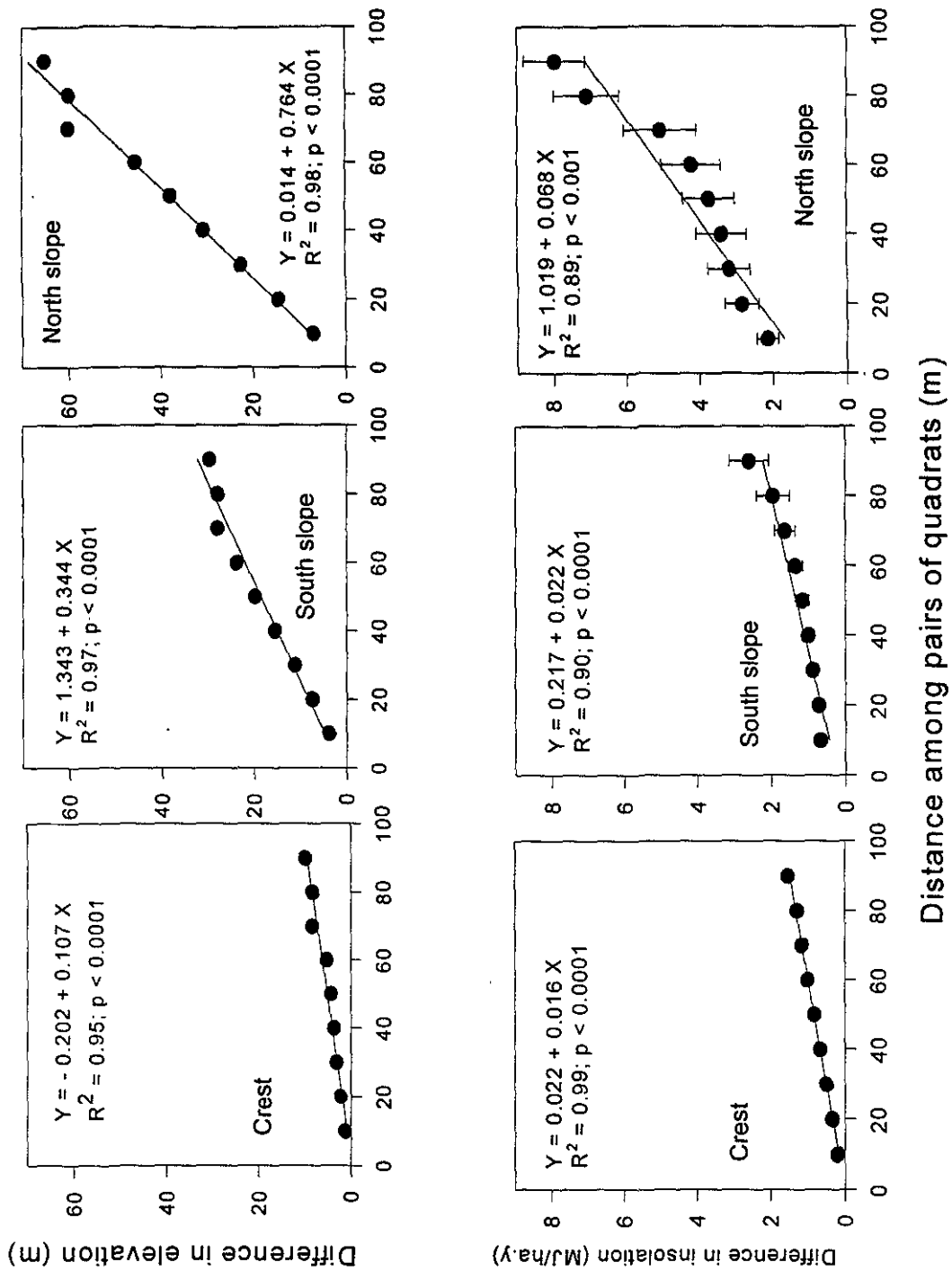
Fig. 11. Spatial pattern of environmental heterogeneity within three contrasting transects. A linear regression was fit to observed values to enable comparison among variables and among transects. Average (and standard error) values of the three 10 X 10 m quadrats located in the same row of the 30 X 100 m transects are given.
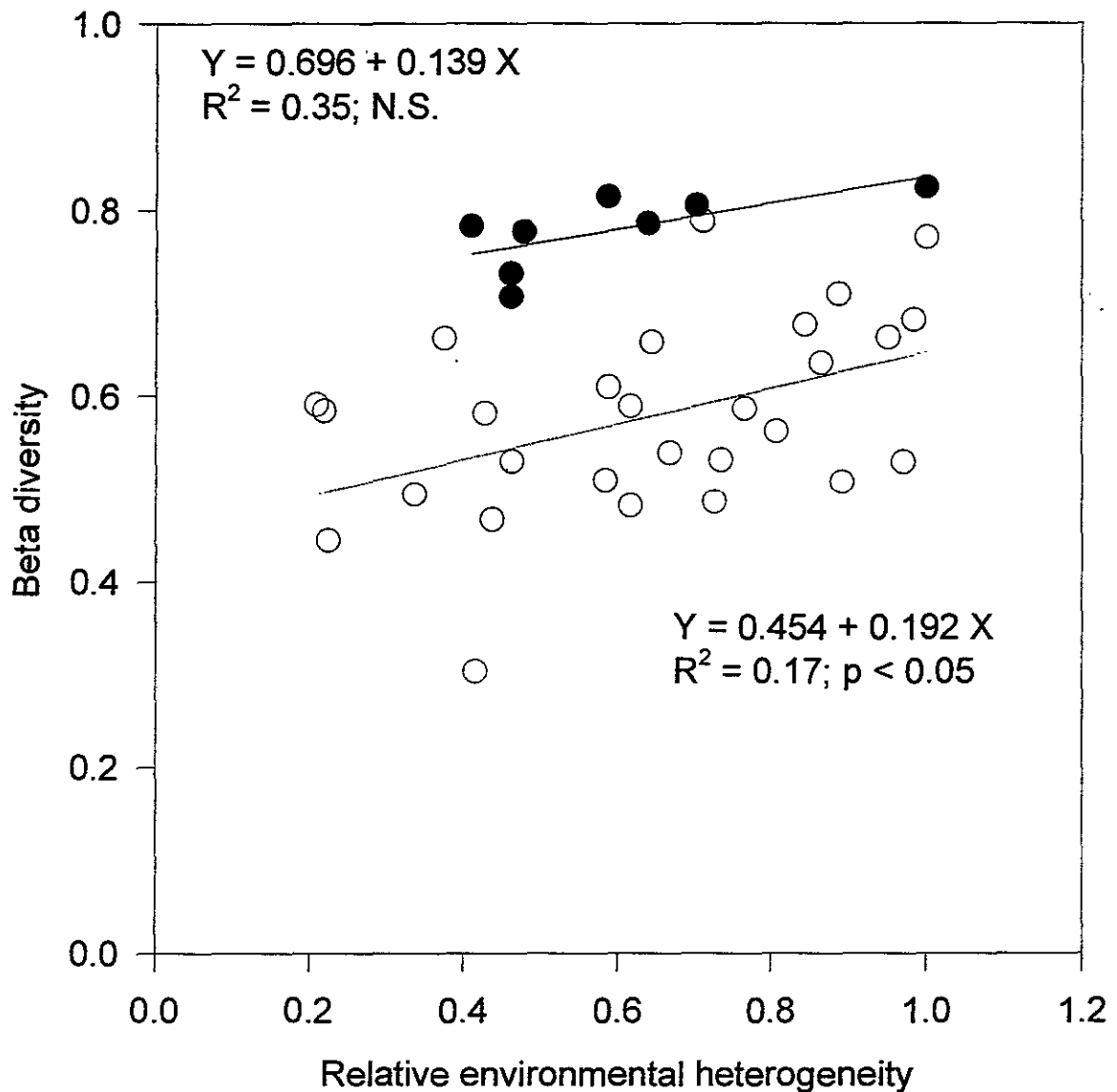
Fig. 12. Relative environmental heterogeneity and beta diversity at the two spatial scales (among and within transects). Environmental heterogeneity was calculated as a combination of differences for the 4 environmental variables among transects or quadrats, and was further standardised to oscillate between 0 and 1 in both cases. White dots represent comparisons among all pairs of the 8 transects; black dots represent average values obtained from the comparisons among all pairs of quadrats within each one of the 8 transects.

heterogeneity increased, when all 10 x 10-m quadrats were compared to each other within the 8 transects. Little dispersion was found around this relationship, but the determination coefficient and the significance level of the resulting model were weak ($p = 0.07$). The slope of the relationship between beta diversity and environmental heterogeneity in the case of the comparisons among the 8 transects was similar to that obtained at the quadrat-based scale. Despite a higher degree of dispersion among comparisons, the determination coefficient and the level of statistical significance was higher ($p < 0.05$; Fig. 12). Beta diversity values among quadrats were, in general, higher than among transects.

Discussion

The magnitude of beta diversity

The watershed study system showed a mosaic of topographic conditions that seems to be translated into a high variability in tree abundance, species richness, species diversity, and species composition. As shown above, these community attributes varied widely among and within transects. Beta diversity, both among and within transects, was generally large, though a large variance in beta diversity values was found. Species similarity among 0.3 ha transects was as low as 0.21. Within transect beta diversity was such that some pairs of 0.01 ha quadrats that are less than 100 m have completely different species compositions, and species-area curves showed steep accumulation rates within all three contrasting transects. Assessments of single species distribution showed a similar picture: most species have a restricted distribution, either among and within transects. Beta diversity within transects was in general higher than the beta diversity among transects.

The observed beta diversity among 0.3 ha transects found in this study is lower than that found for a tropical rain forest in the middle Caquetá area, in Colombia (Duivenvoorden 1995). There, average Jaccard beta diversity among 95 plots of 0.1 ha was higher than 0.80 ($\beta = 1 - C_j > 0.80$), while the average for Chamela was 0.42. Also, a larger proportion of rare species was found at Caquetá, where 59% of the species were present in only one transect, while at Chamela only 50% of the species were found in less than half of the transects. Among transect beta diversity values found at Chamela were very similar to those found for a tropical dry forest within a nearby reserve, at the Sierra de Manantlán, Jalisco, México (Vázquez and Givnish 1998). In that case, beta diversity among 0.1 ha tropical dry forest sites (composed of 10 transects of 0.01ha at an altitude of

1500m) placed 100 m away had a beta diversity ($\beta = 1 - D$, Sorensen similitude index in this case) of 0.4 to 0.5. Vázquez and Givnish (1998) reported a decrease of beta diversity with altitude to as low as 0.3 at 2400 m. Among transect beta diversity at Chamela is larger than that found for an inter-tropical semiarid region at the Tehuacán-Cuicatlán valley, in central Mexico (Montaña and Valiente-Banuet 1998). In that study, pairs of 0.1 ha plots separated by an altitudinal gradient of 100 m had a Jaccard beta diversity around 0.25 (Whittaker's beta diversity = 1.6), for an altitude of 1550m. As in the case of Manantlán, among plots beta diversity decreased with altitude and was close to 0 (Whittaker's beta diversity = 1) at 2350m.

At Chamela, the within transect beta diversity (among 0.01 ha quadrats) was in general larger than the among transect one. This pattern can be attributed to a random sampling effect. A total of 118 species were found in this area, and average richness of transects is 54 species while that of quadrats is only 9 species. The probability of finding the same species within pairs of quadrats is much less than that of finding the same species within pairs of transects. Correspondingly, we found that the variance of among transect beta diversity is also lower than that of among quadrat beta diversity.

The within transect beta diversity at Chamela is again larger than that detected at Tehuacán-Cuicatlán (Montaña and Valiente-Banuet 1998). There, sets of five 0.02 ha quadrats located within a 1 ha sampling area at the same altitude had a Jaccard beta diversity close to 0 (Whittaker's beta diversity $\cong$ 1). A large among quadrat beta diversity, such as that found for Chamela, has been reported for tropical rain forests. In the case of riparian forests within the Pine Ridge savanna in Belize, for example, Meave (1991) showed that 80% of the species (from a total of 51) had a differential distribution along short transects (20 to 100 m long).

Species-area curves within the three contrasting transects at Chamela showed that 43 to 64 species could be accumulated by adding 0.01 ha quadrats up to an area of 0.3 ha. In the case of the tropical forest at Barro Colorado Island, Panama, only 20 to 30 species were accumulated for a similar area, when accumulating data from 0.04 ha quadrats within a 50 ha permanent plot (Hubbel and Foster 1993). In the case of the tropical rain forest at Caquetá (Duivenvoorden 1996), species-area curves showed higher species accumulation rates, reaching 50 and up to 120 species for a similar area, when data from 0.1 ha plots was accumulated.

In synthesis we can say that beta diversity found at the tropical dry forest at Chamela is comparable to that reported for other tropical dry forests, similar or lower than

that detected for tropical rain forests, and higher than that at an inter-tropical semiarid region. Well known altitudinal gradients in species diversity (e.g. Lieberman et al. 1996, Brown 1986) seem to be closely related to decreasing beta diversity with altitude (Vázquez and Givnish 1998, Givnish 1999). Also, precipitation gradients in species diversity could be associated to increasing beta diversity with increasing precipitation (Givnish 1999).

The environmental heterogeneity

The mosaic of topographic conditions found within the watershed system is associated to a high variability in environmental conditions. Within an altitudinal gradient ranging from 40 to 180 m we found contrasting slope conditions, ranging from steep slopes to flat crests. In addition, a high variability in aspect values was found, with two major contrasting conditions: north and south facing slopes. Such variations in slope and aspect values contribute simultaneously to a high variability, among and within transects, in total annual insolation values ranging from as low as 2 MJ/ha.y and up to 17 MJ/ha.y,. Soil characteristics associated to available water holding capacity showed a great variance from very low holding capacity to a rather large one (> 100 l/ha), but such variance did not show any clear among or within transect patterns.

This mosaic of slope, aspect and insolation values is tightly related to water availability for plant establishment and growth. It has been shown for these watersheds that different processes determine soil water content throughout the year (Galicia et al. 1999). At the onset of the rainy season, soil water content is mainly affected by soil characteristics, which are in turn closely associated to topography. During the rainy season, soil water content is instead affected mostly by insolation that affects water evaporative demand. Then, north-facing bottom locations, such as the lower part of the North-facing transect, have greater soil water content for longer periods, due to their topographic position, their water holding capacity, but mostly to their low evaporative demand associated to the lowest insolation values. In contrast, top and middle locations, such as the Crest and the upper part of the South-facing transects, have lower soil water content for shorter periods due to lower water holding capacity, topographic position, but mostly to elevated evaporative demands associated to the highest insolation values (Galicia et al. 1999).

In addition to differences in soil water content, the mosaic of topographic conditions is certainly associated to other differences in conditions and resources for plant establishment and growth. Studies performed along short altitudinal gradients ranging from

crest to bottom of slopes (catena) have shown that soil type, depth, structure, drainage conditions and accumulation of organic matter change along these gradients (e.g. Lawson, and Hall 1970, Lescure and Boulet 1985, Oliveira-Filho et al. 1998). In the case of Chamela, differences in nutrient availability along the altitudinal gradient are also expected from differences in morphopedological processes, organic matter decomposition rates, and nutrient lixiviation and immobilisation (Campo 1995, Cotler et al. in press, Martínez-Yrízar and Sarukhán 1990, Solís 1993).

Differences in disturbance regimes associated to flooding have been found for such short altitudinal gradients along riparian areas (e.g. Meave 1991, Naiman and Décamps 1997), but are not likely to be important within the small watersheds mainstream channel (López-Guerrero 1992). Instead, an important source of disturbance could be water run-off and accompanying materials on very steep slopes such as that at the North-facing transect. Rainfall patterns have been shown to present very erosive rainstorms (García-Oliva et al. 1995). In the case of flat sites with high insolation, such as that at the Crest transect and the upper part of the South-slope one, disturbance regimes seem to be associated to large tree mortality in particularly dry years (Durán et al. in press).

The relationship between environmental heterogeneity and beta diversity

In this work we found that among and within transect beta diversity is associated to environmental heterogeneity, most specifically to slope, elevation and insolation. This relationship was evident by the elevated percentage of total variance in species composition among transects explained by canonical axes that were correlated to such environmental variables. Despite this percentage was low for the within-transect analysis, the sensitivity of beta diversity to environmental heterogeneity was similar at both spatial scales.

The three environmental variables associated to beta diversity, slope, elevation and insolation are closely related to soil water content. Contrasts in soil water content such as those mentioned above among the bottom of the North-facing transect and the Crest and South-facing transects seem to be associated to beta diversity among transects. The relationship between beta diversity and the environmental variables associated to soil water content were most evident for the within transect analysis, and particularly within the North-facing transect, despite the low percentage of variance explained by the canonical axes. We should notice that insolation values modelled here represent incidence of solar radiation with no reference to potential interception by vegetation; further work is needed

to explore the role played by vegetation structure in combination with total annual insolation on beta diversity.

The reduced percentage of variance in species composition explained by canonical axes in the case of within transect beta diversity contrasted to that reported in a similar work undertaken at the tropical dry forest found at Santa Vitória, central Brazil (Oliveira-Filho et al. 1998). There, 5 transects of 30 X 75 m were established over a short-scale altitudinal gradient along the slope of Rio Paranaíba, where only 60 plant species were found. Analysis of the changes in species composition among 50 quadrats of 15 X 15 m showed that the 2 first axis obtained through a CCA analysis explained 13.2% and 5.1% of the total variance in species composition respectively. These axes were correlated to proportional area in canopy gaps, elevation, slope, and soil type. Instead, low variance in species composition explained by CCA was found for the case of 0.1 ha plots at the species- rich tropical rain forest at Caquetá, Colombia (Duivenvoorden 1995). In that case, the first 2 canonical axes explained only 3.2% and 3.0% of the variance in species composition respectively. The low variance in species composition explained by CCA in the case of the within transect analysis at Chamela could be attributed to the elevated regional diversity relative the average species diversity of 10 X 10 m quadrats.

In the case of among transect beta diversity, comparable results to those found at Chamela were reported for the case of the woody vegetation of the Middle Casamance Region, Senegal (De Wolf 1988). The assessment of beta diversity among 141 relevés showed that the two first axis of a CCA analysis had constrained eigenvalues of 0.21 and 0.11 (these values were 0.24 and 0.20 at Chamela). These 2 canonical axes were correlated with topographic position and precipitation. Within a larger region in Northern Kenya, covered with woodland, savanna and shrub-steppe ecosystems comparable results were obtained (Coughenour and Ellis 1992). The 2 principal axes resulting from a detrended correspondence analysis (DCA) had eigenvalues of 0.36 and 0.18 respectively, and were correlated to rainfall, elevation and soil type. Also, analysis of the woody plant diversity at a tropical dry forest in south-western Madagascar showed that two distinct habitats in relation to soil water content presented different species composition (Sussman and Rakotozafy 1994). In the tropical dry forest of north-western Mexico, differences in solar radiation were found to be associated to differences in nurse perennial species distribution (Arriaga et al. 1993).

In synthesis, beta diversity in tropical dry forests has mostly been attributed to topographic and edaphic factors associated to water availability. In the case of Chamela

such variables were elevation, slope and insolation. Nevertheless, as discussed above, the role played by other factors associated to the altitudinal gradient were not assessed. In the case of such short altitudinal gradients in tropical rain forests (e.g. Lawson et al. 1970, Lescure and Boulet 1985, Lieberman et al. 1985), beta diversity has mostly been attributed to differences in soil drainage, flooding, and nutrient availability (e.g. Duivenvoorden 1996, Tuomisto et al. 1995). In the case of Chamela, further work is still needed on the role played by differences in nutrient availability, and disturbance regimes associated to rain patterns and frequency of severe droughts as determinants of beta diversity.

Spatial pattern of beta diversity and environmental heterogeneity

We showed here that among transect beta diversity had a spatial pattern such that closer sites tended to be more similar in species composition, meaning that among transect beta diversity has a spatially autocorrelated structure. It is noticeable that the slope associated to decreasing similarity with distance was low. Within transect beta diversity showed a spatially autocorrelated structure in only 1 of the 3 contrasting transects. The North-facing transect did present such structure, and it was significantly different the spatial structure generate by a random sampling model. In the other two transects, within transect beta diversity spatial structure did not differ from a spatial structure generated by the null model.

We also found that environmental variables had a spatially autocorrelated nature in all 3 contrasting transects, but decreasing similarity in environmental variables with distance was largest at the North-facing transect. Interestingly enough, it was only for this last transect that beta diversity presented a spatially autocorrelated pattern. Within that transect spatial pattern of beta diversity and that of environmental heterogeneity were correlated. These results suggest that in absence of a strong environmental gradient within transect beta diversity does not have a spatially autocorrelated structure. On the contrary, when a clear environmental gradient is present, the spatial structure of within transect beta diversity seems to be closely associated to the spatial structure of environmental heterogeneity. For the case of among transect comparisons, the spatial structure of environmental heterogeneity should be described, and its role as a determinant of the spatial structure of beta diversity should be assessed. For this purpose, a larger number of sampling points are needed (Legendre and Fortin 1989).

In general terms, the spatial structure of beta diversity and its relation to that of environmental heterogeneity has seldom been documented. In the case of the tropical dry

forest at Barro Colorado Island, a spatial structure as that found in Chamela was described, but not related to environmental heterogeneity (Hubbel and Foster 1983). In the case of in the temperate forests of Haut-Saint-Laurent, south-western Quebéc, Canada, the spatial structure of tree species composition was not described, but was attributed not only to environmental heterogeneity but also to spatial processes inherent to the vegetation (Leduc et al. 1992). Further work is still needed in this direction to understand underlying factors of spatial structure of beta diversity.

Beta diversity and conservation issues in tropical dry forest

The existence of a complex mosaic in species composition within the tropical dry forest at the Chamela-Cuixmala Reserve should necessarily be considered in future initiatives for the conservation of this highly diverse ecosystem. High beta diversity within the Chamela-Cuixmala Region at higher spatial scales, among different morphoedaphic units, has also been found (Durán et al. in press). The rugged nature of the landscape found here is common to the pacific coast of eastern Mexico formerly covered by tropical dry forest (Rzedowski 1978, Trejo 1998). Therefore, the results obtained in this study may be relevant for other tropical dry forests. In order to conserve the majority of the regional diversity of these forests, it will be necessary to include the environmental mosaic described here.

Information on the species composition and number of species shared among sites in tropical forests are urgently needed to conserve the enormous biodiversity they support (e.g. Condit 1996, Lawton et al. 1998). Results emerging from the present work indicate that topographic variables, easily assessed in the field or within Geographic Information Systems, such as elevation, slope and aspect (used to model insolation) seem to be good predictors of both the magnitude and the spatial pattern of tree species beta diversity. Local and regional beta diversity modelling (e.g. Burnet et al. 1998, Nichols et al. 1988), based on such topographical features, will certainly be very helpful in the conservation initiatives of the high beta diversity of tropical dry forests.

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Capítulo IV

Dissecting spatial and environmental components

of beta diversity:

the case of a tropical dry forest in Mexico

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INTRODUCTION

Beta diversity is a measure of the differences in species composition among sites (Magurran 1988, Whittaker 1972). Beta diversity has been related to factors such as distance from source of propagules (e.g., MacArthur and Wilson 1967, Kadmon and Pulliam 1993, Brown et al. 1996), species dispersal abilities (e.g., Harrison et al. 1992, Cook and Quinn 1995, Quintana-Ascencio and Menges 1996, Mourelle and Ezcurra 1997, Brown et al. 1996), environmental heterogeneity in space (e.g., Whittaker 1972, Quintana-Ascencio and Menges 1996, Wiens et al. 1993, Mourelle and Ezcurra 1997), biotic interactions (e.g., Hanski 1981, McLaughin and Roughgarden 1993, Tilman and Kareiva 1997, Condit 1996), and random sampling processes (e.g., Connor and Simberloff 1979, Hubbell and Foster 1986, Gotelli and Graves 1996).

Within this set of factors, special emphasis has been given to environmental heterogeneity (e.g., Gauch 1982, Palmer 1993, Whittaker 1967) and distance among pairs of sites (e.g., MacArthur and Wilson 1967, Whittaker 1977) as major determinants of beta diversity. The underlying rationale about the importance of environmental heterogeneity in this respect is that competition has led to differential use of resources by species in the presence of a resource gradient (Whittaker 1972, Rosenzweig 1995). Therefore, an increase in beta diversity is expected, as differences in environmental conditions among sites increase. The rationale underlying the importance of distance among pairs of sites, on the other hand, relies on the island biogeography theory (MacArthur and Wilson 1967). This theory proposes that single species colonization rates decline with growing distance to species source (MacArthur and Wilson 1967); consequently, compositional similarity among islands (sites) decreases as distance among sites increases (e.g. Kadmon and Pulliam 1993). Also, disturbance regimes (e.g. Connell 1978) and biotic interactions (operating within and between species) may lead to spatial structure in species distributions in the absence of environmental heterogeneity (e.g. Connell 1971, Tilman and Kareiva 1997).

The role-played by environmental heterogeneity and distance among pairs of sites among sites as determinants of beta diversity cannot easily be isolated, since these two factors are strongly correlated. In fact, environmental heterogeneity has a spatially autocorrelated structure (Webster 1985, Bell et. al. 1993, Legendre 1993). Thus, the source of the spatial pattern of beta diversity cannot easily be attributed either to distance effects, such as distance-dependent colonization processes, disturbance or biotic

interactions, to distance effects combined with environmental ones, such as the spatial autocorrelation of environmental heterogeneity, or simply to environmental ones.

Attempts to separate the effects of physical distance (PD) from that of environmental heterogeneity (EH) on beta diversity have been addressed during the last decade (Borcard et al.1992, Cody 1993, Leduc et al. 1992). These studies have been able to partition the total inter-site variance in species composition into a PD and EH-related fractions. However, the multivariate approach does not allow for a direct assessment of the response of beta diversity to changes in EH or PD in the absence of one or another.

We propose an alternative way to assess the relative importance of EH and PD on beta diversity. We use a sensitivity analysis that enables the assessment of the relative change on beta diversity resulting from relative changes in EH, PD or both (Fig. 1). In this analysis, we contrast an environmental control model hypothesis against a spatially controlled one. In both cases, a linear relationship between beta diversity and both PD and EH was adopted as the simplest possible model. The rate at which beta diversity changes with PD or EH, expressed as the slope of the resulting linear regression model, will reveal the relative importance of each of the two contrasted models (cases a,b or c; cases d, e and f in Fig. 1). The basal amount of beta diversity (intercept of the linear model) will depend inversely on the amplitude of species distribution. If most species are ecologically or geographically widely distributed, basal beta diversity will tend to be small (case g in Fig. 1), whereas if most species are narrowly distributed the basal beta diversity will tend to be large (case h in Fig. 1).

When analyzing the sensitivity of beta diversity to changes in EH, while keeping PD constant, two possible scenarios may be expected. Beta diversity can be enhanced with increasing EH, or remain constant. If beta diversity increases with EH (case j in Fig. 1) then the species specialization hypothesis can be considered. If beta diversity remains constant (case i in Fig. 1), this hypothesis weakens. Similarly, when analyzing the relationship between beta diversity and PD among sites, while keeping EH constant, beta diversity should increase or remain constant with increasing PD among sites. If beta diversity increases with PD (case l in Fig. 1) then spatially structured processes could be considered. In such case, distance-dependent colonization rates, disturbance rates, and local biotic interactions can be thought to determine community structure. Otherwise, this hypothesis cannot be supported (case k in Fig. 1). Of course, both EH and PD associated processes may determine beta diversity in a given system, very probably in a non-additive
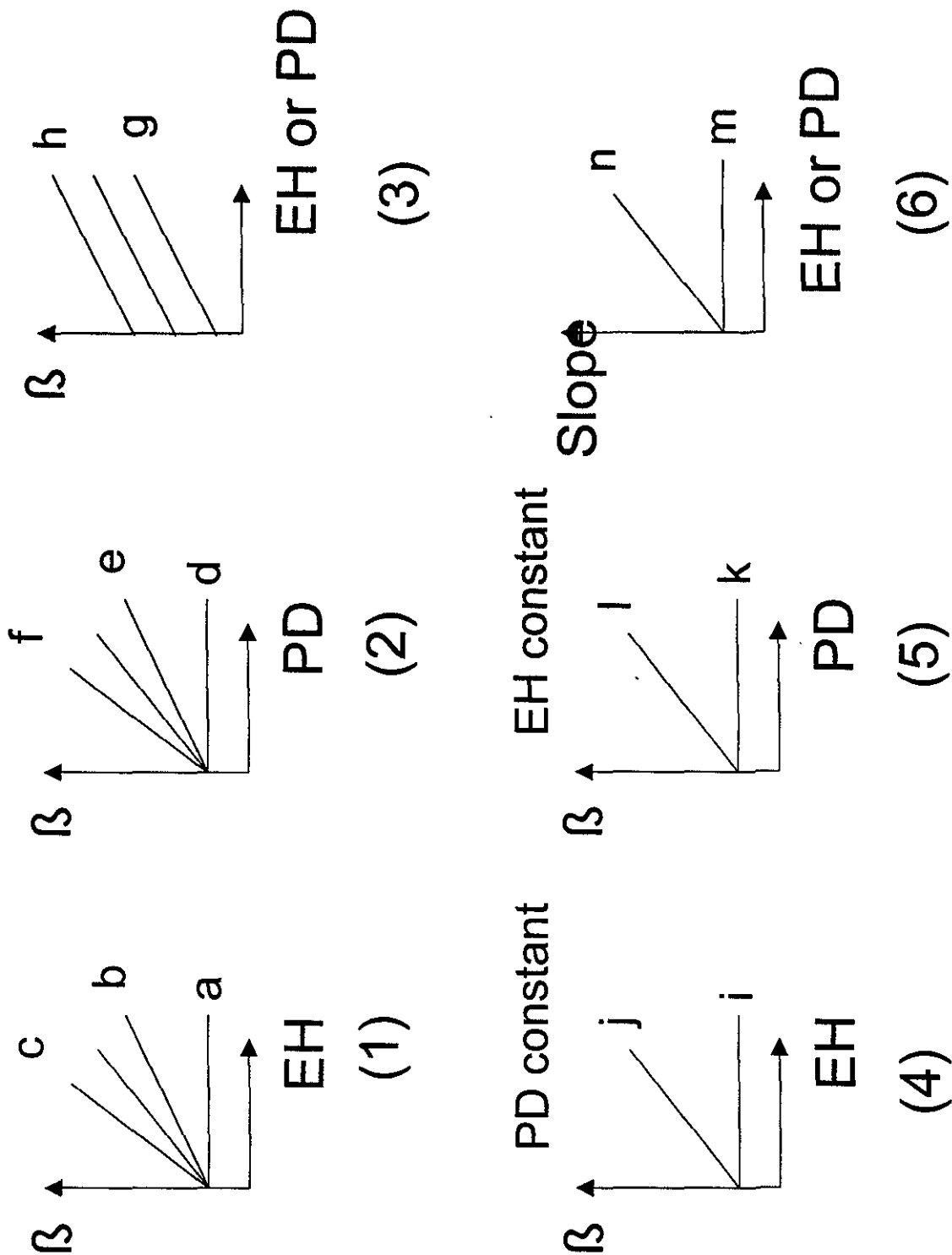
Fig. 1. Possible scenarios resulting from a sensitivity analysis of Beta diversity (β) to environmental heterogeneity (EH) and physical distance (PD). First step of the sensitivity analysis: sensitivity of β to EH (1) and to PD (2) using all the data; within this first step, sensitivity can be null (cases a and d), low (cases b and e) or high (cases c and f), and basal beta diversity can be low (case g in (3)) or high (case h in (3)). Second step of the sensitivity analysis: sensitivity of β to EH while keeping PD constant (4) and sensitivity of β to PD while keeping EH constant (5); sensitivity can be null (cases i and k) or high (cases j and l). Third step of the sensitivity analysis: synergic effects of PD and EH on β (6); sensitivity of β to one of the factors (e.g. PD) can be independent of the other factor (e.g. EH, case m) or vary as the other factor varies (e.g. EH, case n).

but a synergistic way. Synergistic effects between EH and PD can be evaluated by controlling for different levels of one of these factors and assessing how the regression slope or the intercept change (cases m and n in Fig. 1).

We use the previously described sensitivity analysis to study beta diversity in the Chamela tropical dry forest in Western Mexico (Bullock et al. 1995, Gentry 1995; Lott 1993). Other studies have shown that beta diversity of the tree community is noteworthy in this region (Lott et al. 1986, Balvanera 1998, Balvanera et al. in prep.). It has been attributed to differences in water availability along a short altitudinal gradient (Bullock et al. 1995, Lott et al. 1987, Balvanera 1998, Balvanera et al. in prep.). In this paper, we pursue the following aims: i) to assess the isolated and combined effects of EH and PD on tree community beta diversity, ii) to discuss the biological processes associated with the observed beta diversity trends, and iii) to establish general determinants of beta diversity throughout sensitivity analyses.

MATERIALS AND METHODS

Study area

The study was conducted at the Chamela Biological Station of the National Autonomous University of Mexico (19° 30'N, 105° 3′ W), which is part of the Chamela-Cuixmala Biosphere Reserve, in the state of Jalisco, Mexico, south of Puerto Vallarta and only 2 km from the Pacific coast. The climate of Chamela is warm, with a mean annual temperature of 24.9° C. The mean annual precipitation is 748 mm; with 80% of the rain falling in during only four months, from July to October (Bullock 1986, García-Oliva et al. 1991).

Tropical dry forest is the major vegetation type, with small areas along riparian zones of main streams covered by tropical semideciduous forest (sensu Rzedowski 1978). Average canopy height in the dry forest is around 10 m, and most mature trees have diameters at breast height (DBH) between 5 and 10 cm. In the semideciduous forest, average canopy height is around 18 m and trees with DBH larger than 30 cm are common. Some of the most abundant tree species in the dry forest are Plumeria rubra L. (Apocynaceae), Cochlospermum vitifolium (Willd.) Spreng. (Cochlospermaceae), Gliricidia sepium (Jacq.) Kunth ex Steudel (Leguminosae), Comocladia engleriana (Anacardiaceae) Loes., Celaenodendron mexicanum Standl. (Euphorbiaceae), Caesalpinia eriostachys Benth. (Leguminosae), Cordia elaeagnoides DC. (Boraginaceae), Guapira macrocarpa Miranda (Nyctaginaceae), and Bursera instabilis McVaugh & Rzed (Burseraceae).

In the 13000 ha of Chamela region 1120 species of vascular plants that belong to 544 genera and 124 families have been recorded (Lott 1993). Lott et al. (1986) found that the number of tree species (DBH ≥ 2.5 cm) in 0.1 ha plots varied between 92 and 105. This local species richness is among the largest recorded for tropical dry forests around the world (Gentry 1985).

The study was conducted within a granite massive bed (Cotler et al. in press) where three small watersheds (15, 19, and 28-ha in size respectively) run parallel (Maass et al. 1995, Sarukhán and Maass 1990). There, soil is an association of entisol, inceptisol and alfisol (Balvanera et. al. in prep., Cotler et al. in press, Galicia et al. 1995, Solís 1993). The elevation ranges from 40 to 190-m. In the upper part of this altitudinal gradient soils are deeper, and therefore show higher water retention capacity compared to soils of the medium and lower slopes of the watersheds (Galicia et al. 1995, Cottler et al. in press). On the other hand, organic matter content (Galicia et al. 1995) and nutrient availability are higher (Solis 1993, Campo 1995). Soil water content is highly determined by solar radiation interception, associated in turn to watershed topography, and to a lesser extent to soil characteristics. Thus soils water content is higher in the bottom of steep north-facing slopes than in the crest and upper part of south-facing slopes (Galicia et al. 1999).

Sampling design and data collection

Twenty-six rectangular transects were laid along the major altitudinal gradient of the study watersheds, ranging from the main stream channel to the lateral crest. Steep slopes with exposed rock and treeless vegetation were avoided. Transects measured 20 or 30 X 100 m. Each transect was divided into 20 or 30 10 X 10 m quadrats which were considered the basic sampling units. In total, 615 quadrats were established.

Within each quadrat, all trees with a DBH larger than 5 cm were numbered, tagged, and identified. Species were identified from their bark (Pérez-Jimenez and Barajas 1990), non-reproductive attributes and assisted by expert plant taxonomists (E.J. Lott and A. Pérez-Jimenez). Herbarium specimens were collected and are available from the authors. Species names follow nomenclature of Lott (1993).

Within each quadrat, three environmental variables related to soil water content were measured. i) Slope, a topographic variable associated to water run-off and infiltration (Ruhe 1975; Darlymple et al. 1968), was measured at each one of the four corners of each quadrat and averaged. ii) Total annual insolation above forest canopy, a predictor of soil water content (Galicia et al. 1999) as a determinant of water evaporative demand (Ezcurra

et al. 1991, 92), was estimated with the model Joule 2.0 (Ezcurra 1996) that uses slope, aspect and angle to horizon (recorded over the 360 ° around each quadrat). iii) Soil available water holding capacity (AWHC) was estimated by describing a soil core taken at the center of each quadrat (depth < 1 m); depth, texture and stoniness were determined by field methods for each horizon (Balvanera et al. in prep.), and AWHC was estimated using well known databases (Siebe et al. 1996).

To measure physical distance among sites, each transect was geographically referenced using a Trimble Pathfinder GPS with simultaneous differential correction (Trimble Navigation Limited 1994); UTM coordinates resulted from the average of at least 150 corrected points. Only measurements with a standard deviation ≤ 2.0 m for the 150 point coordinates were used.

Models and data analysis

Distribution of environmental variables was described. A principal component analysis (PCA) was performed with the three environmental variables to reduce environmental variation to only one or two major axis. Vegetation data were used to construct data matrices containing species presence-absence, abundance, and basal area as columns and quadrats as rows. Number of trees and number of species per quadrat were calculated; species distribution and local abundance within quadrats were examined.

The 615 quadrats were compared pair-wise, and 14045 pairs of quadrats (out of the more than 180,000 possible combinations) were selected at random with replacement. For each pair of quadrats, beta diversity, physical distance (PD) and environmental heterogeneity (EH) was calculated.

Beta diversity was calculated using presence-absence, abundance a basal area data. Presence-absence beta diversity was calculated as

beta diversity = 1 – Jaccard index,

where Jaccard index is (Magurran 1988)

$$Cj = \frac{j}{a+b+j}$$

being j the number of species found in both sites, a the number of species in site A and b the number of species in site B.

Abundance beta diversity was calculated as

beta diversity = 1 – Morisita-Horn index,

where Morisita-Horn index is (Magurran 1988)

$$C_{mh} = \frac{2\sum (an_i bn_i)}{(da + db)aN.bN}$$

being aN the total number of individuals in site A, an_i the number of individuals of the ith species in A, and

$$da = \frac{\sum an_i 2}{aN2}$$

Basal area beta diversity was calculated using the Morisita-Horn index, where abundance values for each species in each quadrat was replaced by the logarithm of its basal area.

Physical distance (PD) between any two quadrats was simply the linear distance between them, calculated as an euclidian distance among pairs of points with x and y coordinates. Linear distances, irrespective of real distances in the field associated to topography were considered.

Environmental heterogeneity was calculated in two different ways. i) EH_1 was calculated as the Euclidean distance among the pairs of quadrats, where the coordinates of each quadrat were derived from their scores for the two first axis of the principal component analysis performed with slope, insolation and soil available water capacity. ii) EH_2 was calculated as

$$EH_2 = \sqrt{(S_i - S_j)2 + (I_i - I_j)2 + (W_i - W_j)2}$$

where S is slope, I is total annual insolation and W is soil AWHC for any pair of quadrats i and j. To work with relative magnitudes of PD, EH_1, and EH_2, were in relation to the maximum value in each case. To describe inter-quadrat variation of beta diversity, EH and PD we analyzed the coefficient of variation and the degree of kurtosis and skewness departing from a normal distribution for the 14045 values obtained for all pair-wise comparisons.

Spatial structure of slope, insolation, soil AWHC and environmental heterogeneity (EH_1) were described using the 14045 pair-wise quadrat comparisons database. A semivariogram was constructed by calculating the semivariance

$$\gamma_h = \Sigma \, (x_i - x_j)^2/2,$$

where x_i and x_j are the values of the 3 environmental variables taken by all pairs of *i* and *j* points that are separated by distance *h*, as described by Legendre and Fortin (1989) and Rossi et al. (1992) within an ecological context. One hundred and forty different *h* intervals (categories) were considered. To maintain a constant sample size (N = 100) among *h* categories we changed the amplitude of each *h* category.

Sensitivity analyses. To assess the relative importance of changes in PD and EH on beta diversity, we followed the rationale underlying geostatistical tools (e.g. Legendre and Fortin 1989, Clark 1979, Rossi et al. 1992, Webster and Oliver 1990) with *ad hoc* modifications.

The first approach was to relate beta diversity with either PD or EH, using the whole database with 14045 pairs of quadrats for which data were available on beta diversity, PD and EH (cases a, b, c, d, e or f in Fig. 1). In this case, the magnitude of the change in beta diversity produced by changes in PD and EH was assessed without controlling on combined or synergistic effects of the two variables. To avoid errors associated to large degrees of freedom, broad dispersion of points (heteroscedasticity), and non-independence of pair-wise values (*e.g.*, Legendre and Fortin 1989, Clark 1979, Rossi et al. 1992, Webster and Oliver 1990), we used average beta diversity, PD, and EH values per *h* category (N = 100). Data corresponding to PD values with very low frequency (> 2.5%) were excluded. Mean values of beta diversity were fitted to average $Log_{10}(PD)$ using a simple linear model

Beta diversity = a Log(PD) + b.

The same procedure was followed for the relationship between beta diversity and EH. Resulting slopes were compared and used as measures of sensitivity of beta diversity to changes in PD or EH. Ordinate intercepts from the two models were compared and were used to assess basal beta diversity in each case.

The second procedure was to analyze the sensitivity of beta diversity to one of the two factors, while keeping the other one constant (cases i, j, k, and l in Fig. 1). For this purpose, three contrasting dimensions of PD (short = 16 m, middle = 100 m and large = 930 m average distances) were kept constant. In each case, 600 pair-wise quadrat comparisons were used to assess the relationship between beta diversity and EH. As in the previous case, average beta diversity values (N = 50) were fitted to average Log_{10}(EH) values, using the model

Beta diversity = a Log(EH) + b

The same procedure was undertaken to assess the relationship between beta diversity and PD, while keeping EH constant, at three contrasting values of EH (low EH = 0.05, middle EH = 0.38 and high EH = 0.99 average heterogeneity).

The third approach to our sensitivity analysis was to evaluate synergistic effects of EH and PD on beta diversity (cases m and n in Fig. 1). For this purpose, the second procedure was repeated, while keeping constant PD and EH at a set of 15 different values. Synergistic effects of PD on the sensitivity of beta diversity to EH was evaluated by keeping PD constant at 15 different values. For each PD value we obtained the slope and ordinate intercept regressing beta diversity on EH. Then, the resulting set of slope and intercept values were used to regress slope and intercept on PD (N = 15). The procedure was repeated for 15 values of EH, for which the sensitivity of beta diversity to PD, while keeping EH constant, was analyzed; resulting slope and intercept values were regressed on EH.

In all cases, residuals from regressed models were analyzed and points with extreme residual values were down-weighted for model fitting. All procedures of the sensitivity analysis were developed within Excell (Microsoft 1997). JMP (SAS Institute 1996), and Orden (Ezcurra 1992) software were used for statistical analysis.

RESULTS
Environmental heterogeneity
Environmental heterogeneity in the study area was large (Fig. 2 a,b,c). Slope values ranged from 0 to 46.3 degrees (C.V. = 57.9%), and average slope for the 615 quadrats was 16.5 degrees (± 0.4 s.e.). Only 10% of the quadrats presented relatively flat slopes (≤ 5.5 degrees), but distribution of slope values was skewed toward values ≤ 14
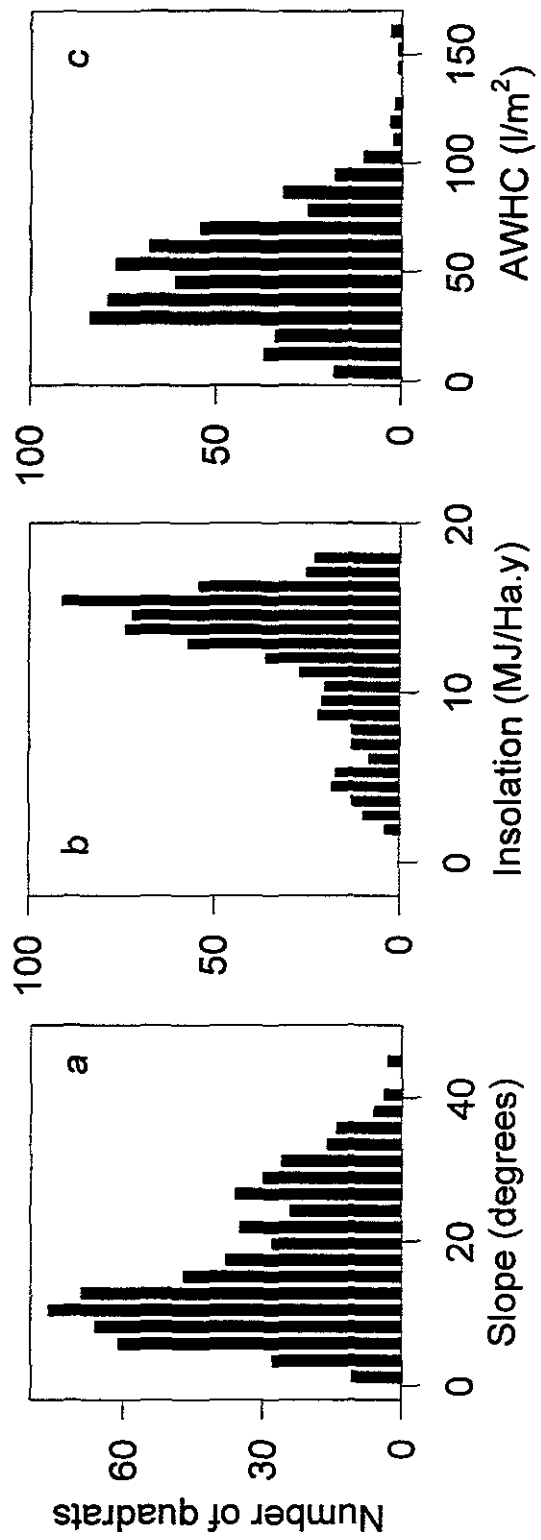
Fig. 2. Environmental heterogeneity. Distribution of the values taken for the 3 environmental variable at the 615 quadrats.

degrees (skewness = 0.61); 25% of the quadrats were found on very steep slopes (≥ 23 degrees). Average values (between 16 and 22 degrees) were less frequent than those expected from a normal distribution (kurtosis = -0.55; Fig. 2a).

Total annual insolation varied from 1.5 to 18.4 MegaJoules/m^2.year (M.J m^{-2} y^{-1}), but heterogeneity was lower for this variable than for slope (C.V. = 30.5%). Average insolation was 12.6 M.J m^{-2} y^{-1} (± 0.2 s.e.); 10% of the quadrats presented very low insolation (≤ 5.8 M.J m^{-2} y^{-1}) and 75% of the quadrats had insolation between 10 and 18 M.J m^{-2}y^{-1} (skewness = -0.99; kurtosis = 0.12; Fig. 2b).

AWHC changed more than three orders of magnitude (C.V. = 50.6%) and ranged from 1.1 to 164 l m^{-2}. Average AWHC was 50.5 l m^{-2} (± 1.0 s.e.); 10% of the quadrats presented very low AWHC (≤ 19 l m^{-2}) and 10% of the quadrats had high AWHC (≥ 85 l m^{-2}; skewness = 0.8; kurtosis = 1.2; Fig. 2c). The three measured variables were independent, except for insolation, that was calculated from slope (r = -0.513; p < 0.00001). Average values of insolation (around 13 M.J m^{-2} y^{-1}) where found mostly for low values of slope (≤ 10 degrees), and both highest and lowest values of insolation corresponded to higher values of slope.

Results from a principal component analysis using slope, insolation and AWHC for 615 quadrats, showed that 86.3% of environmental variation was concentrated in the first axis, and only 0.09% in the second one. The first axis showed a high correlation with slope (r = 0.63; p < 0.0001) and a low one with AWHC (r = 0.32; p < 0.0001). The second axis was less correlated to the same variables (with slope r= 0.20; p < 0.0001, and with water capacity r= - 0.12; p < 0.01). None of these axes were correlated with insolation.

Community structure

We recorded 8148 trees, belonging to 138 species, within the 615 sampled 0.01 ha quadrats. Due to the reduced size of the quadrats, the number of individuals per quadrat was commonly low (Fig. 3a). A quadrat had a minimum of two trees and a maximum of 29. The average number of trees per quadrat was 13.2 (± 0.2 s.e.), which represented less than 0.2% of the total tree sample size. Accordingly, the number of species per quadrat varied from 2 to 17 species (Fig. 3 b). The average number of species per quadrat was 8.7 (± 0.1), equivalent to 6.3% of the total number of recorded species.

Most of the species showed a restricted distribution (Fig. 3 c). Twenty five percent of the total number of species (34) was present in less than three quadrats, and 75% of them (103) were found in less than 6% (40) of the quadrats. Some species showed a

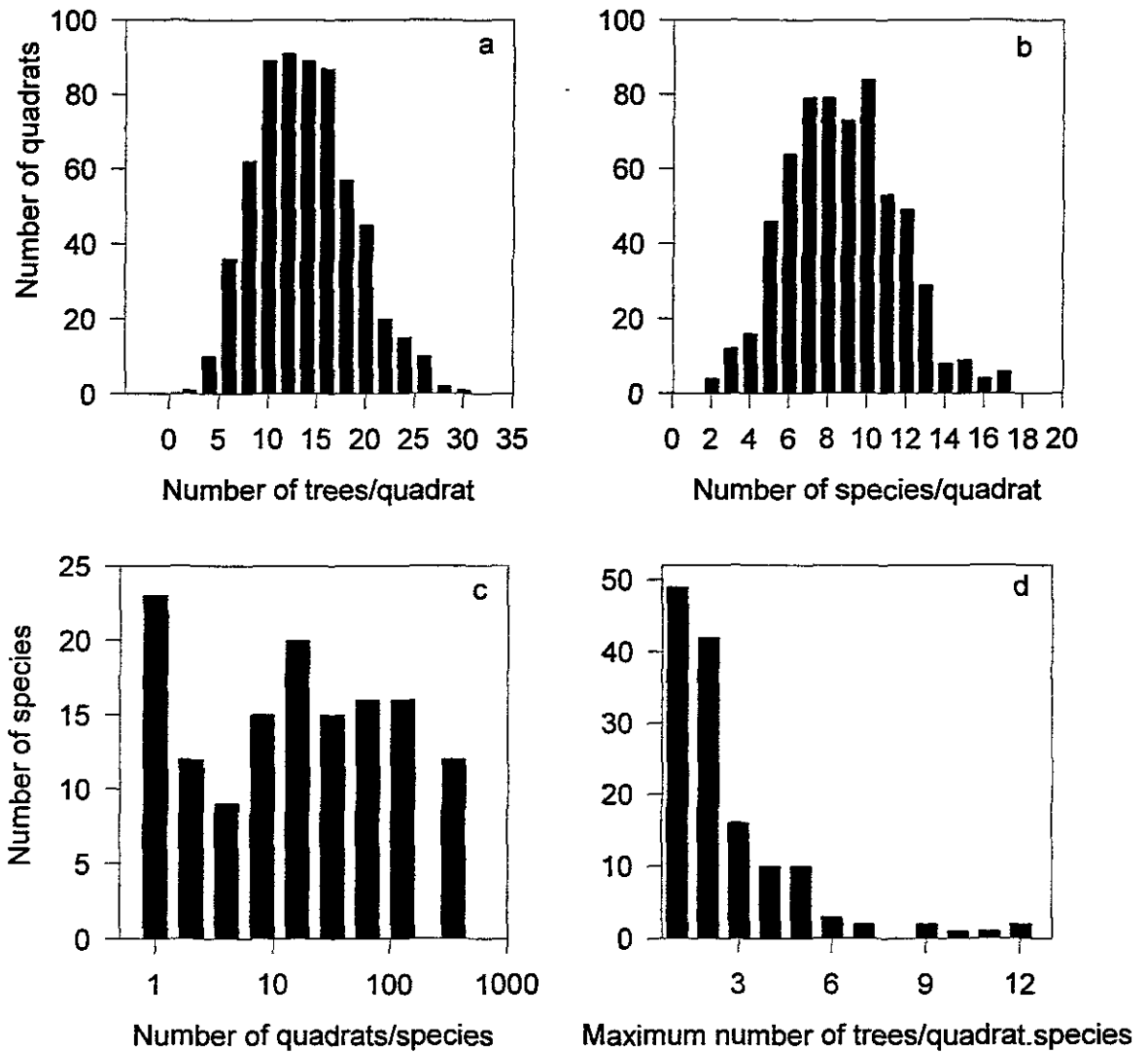Fig. 3. Characteristics of the tree community at Chamela, Jalisco. a) Frequency distribution of the *number* of trees per quadrat, b) frequency distribution of the number of species per quadrat, c) frequency distribution of the amplitude of species distribution, measured as number of quadrats occupied per species, d) frequency distribution of species abundance per quadrat, measured as maximum abundance of species per quadrat.

broad distribution, and 28 species were present in more than 168 quadrats, or 27% of the total number of sampled quadrats. The species with the highest local abundance was *Plumeria rubra* that was present in more than half of the quadrats (347; 56%).

Species abundance was, in general, low in a quadrat basis (1 to 12 trees per quadrat; Fig. 3 d). Almost all species (103) had a maximum abundance of three trees per quadrats, and only eleven of them (8%) presented abundance higher than six trees per quadrat. *Celaenodendron mexicanum* and *Lonchocarpus constrictus* had the maximum abundance of 12 trees per quadrat.

Beta diversity, physical distance and environmental heterogeneity resulting form pair-wise comparison of quadrats

The 14045 pair-wise comparisons among the 615 quadrats showed a large variation in beta diversity, PD and EH (Fig. 4 a,b,c,d,e,f). Beta diversity, however, was generally high (Fig. 4 a,b,c). On average, dissimilarity among pairs of quadrats was 0.8501 (±0.0009) for presence-absence data, 0.7569 (± 0.0017) for abundance data and 0.7524 (± 0.0014) for basal area data. The largest variation was found with abundance (C.V. = 26.1%; Fig. 4 b), and basal area (C.V. = 22.1%; Fig. 4 c), and was smaller with presence-absence data (C.V. = 13.1%; Fig. 4 a). In all three cases, beta diversity showed a frequency distribution skewed towards values close to 1 (skewness = -0.83, -0.72, -0.32 for presence-absence, abundance and basal area data, respectively), i.e., most quadrats tend to have exclusive species composition. Beta diversity values obtained from presence/absence data were highly correlated with those derived from basal area (r = 0.94; p < 0.00001). For this reason, hereafter beta diversity based on basal area will not be considered for further analysis.

Variation in physical distance among sites covered a wide range (Fig. 4 d), varying from 8 up to 3678 m away, but with very few pairs were more than 1,200 m away. Because distance was calculated on the horizontal plane, the estimated length between neighboring quadrats was lower than 10 m due to slope effects. Most of the pairs of quadrats (97.1%) were separated by less than 1085 m. We excluded from following analysis those pairs of quadrats that were further apart than this distance because they were extremely infrequent.

Environmental heterogeneity varied also greatly among pairs of quadrats. Difference values for the three environmental variables showed strongly skewed distributions toward low values (skewness = 0.87 to 1.22). Variation was largest for
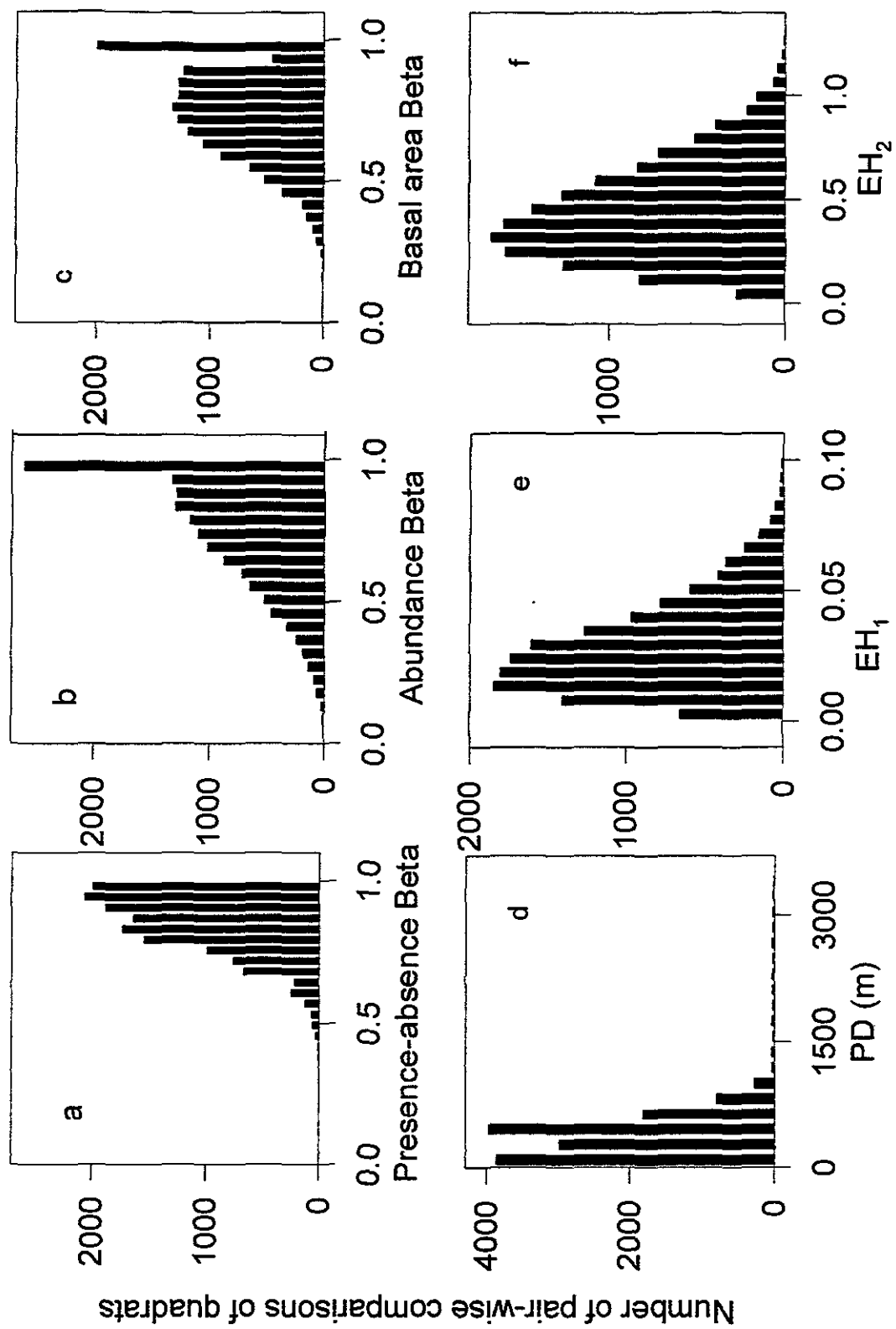
Fig. 4. Results from the 14045 comparisons among pairs of quadrats. Distribution of the values obtained for the 3 measures of beta diversity (a,b,c), for physical distance (d) and for the 2 measures of environmental heterogeneity (e,f).

insolation values (C.V. = 93.7%), followed by slope (C.V. = 85.2%) and lowest for AWHC (C.V. = 74.0%). Measures of environmental heterogeneity EH_1 and EH_2 were not correlated (r = 0.14; but p < 0.0001). They both varied three orders of magnitude, ranging from 0.0001 to 0.1 in the case of EH_1 (Fig. 4 e) and from 0.006 to 1.3 in the case of EH_2 (Fig. 4 f). Distribution of EH_2 was closer to normal (skewness = 0.65; kurtosis = -0.09) than that of EH_1 (skewness = 0.85; kurtosis = 0.45).

Spatial autocorrelation of environmental heterogeneity

All environmental variables, as well as environmental heterogeneity, presented a spatially autocorrelated pattern (Fig. 5). In all cases, variance increased with physical distance from 0 to 200 m. The pattern changed among variables. A semivariance different to 0 at shortest distances (called nugget in geoestatistics) was only present in the case of AWHC (Fig. 5 c) and EH_1 (Fig. 5 d), probably associated to an error inherent to the measurement of this soil characteristic. The slope (Fig. 5 a) and insolation (Fig. 5 b) semivariograms had an oscillating pattern, where period for slope (maximum at 200, 500 and 700 m) was shorter than that for insolation (maximum at 200 and 700 m). These oscillations are probably due to the topography of the 3 parallel watershed, where repeated sequences of flat crests, south-facing slopes and steep north-facing slopes area found in the 3 of them.The semivariogram for AWHC showed maximum variances at 200 m and at more than 800 m. Environmental heterogeneity, as a combination of all 3 environmental variables, showed a logarithmic pattern.

Sensitivity of beta diversity to physical distance and environmental heterogeneity

The sensitivity (slope) of beta diversity to changes in PD was different to that produced by changes in EH, and the same was true for basal beta diversity (intercept). With presence-absence data, beta diversity showed higher sensitivity to changes in PD than in EH_1 (Fig. 6 a). The regression model of beta diversity on PD showed a stronger determination coefficient, steeper slope (p < 0.001), and lower basal beta diversity (p < 0.001) than the regression model of beta diversity on EH_1 (Fig. 6 b). The same results were obtained when using abundance data (Fig. 6 c,d) and when replacing EH_1 for EH_2.

Beta diversity, using presence-absence data, was better explained by inter-site differences in terrain slope (R^2 = 0.75; F = 339; d.f. = 1,114; p < 0.00001) than in insolation (R^2 = 0.68; F = 264; d.f. = 1,114; p < 0.00001). Differences in AWHC had smaller influence

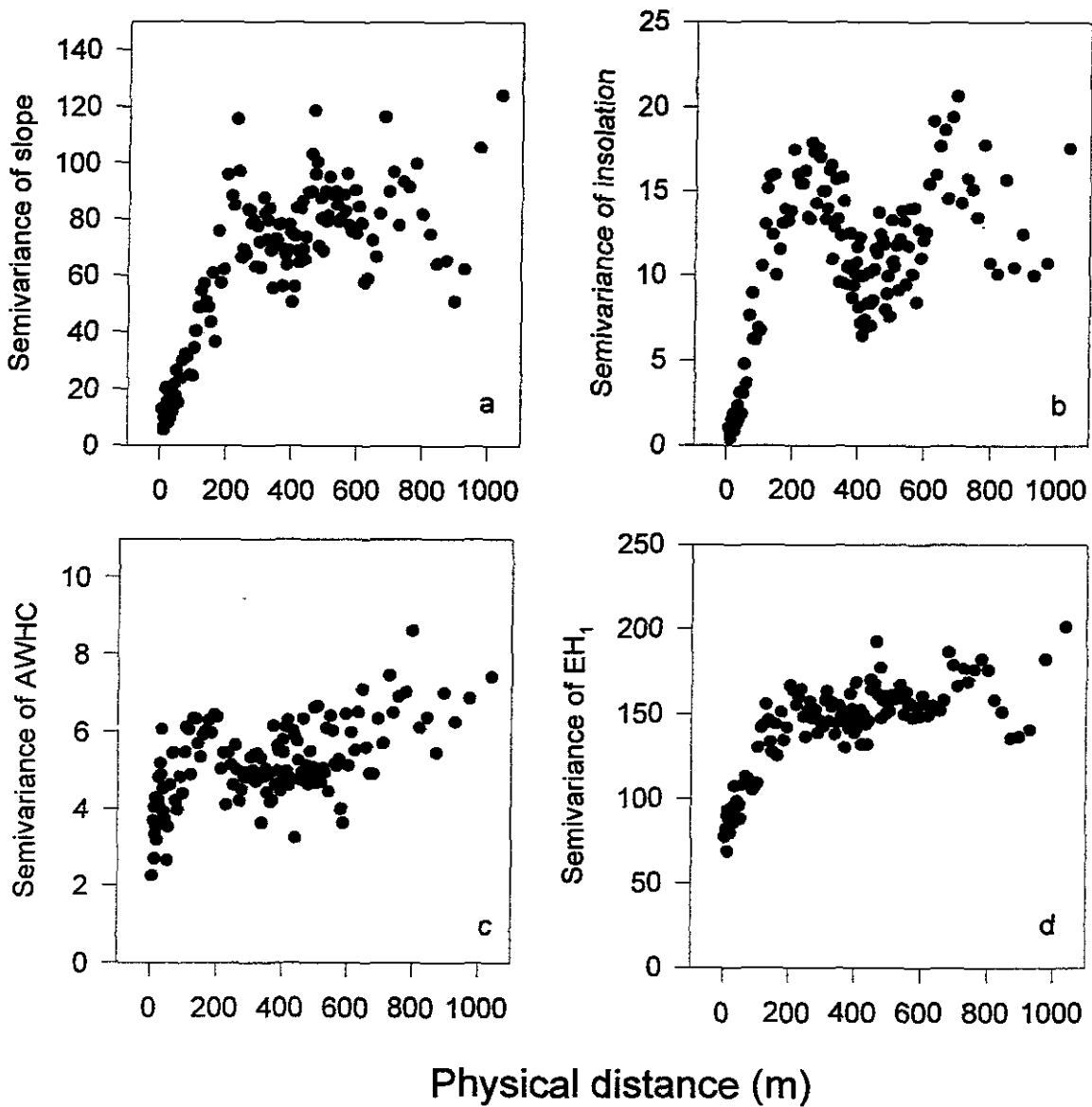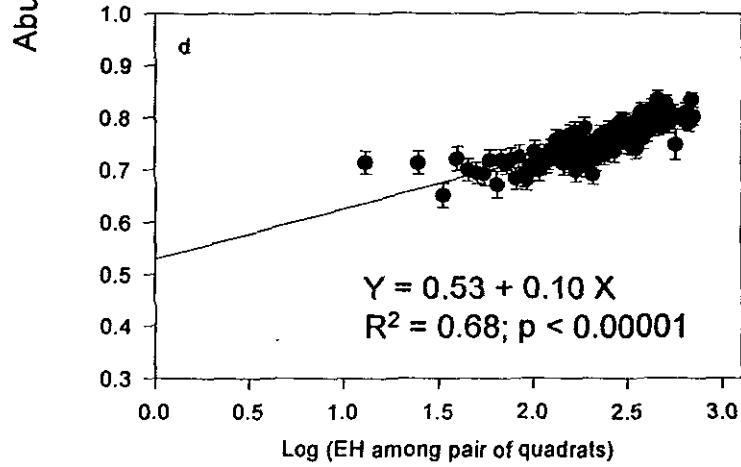Fig.5. Semivariograms of the 3 enviromental variables and EH1.

Fig. 6. First step of the sensitivity analysis of beta diversity to physical distance (PD) and environmental heterogeneity (EH), using all the data base, and two different measures of beta diversity.
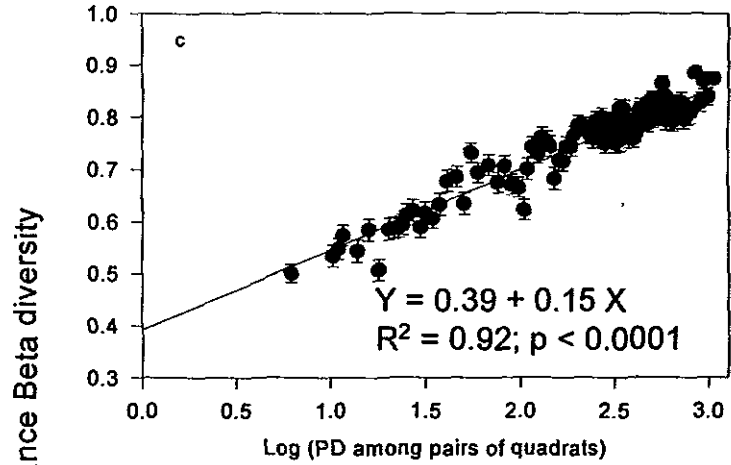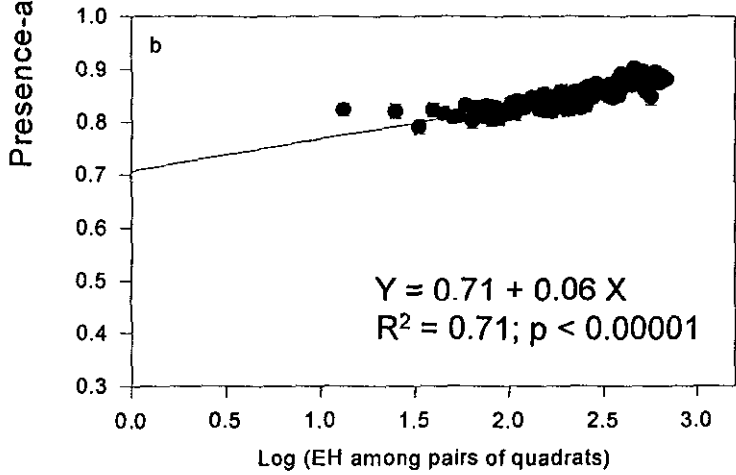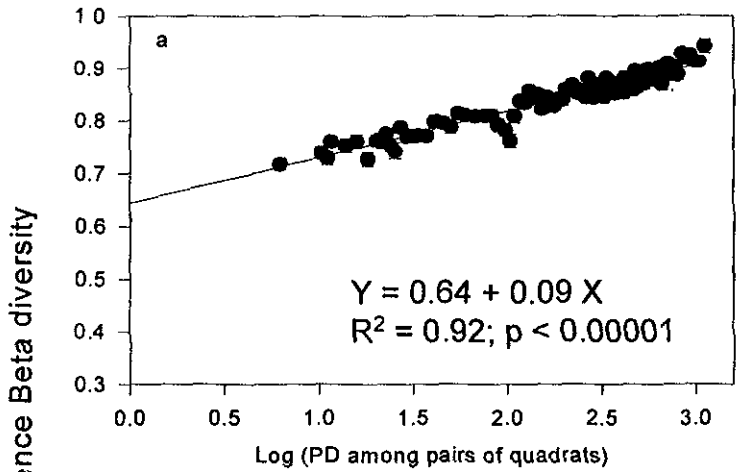
$(R^2 = 0.43; F = 92.0; \text{d.f.} = 1,114; p < 0.00001)$. A similar pattern was found with the use of abundance data.

Sensitivity of beta diversity controlling for distance or environmental heterogeneity

Beta diversity was consistently sensitive to PD changes when keeping EH constant at three different levels (Fig. 7). Beta diversity was not sensitive to EH when keeping PD constant at short (Fig. 7 g,j) and large PD (Fig. 7 i,l). Nevertheless, it is noticeable that when PD was kept constant at an intermediate value, beta diversity was sensitive to EH (Fig. 7 h, k). These trends were found both for presence/absence and abundance data (Fig. 7).

Synergistic effects of PD and EH on Beta diversity

Beta diversity was sensitive to PD when keeping EH constant at various levels (Fig. 8 c,d). A synergistic effect of EH on the sensitivity of beta diversity to changes in EH was observed as: i) an increase in basal beta diversity as EH increased (Fig. 8 a,b), and ii) as a decrease in the magnitude of the sensitivity of beta diversity to changes in PD as EH increased (Fig. 8 c,d). These results were consistent independently of the use of presence-absence (Fig. 8 a,c) or abundance data (Fig. 8 b,d).

Beta diversity was not sensitive to changes in EH when keeping PD constant at most of the considered PD categories (Fig. 8 g,h). Using presence/absence data, this lack of sensitivity tended to be more pronounced as PD increased (Fig. 8 g). Using presence-absence or abundance data, basal beta diversity tended to increase as PD increased (Fig. 8 e,f).

Overall, our results showed the existence of synergistic effects of PD and EH on beta diversity, even when controlling for PD or EH. Basal beta diversity was consistently affected by this synergistic effect and the sensitivity of beta diversity to changes in PD was affected by increasing values of EH. However, sensitivity of beta diversity to changes in EH was not always clear and synergistic effects with PD were not apparent in this case.

Fig. 7. Second step of the sensitivity analysis of beta diversity to physical distance (PD) while keeping environmental heterogeneity constant (EH), and sensitivity of beta diversity to EH while keeping PD constant. Three different levels of PD (short = 16 m, middle = 100 m, long = 930 m) and EH (low = 0.05, middle = 0.38, high = 0.99) were considered. Presence-absence and abundance data were used.

Plot a: LOW EH; Y = 0.62 + 0.09 X; R² = 0.68; p < 0.00001
Plot b: MIDDLE EH; Y = 0.64 + 0.09 X; R² = 0.55; p < 0.00001
Plot c: HIGH EH; Y = 0.07 + 0.07 X; R² = 0.39; p < 0.00001
Plot d: LOW EH; Y = 0.35 + 0.17 X; R² = 0.75; p < 0.00001
Plot e: MIDDLE EH; Y = 0.32 + 0.18 X; R² = 0.69; p < 0.00001
Plot f: HIGH EH; Y = 0.55 + 0.10 X; R² = 0.20; p < 0.001
Plot g: SHORT PD; Y = 0.70 + 0.02 X; R² = 0.02; N.S.
Plot h: MIDDLE PD; Y = 0.60 + 0.09 X; R² = 0.30; p < 0.0001
Plot i: LARGE PD; Y = 0.92 - 0.00 X; R² = 0.00; N.S.
Plot j: SHORTPD; Y = 0.56 - 0.01 X; R² = 0.00; N.S.
Plot k: MIDDLE PD; Y = 0.43 + 0.11 X; R² = 0.20; p < 0.001
Plot l: LARGE PD; Y = 0.81 + 0.02; R² = 0.02; N.S.

Presence-absence Beta diversity
Abundance Beta diversity

Log (PD among pairs of quadrats)
Log (EH among pairs of quadrats)
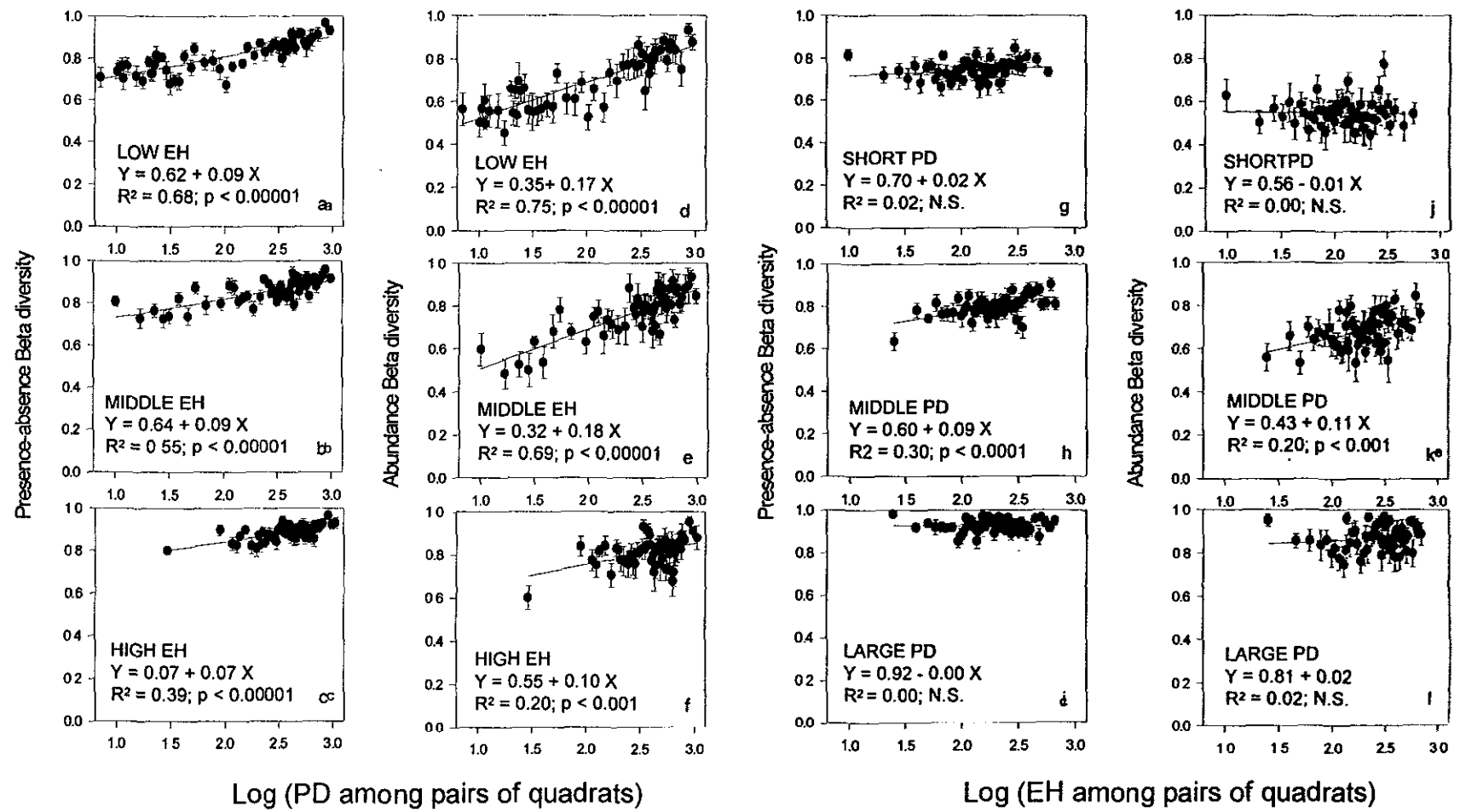
93

Fig. 8. Third step of the sensitivity analysis: synergistic effects of physical distance (PD) and environmental heterogeneity (EH) on basal beta diversity and sensitivity of beta diversity to EH and PD. Presence-absence and abundance data were used. White dots were used to pinpoint values of sensitivity of beta diversity to EH or PD that were not significantly different from 0.
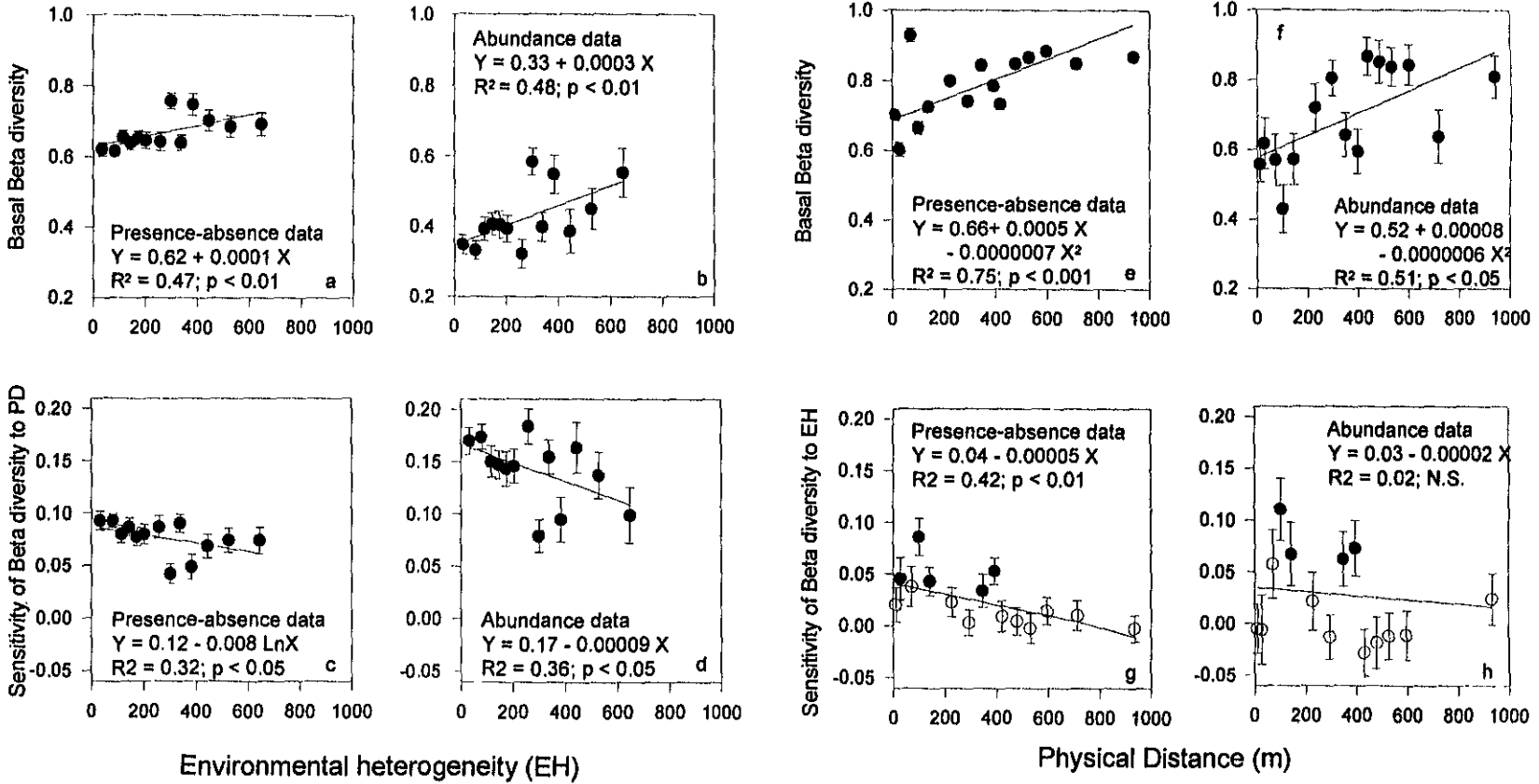
DISCUSSION

Using a sensitivity analysis to assess environmental heterogeneity and spatial components of beta diversity

In this study we found that beta diversity was sensitive to physical distance and to a lower degree to environmental heterogeneity. The sensitivity of beta diversity to physical distance was found even when keeping environmental heterogeneity constant. Nevertheless, sensitivity of beta diversity to environmental heterogeneity practically disappeared, as physical distance was kept constant. Only in the case of physical distance being kept constant to a value of 100 m, beta diversity was sensitive to environmental heterogeneity. Such distance of 100 m is similar to the distance at which environmental heterogeneity was greatest when analyzing semivariograms of environmental variables. We also found synergistic effects of environmental heterogeneity and physical distance on beta diversity.

Our results indicate that the effects of physical distance and environmental heterogeneity on beta diversity are intermingled. They also indicate that physical distance has and effect that is independent of environmental heterogeneity. We also found that most of the effect of environmental heterogeneity is dependent on physical distance, except for the case of sites 100 m apart, where maximum environmental heterogeneity is found. Thus, sensitivity of beta diversity to environmental heterogeneity is affected by the spatially autocorrelated nature of environmental heterogeneity at the scale at which this study was done.

In the watersheds at Chamela, a high basal beta diversity was prevalent in the tree community. Such a high beta diversity can be attributed to the presence of many rare species, each one distributed in a very small proportion of the sampled quadrats, contributing to a higher dissimilarity among pairs of quadrats. Also, the size of each quadrat was small (0.01 ha) and contained only a small number of trees and species.

Our results are consistent with those found in other biological systems. For example, in the case of temperate forests, Borcard and coworkers (1992) found that out of the 18.8% of the variance associated to environmental variables, almost half of it (7.8%) was associated to space as indicated by a spatial autocorrelation analysis of environmental variables.

Biological processes involved as determinants of Beta diversity: the case of the tropical dry
forest

The models used in this paper have allowed us to analyze two different hypotheses on processes associated to beta diversity: a habitat differentiation model and a spatial control model. In this paper our results support a strong spatial control model. Habitat differentiation was also observed, but it was only true through a strong interaction with space.

These findings can be discussed under the limitations of our experimental design. Environmental heterogeneity was only measured with three variables, all related to water availability. The consideration of a wider number of relevant environmental variables, like those associated to nutrient availability (Arriaga et al. 1993, E. Durán pers. com., Trejo 1998), could provide a different perspective. As discussed above, a high frequency of rare species, and a small quadrat size may also influence beta diversity patterns. The relative importance of environmental heterogeneity as a determinant of beta diversity could increase as plot size increases (P. Balvanera unpubl. data), and that of physical distance could change at different spatial scales (e.g. Levin 1992).

Overall, at the spatial scale considered for this study, our results indicate that beta diversity can be attributed to both a habitat differentiation model and a spatially structured one. The habitat differentiation model cannot be separated from its spatial component, due to the spatially autocorrelated nature of environmental heterogeneity. Other spatially structured biological processes such as distance-dependent colonization, disturbance, and *local biotic interactions (e.g., density-dependent predation) are also determining beta diversity in Chamela. Although environmentally related and distance related processes are probably operating simultaneously, our results show that physical distance was relatively more important than environmental heterogeneity.*

It has been argued that changes in water availability for plants determine major changes in species composition and structure in tropical dry forests (Bullock et al. 1995, Sampaio 1995, Sussman and Rakotozafy 1994). It has been shown, for example, that water potential changes among tropical dry forest species (Borchert 1994a, Holbrook et al. 1995) and that changes in soil water availability determines differential distribution of these species (Borchert 1994b). In the case of Chamela, changes in tree species composition along a small-scale altitudinal gradient were attributed to conditions associated to water availability, such as slope and insolation associated to evaporative load (P. Balvanera 1998, P. Balvanera et al. en prep. Cap III). For example, the dominant *Plumeria rubra* is

found preferentially in flat areas, where insolation and evaporative loads are high. In contrast, the co-dominant *Celaenodendron mexicanum* shows greater abundance in steep slopes, (Durán et al. in press; P. Balvanera unpubl. data), where evapotranspiration demands are lower and soil water content is higher (Galicia et al. 1999).

The relative importance of biological processes associated to the spatial control of species colonization rates has seldom been analyzed for tropical dry forests. In general, colonization ability of plant species depends on seed dispersal, vegetative propagation and availability of growing space. Tree recruitment via seed propagation and germination seems to be a rare event in tropical dry forests (Hubbel 1979, Lieberman and Mingguang 1992). At Chamela, for example, *Cordia elaeagnoides* seeds and seedlings have very low annual survival (van Groenendael et al., 1996). Other species show similar seedling mortality rates (M. Franco, pers. com.). On the contrary, tree vegetative propagation through sprouting seems to be one of the most important regeneration mechanisms in tropical dry forests (Murphy and Lugo 1986). Thus, clumped spatial patterns may arise from the prevalence of vegetative propagation over seedling establishment. In fact, distribution of species with vegetative reproduction such as *Gliricidia sepium* and *Comocladia engleriana* present highly aggregated spatial distributions in the same study site (Balvanera 1999, P. Balvanera unpubl. data, Durán et al. in press). These aggregated patterns could explain the high sensitivity of beta diversity to physical distance.

Disturbance is another factor that can contribute to the sensitivity of beta diversity to physical distance. It has been proposed that patchy tree fall and death associated to strong winds and storms following severe droughts are one of the most important disturbance sources in tropical dry forests (Durán et al. in press). Little is known on the regeneration cycle of this system (Durán et al. in press), but it has been shown in greenhouse conditions, that a wind dispersed species such as *Cochlospermum vitifolium* presents higher relative growth rates with higher light availability (Huante and Rincón 1997). This species has been found to present an aggregated spatial distribution in areas homogeneous in soil water availability (Balvanera 1998).

Some biotic interactions that could promote spacing among conspecific individuals, and therefore contribute to non-aggregated spatial patterns. Such is the case of frequency-dependent mortality (e.g. Kenkel 1988) and the Janzen-Connell model of differential seed/seedling mortality with respect to distance to the parental plant (Janzen 1970, Connell 1971). Such processes have been detected in tropical rain forests of Panama (e.g. Condit et al. 1994), and Malaysia (Fangliang et al. 1997). In the case of the tropical dry

forest at Chamela, only the case of *Erythroxylum havanense* has been reported, for which no effects of distance or density on seed survival were found (Gryj and Domínguez 1996).

CONCLUSIONS

Sensitivity analysis provides a useful tool to explore determinants of beta diversity. For the case of the tropical dry forest at Chamela, and for 100 m^2 plots, we provided evidences that physical distance has a relatively greater importance than environmental heterogeneity in determining beta diversity. Our results support a preponderance of a spatial control model, over a habitat differentiation one. The last one is tightly related to the spatial structure of environmental heterogeneity. The vegetative propagation of trees, biotic interactions or the response to disturbance of some species may help to explain the major role played by physical distance. This sensitivity analysis can be used to analyze the role played by different life history characteristics in the observed spatial structures. Also, further studies using sensitivity analysis in other ecosystems could be helpful to reexamine whether variance in species composition among sites, traditionally associated to environmental variables, can also be attributed to spatially structured ecological processes.

Sensitivity analysis can also be useful in the context of biodiversity conservation and management. Development of models that enable the prediction of the sensitivity of beta diversity to changes in its determinant factors could become an important tool for reserve design. At present, reserve design is based on predictions of species diversity using complementary environmental conditions (e.g. Margules 1991, Bojórquez et al. 1993) and environmental heterogeneity (Burnett et al. 1998, Nichols et al. 1998). This approach may shift to a growing emphasis on spatial relationships among and within conserved areas.

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Capítulo V

Discusión general

y aplicaciones al diseño

de estrategias de conservación

Introducción

Esta tesis exploró a través de enfoques conceptuales, empíricos y experimentales algunos determinantes del cambio espacial en la composición de especies. En este capítulo de la tesis se enfatizarán los resultados sobresalientes, resaltando las contribuciones originales en el marco de la teoría general sobre diversidad de especies y discutiendo su importancia para estudios de conservación de la diversidad biológica. Estas contribuciones se presentan, en primer lugar, para el sistema particular de estudio. Los resultados obtenidos en este trabajo representan la primera aproximación a la caracterización y estudio de la diversidad beta en las selvas bajas caducifolias. En segundo lugar, se hace referencia a las aportaciones al conocimiento ecológico en general, y, en particular, se destaca la importancia de los análisis de sensibilidad desarrollados en este estudio para el entendimiento de los procesos y determinantes asociados al recambio espacial de especies. Finalmente, se discuten las posibles implicaciones de los resultados a la luz de los problemas de la conservación de la diversidad biológica, con énfasis en las selvas bajas caducifolias.

Diversidad beta y procesos asociados en una selva baja caducifolia

Características de la diversidad beta de la selva baja caducifolia de Chamela

La selva baja caducifolia de Chamela, Jalisco, presenta una alta diversidad beta de especies arbóreas a escalas lineales que varían entre 10 y 1,000 metros de distancia. Sitios pequeños adyacentes de 100 m^2 comparten alrededor de un 30% de especies, mientras que un distanciamiento de tan sólo 100 m entre ellos puede reducir la similitud florística a menos del 10%.

Asociada a estos niveles de diversidad beta, se detectó una elevada diversidad gama, constituida por 138 especies representadas por árboles con DAP > 5 cm, y una fuerte variación en el nivel de abundancia y diversidad alfa entre sitios de 0.01 y 0.3 ha. La mayoría de las especies fueron raras, es decir, mostraron distribuciones restringidas y abundancias bajas; menos del 10% del total de las especies mostraron amplia distribución y abundancia local elevada. Las especies dominantes como *Plumeria rubra*, *Gliricidia sepium* o *Thouinidium decandrum* mostraron una distribución preferencial, asociada a ambientes más secos, en el caso de las 2 primeras especies, y ambientes más húmedos en el caso de la última especie.
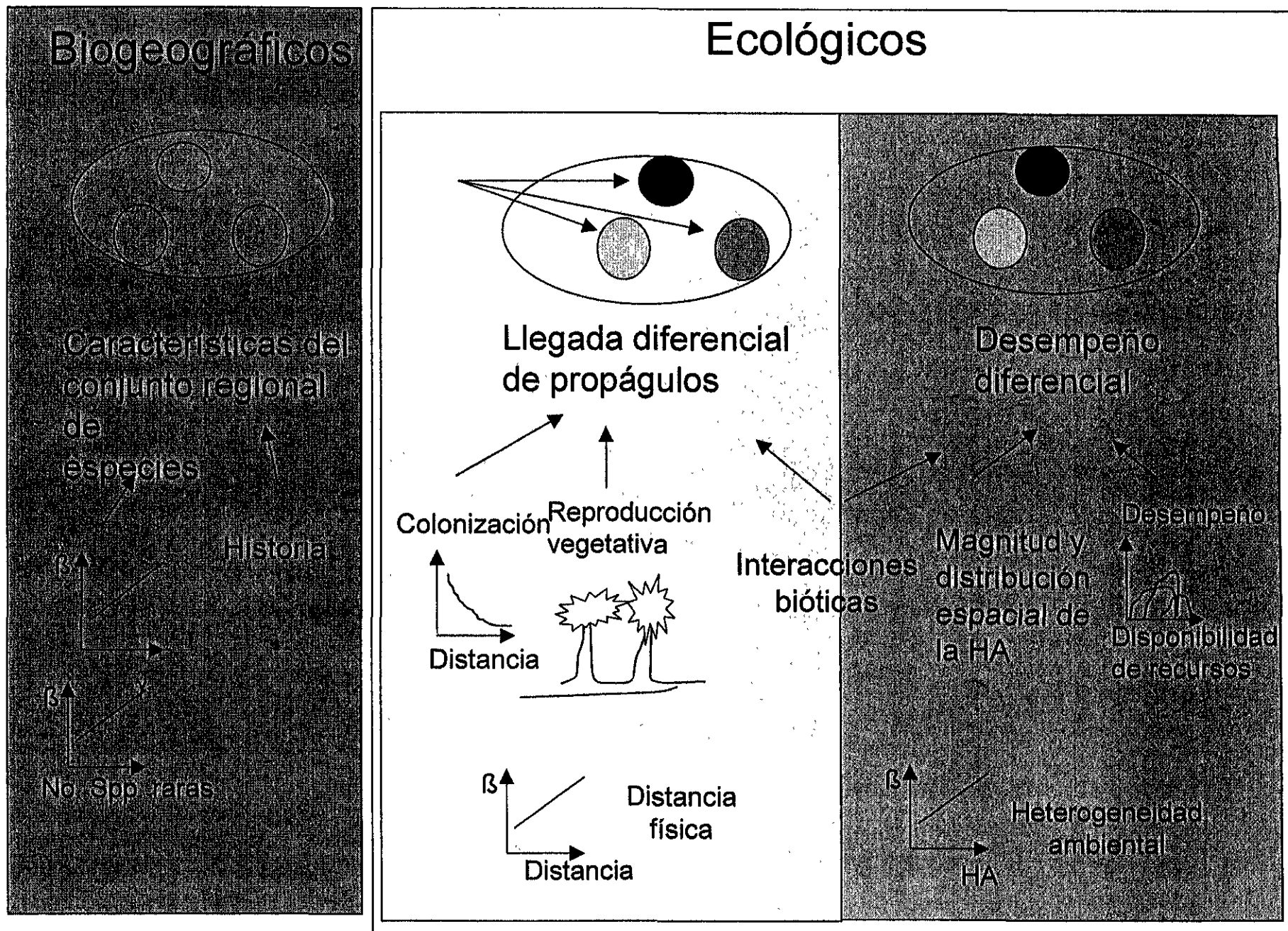
Los patrones de diversidad beta observados en Chamela son consistentes con expectativas teóricas y observaciones empíricas que indican que en los sistemas tropicales ocurre una elevada diversidad beta a diferentes escalas espaciales. A una escala biogeográfica, para muchos grupos de organismos la diversidad beta es mayor en los trópicos que en las áreas templadas (Whittaker 1972, Sheiner y Rey-Benayas 1994). A escalas de paisaje, la diversidad beta aumenta al reducirse la altitud en las zonas tropicales (Lieberman et al. 1996, Vázquez y Givnish 1998). A escalas ecológicas de unas cuantas decenas de metros cuadrados, en la vecindad inmediata de un árbol se presenta una gran variedad de especies distintas; por ejemplo, en la selva húmeda de Barro Colorado, Panamá, Hubbell y Foster (1986) encontraron que un árbol focal se encuentra rodeado, en promedio, por entre 12 y 16 especies diferentes, considerando a los 20 árboles vecinos más cercanos.

Procesos asociados a la diversidad beta en una selva baja caducifolia

Los procesos biogeográficos que afectan la diversidad beta definen al conjunto regional de especies, es decir, al valor de diversidad gamma (Fig. 1). Manteniendo constante una unidad de terreno focal, la diversidad beta se hace mayor a medida que la diversidad gamma aumenta, debido simplemente a un efecto de muestreo, en donde la incertidumbre en la composición de especies de la muestra crece cuando existe un elevado número de especies. Asimismo, la diversidad beta se hace mayor a medida que aumenta la frecuencia de especies raras en la comunidad, ya que con ello se reduce la probabilidad de encontrar las mismas especies en diferentes sitios. Por lo tanto, la elevada diversidad gamma y el gran número de especies raras pueden estar contribuyendo a la elevada diversidad beta observada en la comunidad de árboles en Chamela.

Poco se sabe acerca del origen de la diversidad gamma en Chamela. Se ha pensado que las selvas bajas caducifolias de México se originaron en el occidente del país y sur de Estados Unidos, sobre suelos con baja capacidad de retención de agua; estos bosques ampliaron su distribución con los cambios climáticos post-pleistocénicos (Graham y Dilcher 1995). Debido a esto, se ha reconocido que las selvas bajas caducifolias de México presentan un elevado porcentaje de endemismo de flora (Rzedowski 1991) y fauna (Ceballos 1995). Sin embargo, quedan por investigar los orígenes, o por lo menos las afinidades biogeográficas, de la flora y los procesos que contribuyen a la elevada diversidad regional de árboles en Chamela.

Fig. 1. Determinantes de la diversidad beta.

Biogeográficos

Características del conjunto regional de especies

Historia

β

No. Spp. raras

Ecológicos

Llegada diferencial de propágulos

Colonización Reproducción vegetativa

Distancia

Interacciones bióticas

β

Distancia física

Distancia

Desempeño diferencial

Desempeño

Magnitud y distribución espacial de la HA

Disponibilidad de recursos

β

Heterogeneidad ambiental

HA

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Los procesos ecológicos determinantes de la diversidad beta, podrían dividirse en dos tipos (Fig. 1): i) aquellos asociados a la dispersión, migración de individuos que determina la llegada diferencial de propágulos de las especies a distintos sitios, y ii) aquellos que determinan el establecimiento, sobrevivencia y finalmente el éxito reproductivo de las especies en los distintos sitios.

Factores asociados a la llegada diferencial de propágulos

La llegada de propágulos de las especies a distintos sitios puede depender a su vez de varios factores. Un primer factor, ampliamente estudiado para un gran número de especies animales y vegetales, es la distancia física existente entre los sitios. Se ha discutido que la tasa de colonización de especies está inversamente relacionada con la distancia a la fuente de propágulos (e.g. MacArthur y Wilson 1963, Howe and Smallwood 1982). Suponiendo una misma capacidad de dispersión de las especies y manteniendo constante las condiciones ambientales, puede esperarse que la similitud taxonómica disminuya al aumentar el distanciamiento entre los sitios (e.g. Whittaker 1972, Kadmon y Pulliam 1993).

El efecto del distanciamiento físico sobre la diversidad beta puede ser agudo cuando la capacidad de dispersión de las especies es limitada (Cook y Quinn 1995, Horvitz y LeCorff 1993), como ocurre con especies que sólo, o preponderantemente, se propagan a través de reproducción vegetativa. En ese caso puede esperarse en las especies un patrón espacial muy agregado y por lo tanto una elevada diversidad beta en la comunidad (Crawley 1997). En el Capítulo IV discutí que este puede ser el caso de varias especies en la comunidad de árboles de Chamela, como por ejemplo en *Gliricidia sepium* o *Comocladia engleriana*. Por el contrario, cuando la habilidad de dispersión de las especies es alta la diversidad beta puede disminuir si se mantiene constante la distancia (Mourelle y Ezcurra 1997).

La capacidad de dispersión de muchas especies de plantas depende de interacciones mutualistas con animales frugívoros que actúan como vehículos de dispersión de semillas. Los atributos de los propágulos (tamaño, cantidad y calidad de recursos alimenticios, exposición en la copa, entre otros), el comportamiento de forrajeo de los frugívoros y la forma en la que estos últimos "manejan" a los propágulos determinan la distancia desde la cual la progenie de una planta hospedera puede colonizar otros sitios (e.g. Howe y Smallwood1982, Howe y Westley 1997). En Chamela,

casi el 50% de las especies es dispersada por mamíferos, y un 20 % es dispersada por viento (Durán et al. en prensa).

Aunque ninguno de los factores arriba discutidos fue abordado directamente en este estudio, la estrecha relación observada entre la distancia entre sitios y la diversidad beta, sobre todo cuando se aísla el efecto de la heterogeneidad ambiental, se debe muy probablemente a la influencia de uno o varios de estos factores (ver discusión cap. IV). Queda por investigar el efecto directo del tipo de dispersión (atributos de propágulos y vehículos de dispersión), o del tipo de reproducción (vegetativa o sexual) sobre la diversidad beta observada.

<u>Factores asociados al desempeño diferencial de las especies</u>

El desempeño de las especies en un sitio dado está relacionado con las condiciones del sitio y la disponibilidad de recursos (Fig. 1). Desde los trabajos de Hutchinson (1959) y Whittaker (e.g. 1972), se ha observado que las especies responden de manera diferencial a las condiciones y recursos presentes en el ambiente de una región. Se ha planteado que además de las condiciones ambientales, la competencia interespecífica contribuye a generar una heterogeneidad biótica, creando diferencias espaciales en la disponibilidad de los recursos (e.g. Fangliang et al. 1997, Pacala y Levin 1997). Por lo tanto, puede esperarse que la diversidad beta se vea afectada por las características de la heterogeneidad ambiental, por el grado de especialización de hábitat de las especies y por la naturaleza e intensidad de la competencia.

En el caso de este estudio no se abordó de manera explícita el problema del ámbito de tolerancia ambiental de las especies y de la competencia entre especies. Sin embargo, se abundó en la descripción de las características del ambiente y en la respuesta de especies y de la comunidad al patrón espacial y magnitud de la heterogeneidad ambiental. En Chamela existe una relación evidente entre la heterogeneidad ambiental y la diversidad beta: la magnitud de la diversidad beta aumenta con la magnitud de la heterogeneidad ambiental (Cap. III y IV). En particular, esta relación se encontró considerando al agua disponible en el suelo, evaluada a través de la insolación y la pendiente que determinan la demanda evaporativa, como uno de los factores limitantes más importantes que determinan los cambios en composición y estructura en las selvas bajas caducifolias (Mooney et al. 1995). Por lo tanto, los resultados de este trabajo sugieren fuertemente que las especies de árboles en Chamela se desempeñan de manera diferencial a través de gradientes de disponibilidad de agua

(P. Balvanera datos no publicados). Trabajos realizados en otras selvas bajas caducifolias han documentado la existencia de variadas estrategias de las plantas para enfrentar la prolongada sequía (Holbrook et al. 1995), y la relación que existe entre ellas y su distribución espacial (Borchert 1994).

En este trabajo no se exploraron otras fuentes de heterogeneidad ambiental que pueden ser relevantes para la diversidad beta. Se ha discutido que en Chamela la disponibilidad espacial y temporal de nutrientes del suelo está estrechamente relacionada con la disponibilidad de agua (Jaramillo y Sanford 1995, Campo et al. 1998). Resultados de un estudio que contrasta la composición de especies entre unidades con características topográficas, geológicas y edáficas contrastantes muestran que la cantidad de nutrientes y la profundidad total del suelo contribuye, junto con la disponiblidad agua, a explicar los cambios en composición entre sitios (Durán et al. en prensa, E. Durán datos no publicados).

. La variación temporal del ambiente, asociada por ejemplo a la mortalidad diferencial de las especies, puede también estar contribuyendo a los patrones espaciales de la diversidad beta. Se conoce muy poco acerca de los mecanismos de regeneración de las selvas bajas caducifolias, pero existen evidencias en condiciones de invernadero sobre variaciones en las tasas de crecimiento de las especies, y respuestas diferenciales a la disponibilidad de luz (Huante 1996).

Contribuciones al entendimiento de los procesos asociados a la diversidad beta

La relación entre diversidad beta, heterogeneidad ambiental y distancia

La heterogeneidad ambiental no está dispuesta al azar en el espacio, sino que presenta una auto-correlación espacial (Cap. II, IV). Debido a esto, en estudios correlativos es muy difícil separar el peso relativo de la heterogeneidad ambiental del de la distancia física como determinantes de la diversidad beta. Se confunde la contribución de la heterogeneidad ambiental (que influye sobre el desempeño diferencial de las especies) con la de la distancia entre sitios (que influye sobre la llegada diferencial de propágulos).

En el capítulo II mostramos que existen contados estudios que abordan esta problemática; hasta ahora no ha sido posible separar el efecto de la heterogeneidad ambiental aislado de aquel producido por la distancia (ver Legendre 1993, Borcard et al.

1992, Leduc et al. 1992). En el capítulo III se describió la estrecha relación existente entre la diversidad beta de la comunidad de árboles en Chamela y el patrón espacial de la heterogeneidad ambiental.

En el capítulo IV se exploró el papel jugado por determinantes de la diversidad beta a través de un análisis de sensibilidad. Este análisis permitió evaluar la elasticidad (cambio relativo) de la diversidad beta cuando se modifica, por separado, el nivel de heterogeneidad ambiental y el de la distancia física. Con este método fue posible discutir la contribución diferencial de los procesos asociados a la llegada diferencial de propágulos y la de los procesos asociados al desempeño diferencial de las especies para el caso particular de un bosque tropical caducifolio.

El análisis de sensibilidad basado en áreas de 0.01 ha, indica que existe una importancia preponderante de los factores asociados a la llegada diferencial de propágulos sobre los factores asociados al desempeño diferencial de las especies en gradientes ambientales. La heterogeneidad ambiental y sus efectos sobre la distribución y abundancia de las especies contribuyen a determinar la diversidad beta observada pero sus estos efectos se encontraron íntimamente relacionados con el arreglo espacial de los sitios. En cambio, cuando se mantiene constante la magnitud de heterogeneidad ambiental, la relación de la diversidad beta con la distancia entre sitios se mantiene, destacando así la importancia de los factores asociados a la llegada diferencial de propágulos. Discutimos que otras fuentes de heterogeneidad ambiental, espacial o temporal (nutrientes y/o disturbio), y las interacciones bióticas pueden también estar involucrados en la notable sensibilidad que mostró la diversidad beta a los cambios en la distancia física entre sitios.

El análisis de sensibilidad realizado permite deslindar aquellos casos en los cuales la relación que existe entre el patrón de diversidad beta es sólo un artefacto derivado de la autocorrelación espacial de la heterogeneidad ambiental (e.g. Rossi y Queneherve 1998). Si bien Legendre (1993) desarrolló un método que pondera el peso relativo (porcentaje explicado de la varianza total en composición de especies entre sitios) asociado a la heterogeneidad ambiental y al espacio, el análisis de sensibilidad aquí desarrollado permite analizar la respuesta de beta a medida que aumenta uno de los factores controlando al otro factor. No se trata solamente de un peso relativo de los factores, sino del comportamiento de la diversidad beta ante variaciones en cada uno de los factores. Los efectos sinérgicos, o correlaciones entre los dos factores, dan más información que

un porcentaje de varianza; nos dan indicios sobre los niveles de cada factor en los cuales puede darse este efecto sinérgico y del comportamiento mismo del sinergismo.

El desarrollo del análisis de sensibilidad es un ejercicio original que puede tener un amplio ámbito de aplicación. Puede convertirse en una herramienta útil para evaluar la contribución relativa de diferentes procesos ecológicos asociados a la diversidad beta en distintos sistemas biológicos. Podremos así incidir más profundamente en el entendimiento de los determinantes de la diversidad beta y en particular de aquellos asociados a la relación que existe entre la distribución diferencial de las especies, la heterogeneidad ambiental y el espacio.

La pregunta central de la ecología de comunidades

Regresando a lo que Roughgarden (1989) llama la pregunta central de la ecología de comunidades, esta tesis nos permite tener algunos elementos para contestarla. La pregunta era:

"¿Son las poblaciones presentes en un sitio todas aquellas que llegaron ahí por azar, o sólo son un sub-conjunto especial - aquéllas con características que permiten su coexistencia?.

Los datos aquí presentados nos muestran que son tan importantes los procesos asociados a la llegada de propágulos al sitio, como aquellos que determinan su estancia y coexistencia en el. Entonces, es posible replantear la pregunta de Roughgarden en dos sentidos generales: i) ¿cuál es el papel relativo que juegan los procesos asociados a la llegada de propágulos con respecto a los que afectan el éxito diferencial de las especies en la composición de especies de una localidad? y ii) ¿varía este papel en distintos sistemas biológicos y distintas escalas espacio-temporales? El estudio de los determinantes de la diversidad beta brinda la posibilidad de explorar estos procesos. El contraste en la composición de especies entre sitios puede utilizarse para desarrollar tratamientos que permitan controlar y probar el efecto de los distintos procesos involucrados a través de un "experimento natural".

Implicaciones para la conservación de la diversidad

Los resultados obtenidos en esta tesis derivan conocimiento que puede ser importante para desarrollar iniciativas de conservación de la diversidad biológica de la

selva baja caducifolia en Chamela y la de otros sistemas en general. Una pregunta importante de confrontar en este contexto es: ¿cómo conservar sistemas diversos cuya composición de especies en el espacio es tan variable? La existencia de una elevada diversidad beta en un ecosistema, asociada a una elevada riqueza regional de especies y una elevada frecuencia de especies raras, nos pone ante un reto importante de conservación biológica.

Las propuestas para la identificación de áreas prioritarias para la conservación y el diseño de reservas, o redes de reservas, se han basado en listas florísticas y faunísticas (e.g. Grehan 1993, Pressey et al. 1993) y en la relación que existe entre la distribución de especies y la heterogeneidad ambiental (e.g. Margules y Austin 1991, Stokland 1997, Bojórquez-Tapia et al. 1993). Sólo recientemente se ha planteando que la magnitud de la heterogeneidad ambiental (Burnett et al. 1998, Nichols et al. 1998) puede ser utilizada como predictor de la diversidad local de especies.

Los resultados de esta tesis muestran que la distancia entre sitios puede ser tan importante o más importante que la heterogeneidad ambiental como determinante de la diversidad. ¿Sería posible utilizar la distancia entre sitios como herramienta para diseñar una red de áreas naturales protegidas? Tratando de contestar a esta pregunta, se sintetizaron los resultados obtenidos en este trabajo para generar propuestas más generales.

Utilizando los métodos desarrollados en el Capítulo IV, repetimos el análisis de sensibilidad de la diversidad beta a la distancia física y la heterogeneidad ambiental para cuadros de 0.1 ha. Este tamaño mayor tamaño de cuadro es comparable en superficie, aunque no en diseño, con los datos derivados de transectos ampliamente utilizados para la evaluación rápida de la diversidad (ver Lott et al. 1987, Gentry 1995, Trejo 1998 para datos de selvas bajas caducifolias). Los resultados derivados del este análisis (Fig. 2), establecen una clara relación entre la distancia física y la magnitud de la diversidad beta. Utilizando estos modelos es posible predecir a qué distancia dos puntos presentan la diversidad beta máxima, es decir cuando estos dos sitios ya no comparten ninguna especie (Fig. 3). Es necesario suponer para este fin que la tendencia observada entre diversidad beta y distancia física se mantiene a medida que aumenta la distancia más allá de la zona estudiada.

El análisis de sensibilidad nos permite aislar el efecto de la heterogeneidad ambiental del efecto del espacio. Sin embargo, no es posible en el paisaje aislar el efecto de distancia del de heterogeneidad ambiental. De hecho, se ha propuesto que existe una
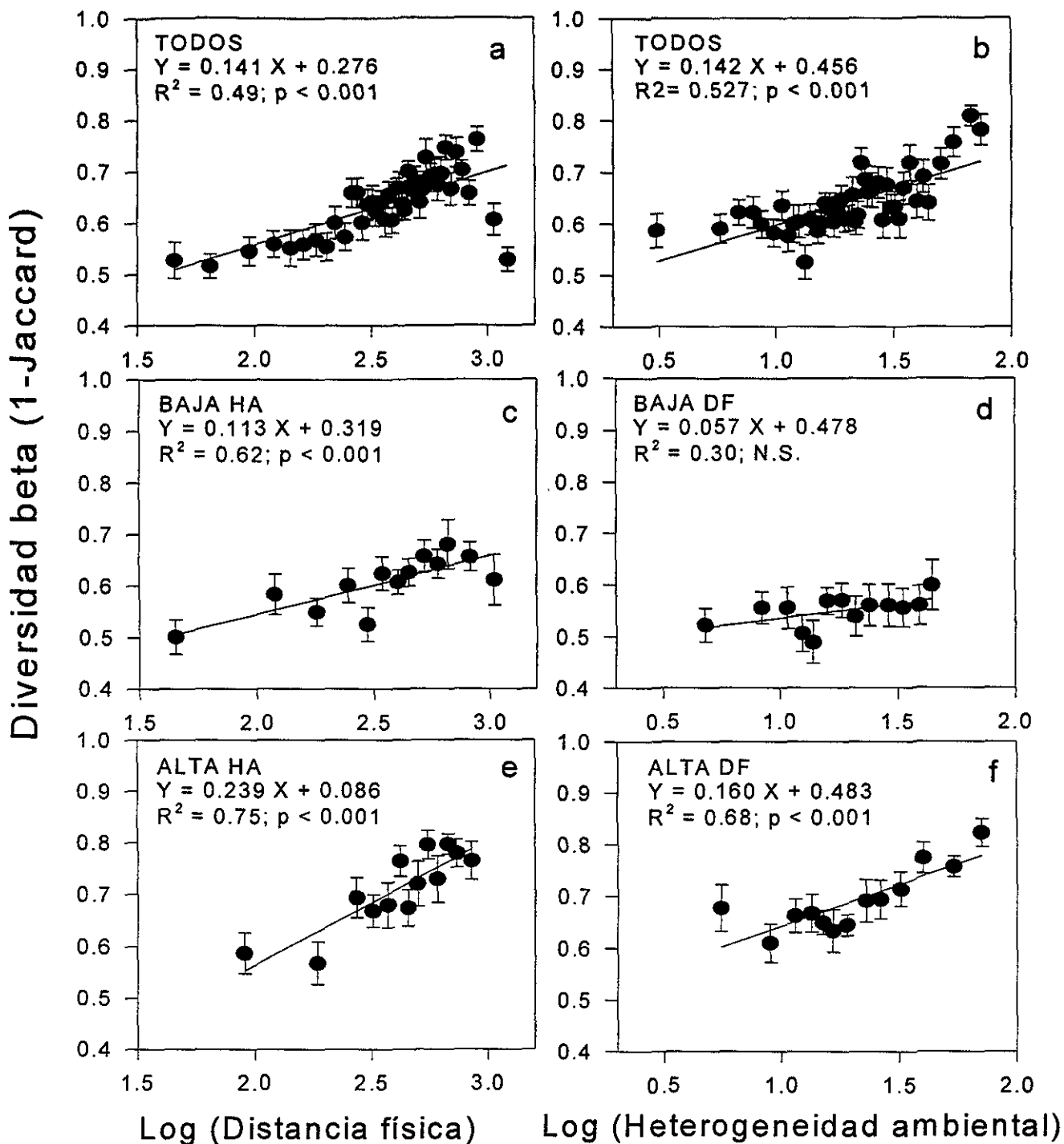
Fig.2. Análisis de sensibilidad de la diversidad beta a la distancia física y a la heterogeneidad ambiental para cuadros de 0.1 ha. La metodología sigue los pasos descritos en el capítulo IV. Se presentan datos para 800 comparaciones entre pares de cuadros utilizando datos de presencia/ausencia. a) y b) Primer paso del análisis de sensibilidad de la diversidad beta a la distancia física y la heterogeneidad ambiental, utilizando todos los datos. c) d) e) y f) Segundo paso del análisis de sensibilidad de la diversidad beta: c) y e) análisis de la sensibilidad de la diversidad beta a la distancia física manteniendo constante la heterogeneidad ambiental en dos niveles contrastantes (baja = 0.04, alta = 0.9 valores promedio), d) y f) análisis de la sensibilidad de la diversidad beta a la heterogeneidad ambiental manteniendo la distancia física constante en dos niveles contrastantes (corta = 131 m, larga = 806 m valores promedio).
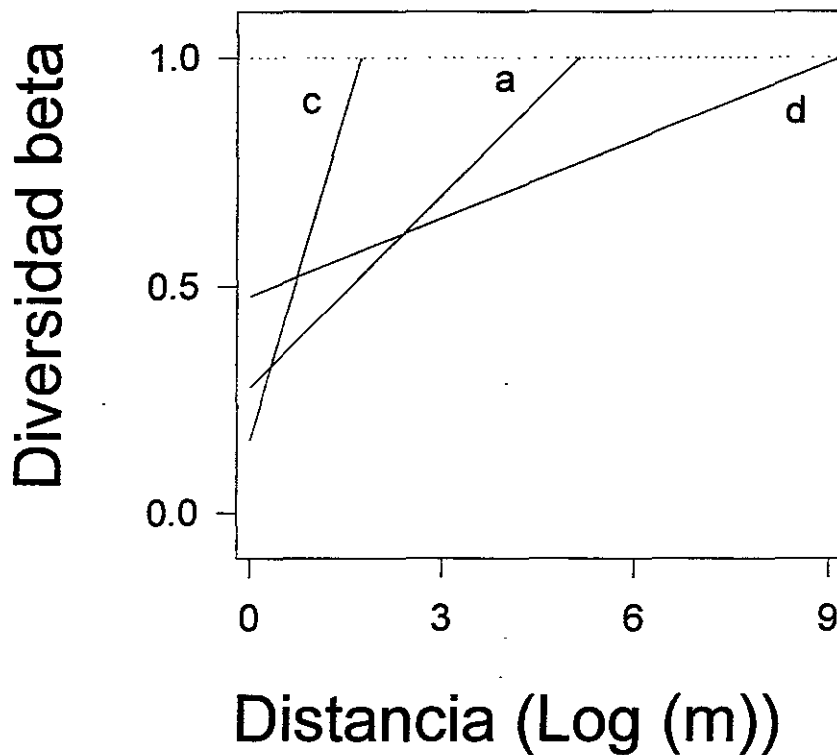
Fig. 3. Modelo hipotético de la sensibilidad de la diversidad beta a la distancia entre pares de sitios de 0.1 ha construida en base a los datos de la Fig. 2. Se presentan 3 posibles modelos: a) todos los datos sín control sobre la magnitud de la heterogeneidad ambiental, b) heterogeneidad ambiental baja, c) heterogeneidad ambiental alta. A partir de este modelo podemos sugerir que a una distancia de 130 Km entre pares de cuadros la diversidad beta es máxima, es decir que 2 pares de cuadros no comparten ninguna especie. Esta distancia varía en función de la heterogeneidad ambiental. El modelo utilizado en él texto es únicamente el modelo a) puesto que representa las condiciones promedio de heterogeneidad ambiental observadas en el área de estudio.

relación linear entre la distancia entre pares de sitios y la magnitud de la heterogeneidad ambiental que es consistente a escalas espaciales que van desde 1 hasta 10^8 m (Bell et al. 1991). Proponemos, más bien, que la distancia puede ser utilizada como herramienta de predicción puesto que incluye tanto el efecto de la heterogeneidad ambiental, a través de su autocorrelación espacial, y el de procesos ecológicos dependientes de la distancia.

Utilizando entonces el análisis desarrollado para los cuadros de 0.1 ha, cuando no se controla la magnitud de la heterogeneidad ambiental, podemos decir que la composición de especies es totalmente distinta a distancias de alrededor de 130 km. Esta distancia alcanza al sur los límites del estado de Colima y al norte una zona cercana a Puerto Vallarta. Este resultado es consistente con el obtenido por Trejo (1998) quien censó la comunidad de árboles de selvas bajas caducifolias en veinte localidades de la República Mexicana utilizando sitios de 0.1 ha. Sus resultados muestran una similitud florística promedio entre sitios menor al 10%, (de un total de 900 especies). La mayor similitud florística fue de 44% y se presentó entre dos sitios distanciados por sólo 20 Km. Cage señalar que estos cálculos fueron hechos en base a la selva baja caducifolia; el tipo de vegetación encontrado a 130 Km hacia la Sierra Madre Occidental es muy distinto y es probable que estos cálculos no sean aplicables en esas condiciones.

Tomando 130 km como radio de demarcación espacial de áreas florísiticamente totalmente disímiles (cuando diversidad beta = 1.0), podemos plantear una estrategia para la conservación de las selvas bajas caducifolias en México. En México, las selvas bajas caducifolias se encuentran en la península de Baja California, la costa del Pacífico Mexicano, la cuenca del Balsas, la depresión central de Chiapas y la península de Yucatán. Estas selvas no sólo presentan una elevada diversidad beta, sino también una elevada diversidad alfa y un porcentaje alto de endemismos (Trejo 1998). La conservación de tan elevada y peculiar diversidad de especies arbóreas está en peligro por las elevadas tasas de deforestación a la que están sujetos en la actualidad estas selvas (Masera et al 1992).

Hasta el momento, existe un número pequeño de áreas naturales protegidas que alberguen este tipo de vegetación. La reservas de La Sepultura en Chiapas, Chacahua en Oaxaca, Manantlán y Chamela-Cuixmala en Jalisco(SEMARNAP 1995) y Sierra de Huautla en Morelos son las únicas que protegen a las selvas bajas caducifolias. Estas reservas se encuentran muy distanciadas, a distancias muy superiores a los 130 km recomendados en este estudio, excepto los casos de las reservas de Chamela-Cuixmala y Manantlán. De acuerdo con los resultados obtenidos aquí, la red actual de reservas de

selvas bajas caducifolias es insuficiente. Dada la enorme distancia que existe entre ellas, es posible que entre las reservas se encuentren comunidades de selva baja caducifolia muy distintas en composición de especies de plantas a las ya representadas en las actuales reservas. Estas comunidades localizadas entre las diferentes reservas no están representadas dentro la red actual de protección. Si bien no es posible pensar en un sistema de protección de selvas bajas caducifolias llegara a tener una densidad tal que hubiera una reserva cada 130 Km, si es posible usar los resultados de este trabajo para trabajar en la dirección de tener una mejor red de reservas de este tipo de ecosistema.

Los modelos aquí propuestos pueden ser utilizados fácilmente para otros ecosistemas. Para ello es necesario saber cuál es la sensibilidad de la diversidad beta a cambios en el valor de sus determinantes para los sistemas estudiados. Se ha propuesto que el estudio de la diversidad beta es fundamental para el diseño de reservas e identificación de áreas prioritarias para la conservación (Blackburn y Gaston 1996; Williams 1996). En este trabajo presentamos sólo uno de los múltiples frutos que pueden obtenerse de esta avenida de la investigación ecológica.

Consideraciones finales

El estudio de la diversidad biológica ha fascinado a los científicos por ser una de las expresiones más asombrosas de la vida. El entendimiento de los procesos asociados a esta diversidad cobra particular urgencia a fines del siglo XX por la alarmante tasa a la que estamos destruyéndola. El énfasis por mucho tiempo ha sido ¿cuántas especies caben en un área?. Sin embargo, el creciente entendimiento de la complejidad de los sistemas biológicos, pero sobre todo de la gran heterogeneidad que presentan estos sistemas entre ellos y al interior de ellos, nos hace dirigir la mirada en una dirección distinta: ¿porqué no se encuentran las mismas especies en todos lados?.

La diversidad beta es justamente el componente de la diversidad de especies que mide esos cambios en composición de especies entre sitios. En esta tesis revisamos los distintos factores a los cuales está asociada la diversidad beta, y los documentamos para un sistema que requiere urgentemente estrategias para la conservación de su elevada diversidad: las selvas bajas caducifolias. La aventura que emprendimos al explorar tanto los aspectos conceptuales de la diversidad beta cómo el hecho de poder medirla, tocarla, y escudriñarla en el campo nos condujeron al entendimiento de cómo está determinada por heterogeneidad de los sistemas biológicos. Entre dos sitios, no sólo cambian las

condiciones ambientales y por lo tanto la respuesta diferencial de las especies a esas condiciones, sino también cambia la disponibilidad de propágulos de las especies, y las interacciones complejas que establecen las especies entre ellas. Es fundamental poder deslindar el efecto de cada uno de estos factores para entender los determinantes de la diversidad beta, y el análisis de sensibilid

ad aquí propuesto es uno de los posibles acercamientos a esta pregunta.

De manera general, pensamos que el entendimiento del contexto espacial de los sistemas biológicos, en general, y el de la diversidad beta, en particular, es una avenida de la investigación ecológica que está apenas iniciando y que se va a desarrollar ampliamente en el futuro debido a los vertiginosos desarrollos tecnológicos y conceptuales que se están dado. en áreas afines ha estado presente por sólo un par de décadas, y que los desarrollos tecnológicos y conceptuales del futuro. Considerando la necesidad urgente de privilegiar algunas zonas del planeta con condiciones peculiares de manejo y protección, el entendimiento de la diversidad beta y en general de la heterogeneidad espacial nos permitirá serán herramientas indispensables en el futuro para la eficientes selección de estas zonas.

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